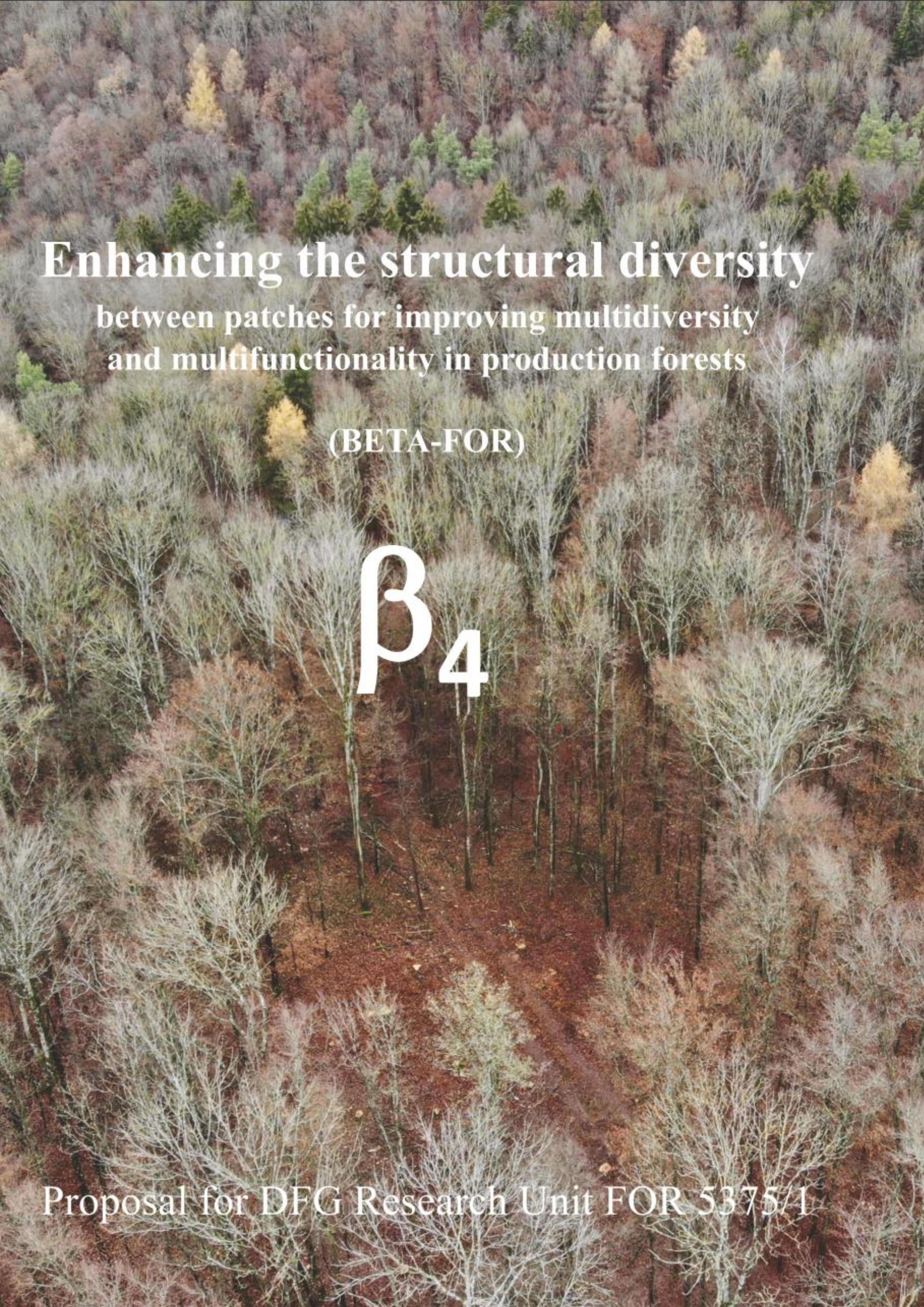


Enhancing the structural diversity

between patches for improving multidiversity and multifunctionality in production forests

(BETA-FOR)

β_4

Proposal for DFG Research Unit FOR 5375/1

Enhancing the structural diversity
between patches for improving multidiversity and multifunctionality in production forests

(BETA-FOR)

Jörg Müller, Michael Scherer-Lorenzen, Christian Ammer, Nico Eisenhauer, Dominik Seidel, Bernhard Schuldt, Peter Biedermann, Thomas Schmitt, Claudia Kuenzer, Martin Wegmann, Simone Cesarz, Marcell Peters, Heike Feldhaar, Ingolf Steffan-Dewenter, Alice Claßen, Claus Bässler, Goddert von Oheimb, Andreas Fichtner, Simon Thorn, Wolfgang Weisser

$$\beta_4$$

Proposal for the 1st phase (2022-2026) of the DFG Research Unit FOR 5375/1

(DFG Forschergruppe FOR 5375/1 – BETA-FOR)

Fabrikschleichach, October 2021

DOI: 10.25972/OPUS-29084

Cite as: Müller, J., Scherer-Lorenzen, M., Ammer, C., Eisenhauer, N., Seidel, D., Schuldt, B., Biedermann, P., Schmitt, T., Kuenzer, C., Wegmann, M., Cesarz, S., Peters, M., Feldhaar, H., Steffan-Dewenter, I., Claßen, A., Bässler, C., von Oheimb, G., Fichtner, A., Thorn, S., Weisser, W. (2021): BETA-FOR: Enhancing the structural diversity between patches for improving multidiversity and multifunctionality in production forests. Proposal for the first phase (2022-2026) of the DFG Research Unit FOR 5375/1. Fabrikschleichach (DOI: 10.25972/OPUS-29084)

Fotos Einband: M. Wegmann, C. Moning, B. Huber

Table of Contents

Overall Description of the Research Unit and the Coordination Proposal

Enhancing the structural diversity between patches for improving multidiversity and multifunctionality in production forests (BETA-FOR)

Prof. Dr. Jörg Müller, Julius-Maximilians-Universität Würzburg (Speaker)

Summary

Natural forests form a diverse mosaic of different successional stages, with variability in environmental conditions and species compositions both determining the overall ecosystem functions. The recently observed consistent loss of β-diversity across ecosystems indicates increasingly homogeneous communities in patches of landscapes, mainly caused by increasing land-use intensity. Biodiversity is related to numerous ecosystem functions and stability. Therefore, decreasing β-diversity is also expected to reduce multifunctionality. Over centuries, a focus on timber production has on the one hand, considerably homogenized the structure and compositions of temperate forests. On the other hand, forest management constantly creates disturbances on different scales, which may create heterogeneity. Interestingly, these contrasting effects have not been studied in detail, and the impact of forest management practices on β-diversity and β-multifunctionality is still lacking empirical evidence. This is based mainly on the paucity of experimental studies on β-diversity and ecosystem functions at the landscape scale. Recent forest diebacks have rapidly accelerated the need to investigate the role of between-stand heterogeneity on diversity and ecosystem functions as a baseline for long-lasting management strategies. To assess the impact of homogenization and to develop guidelines to reverse its potentially negative effects, we combine expertise from forest science, ecology, remote sensing, chemical ecology and statistics in a collaborative and experimental β-diversity approach. Specifically, we will address the question whether the Enhancement of Structural Beta Complexity (ESBC) in forests by silviculture or natural disturbances will increase biodiversity and multifunctionality in formerly homogeneously structured production forests. Our approach will identify potential mechanisms behind observed homogenization-diversity-relationships and show how these translate into effects on multifunctionality. At eleven forest sites throughout Germany, we selected two districts as two types of small ‘forest landscapes’. In one of these two districts, we established ESBC treatments (nine differently treated 50x50 m patches with a focus on canopy cover and deadwood features). In the second, the control district, we will establish nine patches without ESBC. In the Würzburg University Forest Sailershausen, three district pairs are located that serve as intensive study sites with a refined version of ESBC treatments. Here, we will conduct additional sampling of biodiversity, ecosystem functions, and environmental variables, to maximize our mechanistic understanding and to develop a simplified sampling design for long-term monitoring. This will be done at one site per climate region, where the response of trees and associated flora and fauna to ESBC-treatments will be recorded including years with extreme climate conditions. Comprehensive measurements from all eleven sites and repeated rapid assessment in six long-term monitoring sites will allow generalization of our findings for a variety of forests in Germany. By a comprehensive sampling, we will monitor 18 taxonomic

groups and measure 21 ecosystem functions, including key functions in temperate forests, on all patches. The statistical framework, will allow a comprehensive biodiversity assessment by quantifying the different aspects of multitrophic biodiversity (taxonomical, functional and phylogenetic diversity) on different levels of biodiversity (α-, β-, γ-diversity). To combine overall diversity, we will apply the concept of multidiversity across the 18 taxa. We will use and develop new approaches for quantification and partitioning of multifunctionality at α- and β- scales. Overall, our study will herald a new research avenue, namely by experimentally describing the link between β-diversity and multifunctionality. Furthermore, we will help to develop guidelines for improved silvicultural concepts and concepts for management of natural disturbances in temperate forests reversing past homogenization effects.

Study sites

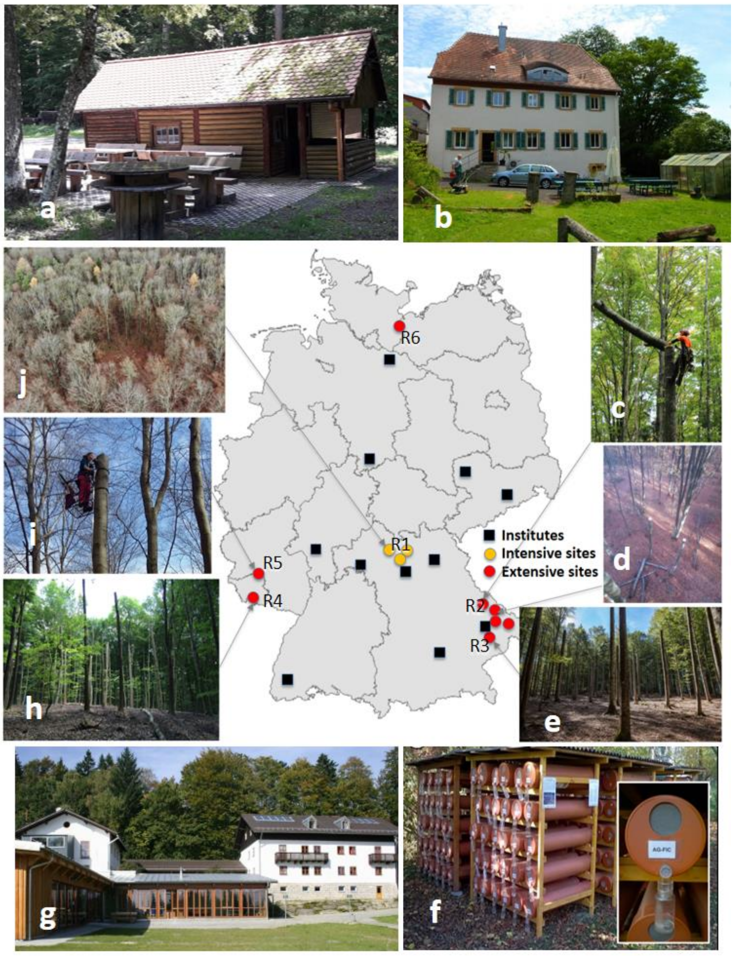


Fig. 1: Distribution of institutes involved in the Research Unit, intensive sites in the University Forest Sailershausen and extensive sites across Germany, R1-6 indicate different climate regions. Pictures show facilities and experimental sites: a) forest hut in the University Forest with Wi-Fi, b) Fieldstation Fabrikschleichach with labs and rearing station, c),d) & e) interventions to enhance structural heterogeneity in the Bavarian Forest, f) rearing station for deadwood available in Fabrikschleichach and the Bavarian Forest, g) meeting house of the National Park with overnight accommodation for workshops and retreats, h) experimental site in the Saarland, i) experimental site in the Hunsrück, j) drone picture of experimental gap in the University Forest.

The proposed study aims to test the effects of an enhanced β-complexity in forests. To test this, we established experimental interventions in 11 districts, each composed of forest units of a size of 10-20 ha, as model landscapes for our experiments across Germany (Fig. 1). In order to achieve a paired design, a further 11 comparable districts are identified as controls for these districts. The forests cover various soil and climate conditions as well as different ownerships. They range from acidic beech-spruce-fir mixed forests, to mixed beech-spruce forests, to mixed beech-oak forests. In a subset of three out of the 11 district pairs, we established so-called intensive sampling sites in the University Forest Sailershausen, which belongs to the Julius-Maximilian University of Würzburg and offers ideal logistical conditions for intensive measurements. Here, we refine the variation in structural heterogeneity by adding treatments that might be relevant for silvicultural practice.

List of projects

	Project leader and Co-PIs	Subproject	Institution
CM	**Jörg Müller**	Administrative coordination, ensuring equal opportunities, workshops	JMU Würzburg
SPZ	**Jörg Müller** **Michael Scherer-Lorenzen** **Christian Ammer** **Nico Eisenhauer**	Scientific coordination, site management, knowledge transfer, background data, data management, statistics	JMU Würzburg JMU Würzburg U Freiburg U Göttingen iDiv, U Leipzig
SP1	**Christian Ammer** **Dominik Seidel** **Bernhard Schuldt**	Forest structure and tree physiology	U Göttingen U Göttingen JMU Würzburg
SP2	**Peter Biedermann** **Thomas Schmitt**	Volatilome and symbiosis	U Freiburg JMU Würzburg
SP3	**Claudia Kuenzer** Martin Wegmann	Novel Earth Observation techniques for forest structure analysis and multi-scale characterization	JMU Würzburg
SP4	**Simone Cesarz** **Nico Eisenhauer**	Soil biodiversity and functioning	iDiv, U Leipzig
SP5	**Michael Scherer-Lorenzen** **Marcell Peters**	After life – decomposition	U Freiburg JMU Würzburg
SP6	**Heike Feldhaar** **Ingolf Steffan-Dewenter** **Alice Claßen**	Plant-animal interactions - pollination, parasitism, and seed dispersal	U Bayreuth JMU Würzburg
SP7	**Claus Bässler**	Dead wood microbial diversity	GU Frankfurt
SP8	**Goddert von Oheimb** **Andreas Fichtner**	Understorey plant assemblages and primary production	TU Dresden LU Lüneburg
SP9	**Jörg Müller** **Simon Thorn** Wolfgang Weisser	Multifunctionality and higher trophic level diversity	JMU Würzburg JMU Würzburg TU München

1. State of the art and preliminary work

Homogenization and its impact on structural properties, biodiversity, ecosystem functions, and their interactions

Homogenization and β-diversity

During the last three centuries, the impact of humans on the globe has escalated to the point that this period has been termed the Anthropocene due to the global reach of the human footprint (Crutzen 2002). Habitat loss, overexploitation of biological resources, pollution, invasive species, and climate change have been identified as the main drivers of accelerated global species extinction (Barnosky et al. 2011; Maxwell et al. 2016; Sala et al. 2000). The loss of species happens at different spatial scales: at a local scale (α) e.g. by removal of resources, such as the extraction of wood from a small forest patches (Müller and Bütler 2010), resulting in the loss of species from local communities (α-diversity) (Newbold et al. 2015). At the landscape scale (γ), species loss happens by a decrease of dissimilarities between local communities (β-diversity) (Fig. 2), a phenomenon also known as ‘biotic homogenization’ and that often exceeds the extent of local loss in many anthropogenic landscapes (McGill et al. 2015). This term was originally used to describe the replacement of native by non-native generalist species (Olden et al. 2016), but is now more broadly applied to various human-induced homogenizations of communities in terms of their taxonomic, functional, and phylogenetic composition across locations (Gossner et al. 2016; Mori et al. 2018; Tscharntke et al. 2021). Any kind of homogenization results in lower β-diversity. While the effects of land use on α-diversity of different trophic levels have been thoroughly investigated (Allan et al. 2014; Laliberte et al. 2010), much less attention has been paid to spatial homogenization (β-diversity) and species loss at the landscape scale (γ-diversity), primarily due to the much more difficult feasibility of replicated studies at that scale.

BOX 1: Beta-Diversity

Alpha (α)-diversity describes the diversity within a plot, forest patch or a single stream. Gamma (γ)-diversity describes the diversity of all plots, forest patches or streams of a region, forming the regional species pool. Beta (β)-diversity links the two and was first described by Whittaker (1960, 1972) as “the extent of differentiation of communities along habitat gradients”. Whittaker (1960, p. 321; 1972, p. 214) defined beta diversity as $\beta = \gamma/\alpha$ (multiplicative beta based on species richness), and his original measure for “turnover” of species composition was $\beta - 1 = (\gamma - \alpha)/\alpha$, which is a function of $\gamma - \alpha$ (the difference of gamma and alpha, i.e., additive beta). However, Whittaker’s original concept was much more general as the restriction to multiplicative or additive β. This plurality of concepts has persisted in β-diversity research to this day, with several summarising studies that recommend different approaches, depending on the question, the available data, and whether the orientations is practical or theoretical (Anderson et al. 2011; Chao et al. 2019c; Ellison 2010; Jost 2007; Jurasinski et al. 2009; Mori et al. 2018). A step forward in the jungle of different diversity measures was Hill's (1973) work. Using a diversity order $q \geq 0$, he showed that species richness, Shannon diversity or Simpson diversity, can be integrated into a continuum of diversity measures and linked through an increasing weighting from rare ($q=0$) to common ($q=1$) to dominant ($q=2$) species respectively, - the so called Hill numbers. Such a continuous weighting seems promising, because some ecosystem functions might be driven more by rare and others by more dominant species. Moreover, there has been an intense debate about whether to partition γ-diversity additively or multiplicatively into α and β (Jost 2010; Veech and Crist 2010a, 2010b), with the latter often being favoured due to its independence of beta from α (but see Anderson et al. 2011; Veech and Crist 2010b). Jost et al. (2011) actually showed that both the additive and the multiplicative approach based on Hill numbers converge to the same classes of dissimilarity measures for all $q \geq 0$. Baselga (2010, 2012) decomposed the dissimilarity into species “turnover” and “nestedness” parts, which might be of interest in biodiversity and ecosystem functions (BEF) research. However, this has been and is still restricted to $q = 0$ (Soares et al. 2020). Because functional and/or phylogenetic β-diversity can be important for the assessment of ecosystem functions, beta diversity frameworks that can be easily extended to functional or phylogenetic diversity (see Chao et al. 2019a) are of particular interest in our RU. Therefore, we will follow the concept of β-diversity along the Hill numbers and their generalizations for taxonomic, functional, and phylogenetic diversities. For partitioning of γ-diversity of our districts into α and β, we will follow the multiplicative approach. Moreover, we plan to incorporate the idea of ecosystem functions in the same framework as for species diversity along the framework of Hill numbers (Mori et al. 2018).

The very few empirical studies on β-diversity revealed new insights into the anthropogenic homogenization effect of communities at the landscape scale. A recent large-scale, multitrophic and cross-regional study demonstrated that high crop heterogeneity measured as heterogeneity between patches increased γ-diversity in agricultural landscapes (Sirami et al. 2019). Gossner et al. (2016) showed that land-use intensification in grasslands leads to reduced β-diversity by homogenization of multitrophic communities below and above ground. In turn, increasing the variability between habitat patches during restoration of prairies has been shown to increase β-diversity (Grman et al. 2018). The appropriate quantification of β-diversity has been an intensive field of research with many different approaches developed since Whittaker's beginnings in 1960 (for the orientation in this RU see Box 1).

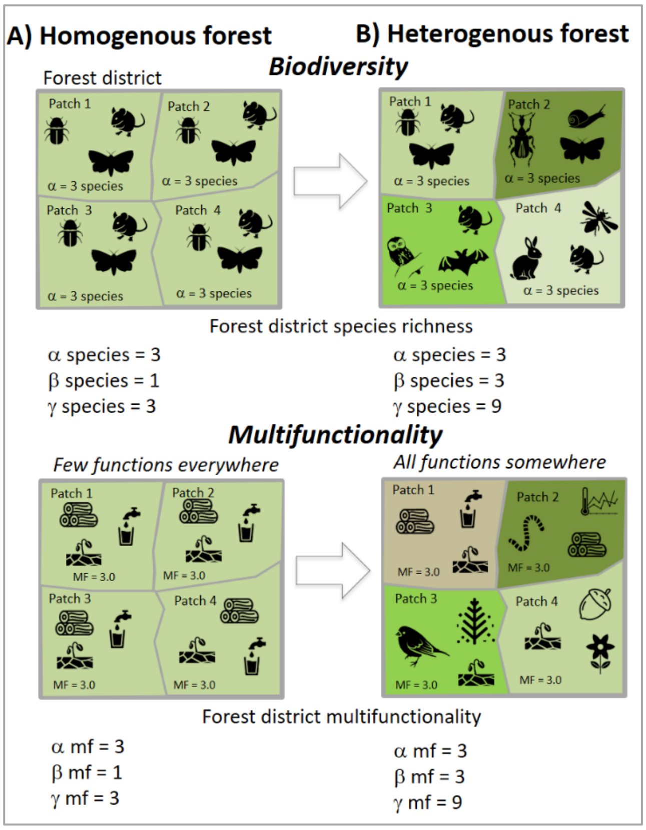


Fig. 2: Conceptual figure how α-, β- and γ-diversity in a homogeneous landscape (A) and a heterogeneous landscape (B), here as an example from forests, might affect multifunctionality. For simplicity, the same number of species and sufficiently fulfilled functions per forest patch is assumed (only functions above a critical threshold according to the threshold approach are displayed; see Mori et al. 2018). β-diversity was calculated as $\beta = \frac{\gamma}{mean\ \alpha}$ (Chao and Chiu 2016). β-functionality was calculated in analogy to diversity (Mori et al. 2018). The turnover of ecosystem functions between the patches by ESBC increases multifunctionality of the district. This can be described as shift from a '*Few functions everywhere landscape*' (mid-aged mixed forests provide some timber, some habitats, and deliver a set of ecosystem functions at similar rates in all patches) to a '*All functions somewhere landscape*', with very different patches providing single functions at maximum in some patches.

Biodiversity-ecosystem functioning relationships

In the last 25 years, much ecological research has been done on the question of whether and how biodiversity contributes to ecosystem functioning and stability, and how these relationships ensure the benefits people gain from nature, in the form of ecosystem services (Cardinale et al. 2012; Isbell et al. 2017; Naeem et al. 2012). The relationship between biodiversity and ecosystem functions (BEF) such as productivity is well understood from observational, theoretical and experimental approaches on the local, within patch (α-diversity) scale (Duffy et al. 2017; Soliveres et al. 2016; Tilman et al. 1997). It has been shown that increasing diversity at one trophic level (in most studies plants) also increases associated diversity at other trophic levels so that "diversity begets multidiversity" (Eisenhauer et al. 2013; Scherber et al. 2010). Moreover, a meta-analysis across terrestrial and marine ecosystems summarized that species-rich communities simultaneously maintain multiple functions ("multifunctionality") at higher levels than species-poor ones, with particularly strong effects of higher trophic levels (Lefcheck et al. 2015). The strength of the BEF relationship has been found to increase with an increasing number of functions taken into account (Hector and Bagchi 2007; Isbell et al. 2011; Meyer et al. 2018) calling for studies on multidiversity and multifunctionality (Eisenhauer et al. 2019b).

Multifunctionality at the landscape level is different from multifunctionality at the local (patch) level, as different patches can contribute different functions to landscape-level γ-multifunctionality (Simons et al. 2021). However, the between-patch contribution to multifunctionality at the landscape level is expected to be low in homogeneous landscapes, because similar species compositions provide similar ecosystem functions (Fig. 2A).

Moreover, more similar compositions of species across patches display less spatial and temporal asynchrony of populations than in heterogeneous landscapes (Blüthgen et al. 2016; Loreau et al. 2021). Both probably have significant consequences for the functioning of ecosystems at the γ-scale (Craven et al. 2018; van der Plas et al. 2016b; Wang and Loreau 2016). Such a translation of reduced β-diversity into reduced γ-multifunctionality was summarized conceptually in the landscape insurance hypothesis (Loreau et al. 2021), that states that "biodiversity provides spatial insurance for ecosystem functioning by virtue of spatial exchanges among local systems in heterogeneous landscapes". Theoretical modelling supports also the importance of a high β-diversity for γ-diversity and γ-multifunctionality of a landscape (e.g. Wang and Loreau 2016).

Only very few studies have investigated the effect of β-diversity on important functions or multifunctionality in real landscapes. Hautier et al. (2018) showed increasing landscape multifunctionality with increasing β-diversity of plants, which also translates into higher β- and γ-stability of primary productivity (Hautier et al. 2020). Similar results were found in restored prairies, i.e. γ-multifunctionality increasing with increasing β-diversity (Grman et al. 2018). This finding was interpreted by the authors as effects of β-diversity on individual abundances at higher trophic levels promoting overall ecosystem services. A third study on a very large scale in Australia, however, did not find significant relations between α- or β-diversity with primary productivity (Burley et al. 2016). Other studies also found evidence that increased β-diversity enhances landscape-level multifunctionality without discussing the results explicitly in terms of β-diversity measures. For example, Simons et al. (2021) found that multifunctionality at the landscape scale in Germany can be increased if different types of managed forests are combined at the landscape level.

The relationship between biodiversity and ecosystem functions at the α-level has been well studied for different ecosystems, such as forests or agricultural land (Scherer-Lorenzen 2014; Soliveres et al. 2016; Tilman et al. 2001; van der Plas et al. 2018; Weisser et al. 2017). How these relationships upscale to the landscape level, however, remains a field of research that has hardly been touched (Eisenhauer et al. 2019b) and which has been identified as one of the most important research questions for the future in BEF studies (van der Plas 2019). However, classical BEF studies, which experimentally manipulate biodiversity, are often restricted to small scales only. Currently, there are three main approaches that attempt to clarify these questions: First, pure modelling approaches that try to test effects of biodiversity on multifunctionality in virtual landscapes with virtual species (Loreau et al. 2003; van der Plas et al. 2019; Wang et al. 2021). Second, the approach of assembling the information gained from field observations of different local patches into new, virtual landscapes composed of different combinations of those patches, and inferring the multi-functionality of such assembled patch assemblies (Ebeling et al. 2020; Schall et al. 2018a; Schwenk et al. 2012; Swanson and Franklin 1992; van der Plas et al. 2019). These applications assume that theoretical combinations of local patch diversity and functions form the overall γ-diversity and multifunctionality additively. However, this ignores potential interactions between patch types located in the vicinity (e.g. edge effects, species with multi-habitat requirements, Le Provost et al. 2021). Hence, the functionality of a forest related to β-diversity is probably more than the simple sum of its single patches. How misleading an virtual upscaling from observations at the patch to a landscape scale might be, can be seen in the current debate on fragmentation, where α-scale (patch) studies predominantly observe negative effects of fragmentation on biodiversity, while γ-scale (landscape) studies detect the opposite (Fahrig 2019). Third, experimental approaches actively manipulate heterogeneity, as in mesocosm experiments with artificial ponds (Hammill et al. 2018). Such an approach allows more rigorous studies under controlled conditions, but rarely corresponds to conditions in real landscapes. In addition, there is more often only the virtual formation of landscapes from field observations of patches and only rarely the real replication of "landscapes" with different heterogeneity levels, which limits the derivation of real β-diversity effects on the diversity and multifunctionality of landscapes.

Manning et al. (2019) classified BEF research into three clusters, from small-grain highly controlled BEF studies, to small grain observational studies to large grain uncontrolled studies, based on the degree of control and spatial scale. They advocate more transfer of biodiversity-ecosystem function research to the scale of 'real-world' ecosystems. However, no study exists, attempting to experimentally manipulate β-diversity in real-world landscapes at any scale, and this replicated and with control landscapes. We are aware of only one experiment aimed at investigating the above-mentioned potential non-additive effects of β-diversity on single ecosystem. This looked at functions in grasslands (van der Plas 2021) using a patch size of only 1x1 m. The complete lack of experimental approaches at the landscape level seems surprising, since manipulative interventions with significant impacts on α- and β-diversity happen regularly in agriculture or commercial forests. However, manipulating landscapes in a well-replicated way is laborious and hard to achieve. Nevertheless, in light of the strong indication for the major changes and high functional importance of β-diversity, expanding BEF studies to the β-scale has been identified as an urgently needed research avenue (Mori et al. 2018; van der Plas 2019).

Forest management, forest biodiversity and ecosystem functioning

Natural forests form a diverse mosaic of different successional stages with different environmental conditions and species compositions (Franklin et al. 1981; Hilmers et al. 2018), most pronounced between early, optimum and late stages. In temperate forests, the diversity of plants and animals is lowest in the optimum phases with dense homogenous forests (EO, MO, LO in Fig. 3a), as we find today in European commercial forests (Fig. 3a, 3c). In addition, the differences in species composition are large between the very early and very late stages compared to the optimum stages (Fig. 3b). These, in turn, determine the ecological functions provided by forests on α-, β- and γ-scales (Ratcliffe et al. 2017).

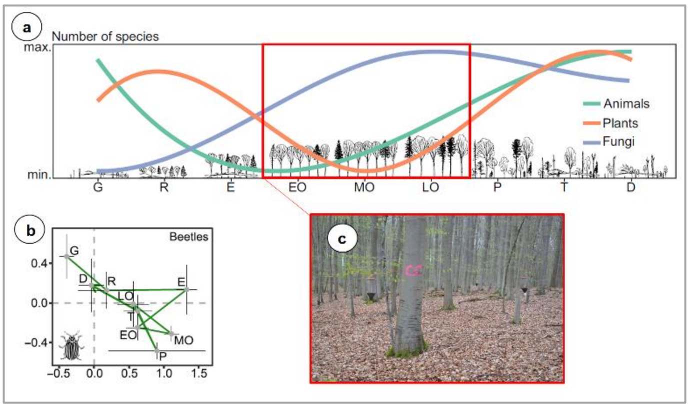


Fig. 3: Changes in (a) species number of three kingdoms and the composition of (b) beetle species communities based on ordinations along the successional gradient: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid-optimum; LO, late optimum; P, plenter; T, terminal; D, decay (from Hilmers et al. 2018). Most of European forests are production forests and are nowadays in the optimum stages (c) indicated by the red box. This most common stage nowadays is focus of our Research Unit.

Silviculture manages tree regeneration and individual tree growth predominantly by controlling canopy closure of patches by interventions, such as thinning, shelterwood cutting, gap felling, single tree cutting). Thus, it influences the abiotic environment with profound effects on plant, animal and microbial communities. While some silvicultural concepts focus on high within-patch heterogeneity (Plenter forestry), others end up in high between-patch heterogeneity, e.g. age class forests with clearcutting (Schall et al. 2018a). Both vertical and horizontal heterogeneity of forest patches have proven to be positive for the diversity of different species groups in temperate forests, although horizontal heterogeneity was more important across different taxonomic-functional groups in animals, plants and fungi than vertical heterogeneity (Heidrich et al. 2020; Schuldt et al. 2019). Different stand types and tree species compositions have also proven to result in different ecosystem functions of forests, with pronounced trade-offs in terms of different functions (Simons et al. 2020). On the local patch scale, it has been shown that tree diversity can increase productivity (Ammer 2019). Tree diversity also temporally stabilizes forest productivity (Jucker et al. 2014; Morin et al. 2014; van der Plas et al. 2016b). Multitaxa studies showed that tree diversity effects on ecosystem multifunctionality are mediated by higher trophic level interactions, such as decomposers (Fujii et al. 2017; Schuldt et al. 2014). This calls for a diversification of forests (Messier et al. 2021) and more multitaxon approaches (Eisenhauer et al. 2019b; Seibold et al. 2018).

The management focus on productivity has shaped both α-diversity and β-diversity of European forests for millennia (Grove 2002). The majority of forests were cleared for cropland, and the structure of the remaining forests changed considerably over centuries. In the Middle Ages, multipurpose forest management created a heterogeneous forest landscape of native tree species, with coppicing for firewood and tanning bark promoting early successional stages and pastures for livestock feed, delivering veteran trees and deadwood for forest specialists, that are nowadays highly threatened (Miklin et al. 2018). In contrast, modern forestry has focused increasingly on timber production since the late 18th century (Rackham 2008; Radkau 2007; Schelhaas et al. 2003). To reach this goal, in the 20th century forestry mostly relied on evenly-aged conifer-dominated homogeneous forests. Depending on tree species composition and ownership, any of those forests were finally logged by clear cutting, creating large openings. The reduction of old-growth trees by overexploitation was common (e.g. Endres 1929), and ever since the early work of Hartig (1808) the removal of dying and dead trees was recommended by foresters to suppress pest species. As a result, numerous deadwood-related species disappeared from many forests of Central Europe (Speight 1989). Alternative silvicultural systems, such as the shelterwood or the group selection system, were applied as well. Although not all mature canopy trees are removed initially under these practices, they also lead to even-aged forests after the final harvest intervention. Moreover, over the last hundred years, the distribution of age classes, which can also create heterogeneity in a landscape (Schall et al. 2018a), has not been observed in age-class forests. Thus, a bias in the development phases towards more mature, closed homogeneous production forests can be found throughout Europe today (Schelhaas et al. 2003). These human activities have caused structurally simplified production forest landscapes compared to previous natural forests throughout Central Europe, substantially leading to homogenization of communities across many taxa (Eckelt et al. 2018; Grove 2002; Ódor et al. 2006).

Since the late 1950s, a shift from clear-cutting to silvicultural strategies aiming at continuous cover started in many countries of the global North (Pommerening and Murphy 2004; Puettmann et al. 2015). These practices have increased the vertical heterogeneity of forests by avoiding larger gaps. In these forests, regeneration is established under the canopy of mature trees many years ahead of the final harvest. In consequence, about 80% of the oak and beech forests in Germany now show two or more vertical layers, i.e. shifting towards a homogenization of multiple layers all over (www.bundeswaldinventur.de, Fig. 4). While patch dynamics in natural forests create a spatially heterogeneous canopy cover on the landscape level, forests that are managed under the continuous-cover paradigm are characterized by low availability of light on the ground and low diurnal temperature range at the forest floor (De Frenne et al. 2019; Ehbrecht et al. 2019). Even thinning does not lead to a substantial increase in light availability across all vegetation layers. Another feature of forests managed with the continuous-cover approach is that trees are typically harvested before their half-life at the latest, in order to avoid infestation by fungi or to reduce the risk of tree loss due to natural disturbances (Knoke 2003). The development of deadwood features on over-mature and dead trees is thus effectively suppressed (Larrieu et al. 2017; Moning and Müller 2009) without explicit intent to leave retention trees (Bauhus et al. 2009). As a consequence, habitat availability for many deadwood species is much lower in production forests than in natural forests (Müller and Bütler 2010; Speight 1989). Multitaxon studies on the consequences of this homogenization of light and deadwood availability have shown that multi-layered forests seem to have less diverse communities than multiple single age-class forests at the landscape level (Schall et al. 2018a). Hence, between-patch heterogeneity is apparently more important for the diversity of various taxa than within-patch heterogeneity for overall forest diversity. Accordingly, a study on oribatid mites has shown a substantial decrease in β-diversity from natural forests with high between patch heterogeneity to production forests with homogenous structures at the scale of a district (Mori et al. 2015).

Fig. 4: In many commercial forests in Central Europe shelter wood cutting has led to homogenisation in the form of two-layer stands excluding gap phases on large areas.

Reciprocally, natural disturbances seem to have positive effects on between-patch diversity in former homogenized forests (Senf et al. 2020; Sommerfeld et al. 2018; Turner et al. 2003). Here, early successional stages seem to be important in forests for high α-, but particularly high β-diversity due to distinct communities adapted to different environmental conditions (Hilmers et al. 2018; Swanson et al. 2011, Fig. 3b).

The awareness of the lack of heterogeneity in most Central European production forests today has provoked a number of new ideas for improving heterogeneity at multiple spatial scales. Retention forestry is one concept developed originally in the boreal zone and applied particularly in clear-cutting systems (Lindenmayer et al. 2012). Based on the observation that even large-scale disturbances always leave parts of the forest unimpaired (Donato et al. 2012), a management concept has evolved that retains groups of trees or deadwood after harvesting. These legacies should promote biodiversity and ecosystem functions (Heikkala et al. 2016b). This idea is now also being applied in temperate forests, with around 5 to 10 habitat trees per hectare, and deadwood in particular being left in the forest after timber harvesting measures (Dörfler et al. 2017). This demonstrably leads to a promotion of deadwood-bound species at the level of the patch but also at the level of the landscape (Dörfler et al. 2018; Roth et al. 2019; Sandström et al. 2019).

Another idea for creating within-stand heterogeneity is to induce premature senescence (Cavalli and Mason 2003; Speight 1989) in younger forests to accelerate the aging process. It mimics the historically applied pollarding of trees for cattle fodder. The resulting early ageing and formation of tree cavities and other microhabitats promotes species that need over-mature trees (Sebek et al. 2013). Coppicing, which was widespread in the Middle Ages and served to produce firewood, has a similar effect. Here, trees, especially oaks and hornbeam, were cut back to the stump about every 20 years. The stumps treated in this way then sprout again. This results in tree stumps with many rotten parts. Today, the remnants of these coppicing forests represent valuable habitats, especially for saproxylic beetles (Bussler et al. 2020; Sebek et al. 2013). A further option is to manage production forests for old-growth features, for example by prolonging the rotation cycle and by creating structural components that are typical for old-growth forests (Bauhus et al. 2009). Extending the rotation period in European beech, for example, to over 150-200 years, increases the amount of microhabitats (Larrieu and Cabanettes 2012; Paillet et al. 2019) and promotes lichen, bird and snail diversity (Moning and Müller 2009).

Similarly, to restore forest heterogeneity, Keeton (2006) developed the concept of enhancing structural complexity (ESC) by increasing the variation in vertical and horizontal canopy density and in different types of deadwood within stands. The effectiveness of such measures was recently tested in a LiDAR study for temperate forests (Heidrich et al. 2020). It showed that increasing the horizontal heterogeneity within a hectare of forest promotes the richness of a large number of species groups in plants, fungi and animals. The diversity of deadwood structures in terms of tree species and structure types also promoted the diversity for fungi and beetles. The latter results were confirmed in an experiment on deadwood diversity and quantity. It was not the mere quantity but the diversity of deadwood structures that promoted the diversity of deadwood inhabitants (Krah et al. 2018; Seibold et al. 2016).

In general, the ESC strategy appears promising for promoting biodiversity and presumably also enhancing the diversity of ecosystem functions, but this concept had no explicit β-diversity focus. However, according to observations from non-managed forests, the spatial differentiation between forest patches with such a treatment should lead to different communities (β-diversity) and by this to a higher γ-diversity (Fig. 2, Begehold et al. 2015; Hilmers et al. 2018; Kortmann et al. 2021).

A recently emerged aspect additionally calls for a better understanding of heterogeneity and β-diversity in forests: The temperate forests of Central Europe have also been experiencing increasingly severe disturbances, such as wind, insect outbreaks, drought and fire in recent years (Seidl et al. 2014). In the course of these events, the death of individual trees, groups of trees and even entire stands is becoming more frequent (Senf et al. 2019). Interventions after disturbances significantly change the pattern of disturbed areas also in temperate forests (Sommerfeld et al. 2018). The previously scarce resource of deadwood is emerging in many places. This raises the question of how this situation can be utilised in the best possible way to remedy previous deficiencies in terms of biodiversity and ecosystem functions in homogenized commercial forests and to make them more resilient in a future climate.

In this context, decisions to remove dead trees and quickly reforest such disturbed areas or to leave them at least partially unmanaged and wait for the establishment of natural regeneration have critical implications for the spatial heterogeneity and diversity of many species groups (Thorn et al. 2018). Such early successional stages, unmanaged, with high deadwood diversity and light on the forest floor are among the rarest forest habitats worldwide today (Noss et al. 1999). Recent meta-analyses show that substantial parts of disturbed areas would have to be left in place in order to preserve the species typical of these habitats (Thorn et al. 2020) and would, in some cases, even be the economically more reasonable option. Nevertheless, many management decisions are often made without deeper economic and ecological considerations. Even in protected areas in Europe and Asia, salvage logging occurs regularly (Müller et al. 2019). Research of natural disturbance events has always the major problem that it can hardly be planned spatially and temporally. Many studies are therefore of limited value since a clear design of disturbances is missing. Therefore, targeted disturbance experiments were called for early on. However, these were rarely implemented (but see Heikkala et al. 2016a; Spence 2001).

In summary, (i) heterogeneity in forests is highly relevant for biodiversity and ecosystem functions, (ii) our understanding of how α- and β-diversity determines γ-diversity and γ-multifunctionality of temperate forests is limited, and (iii) climate change has taken the baton and is changing forest heterogeneity. These findings urgently call for approaches addressing the interplay of different scales, taxonomic groups and ecosystem functions in a controlled field experiment. The fact that manipulations in production forests are common and only need to be set up in a design suitable for research, makes forests an ideal ecosystem for general research on the relationships between β-diversity and γ-multifunctionality (Mori et al. 2013). Additionally, the results of such experiments will be of high value for adjusting forest management practices towards preserving biodiversity and various ecosystem functions. In this Research Unit (RU), we propose to provide an experimental study of manipulating β-diversity at the landscape scale, to investigate the effect on biodiversity and multifunctionality of a landscape, using forests as a model system. Therein, we plan to measure 18 taxonomic groups from a wide range of trophic levels and kingdoms, together with 21 of the most important ecosystem functions in temperate forests in a collaborative research approach within our real world experiment.

Preliminary work

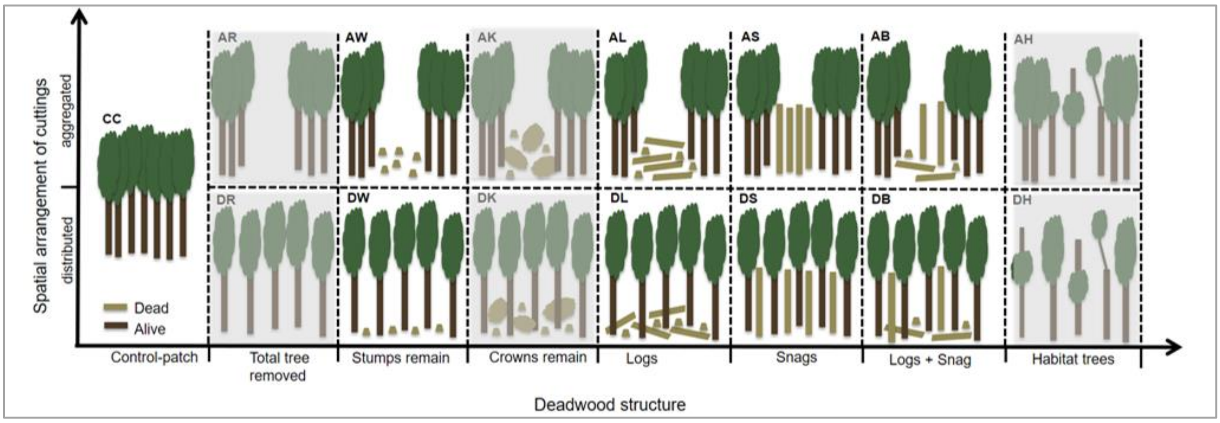


Fig. 5: ESBC treatments on the 50x50m patches realized in each ESBC district. Shaded treatments are realised only at the three intensive sites in the University Forest Sailershausen.

In order to be able to study the effects of α- and β-diversity on γ-diversity and γ-multifunctionality of forests under real world conditions on site, district, and patch level (Fig. 5, 6), we have recruited a number of landowners who agreed to make their land available for experimental interventions and research, even over a longer period. With the help of substantial seed money by the German Federal Environmental Foundation, among others, we already established 11 districts with interventions to Enhance Structural Beta Complexity (ESBC) in 6 climatic different regions in Germany, in the years 2016, 2017 and 2018. In each of the districts with a size of 10-20 ha, we changed the canopy cover and deadwood resources in 50x50 m patches with the same set of interventions (Fig. 5). High stumps were created by harvesters or tree climbers.

As a result, the interventions in the different districts took place in years with different climatic conditions. In the meantime, the deadwood structures created have been colonised by insects and fungi, and the ground vegetation in the gaps has responded to the increased light availability. Now is the perfect time to study these responses in the context of beta diversity.

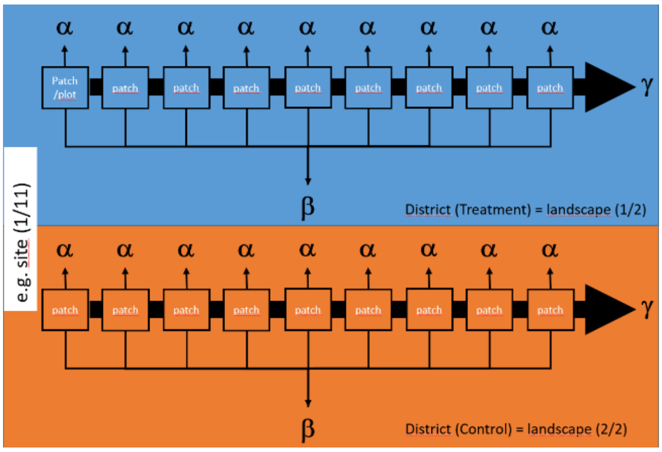


Fig. 6: Schematic representation of the ecosystem elements site, district, and patch in relation to derived diversity levels for an exemplary site.

For the RU, we already envisioned control districts. These districts of similar soil, climate and tree compositions will be selected in the vicinity. This has already been done in the university forest. In the other forests, this has been agreed with the owners and will be set up immediately after this proposal has been approved. Since no interventions are necessary, establishment is much easier. In total, the design will consist of 11 pairs of districts as shown schematically in Figure 6.

On part of the ESBC districts, the applicants have already started extensive measurements, partly even before the interventions started (university forest). Most of the planned research methods for quantifying biodiversity of different taxa, forest structures as well as ecosystem functions have already been tested for their feasibility in this environment. In addition to some established methods, we have also tested new methods in the forest patches for their suitability in temperate forests (Fig. 7). As a result, an extensive treasure trove of data has already been acquired in preparation of the RU, which will make it easier for the PhD students or postdocs in the RU to prepare initial publications at an early stage.

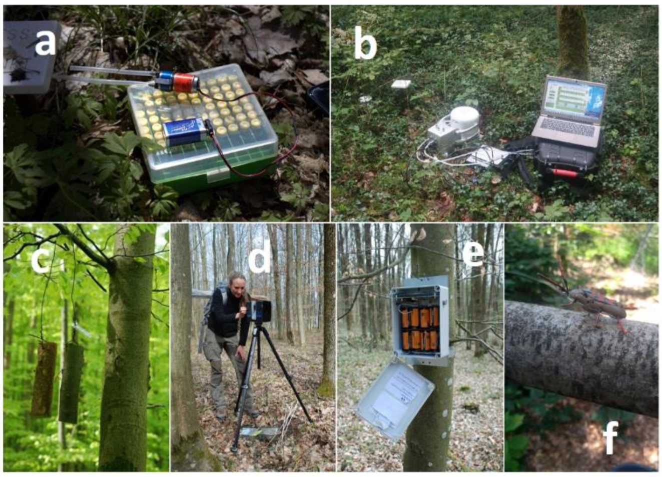


Fig. 7: Different new methods have been tested successfully by the consortium in advance: (a) patch-specific volatile profiles can be estimated by dynamic headspace analysis; (b) Picarro to measure CO_2 fluxes; (c) standardized deadwood as common substrate to measure fungi and bacterial communities by metabarcoding; (d) terrestrial laser scanning allows patch-specific high-resolution measurements of forest structures; (e) sound recorders allow highly standardized measurements of breeding bird communities; (f) artificial insect dummies to measure predator pressure.

For example, we have successfully tested single tree canopy fogging as a method to estimate caterpillar densities, linked them to defoliation as a measure of herbivory resistance and to terrestrial LiDAR and satellite metrics (Bae et al. 2021; Leroy et al. 2021). Moreover, we have successfully tested a new very cost-effective meta-barcoding approach to identify parasitoids in caterpillars using Sequel II (PacBio). To expand the range of dummies used for the assessment of predator pressure we successfully tested not only the existing caterpillar dummies but also adult insects (Fig. 7f).

A measurement of canopy openness by terrestrial laser scanning in five districts, three of them treated with ESBC in the University Forest, showed a wider range of horizontal heterogeneity between the patches resulting from our intervention (Districts B, C and D), and thus the effectiveness of our treatments. To have a replicated control block for each ESBC, we established another two Districts (E and F), both showing comparable ranges of canopy openness as A, B, C and D before treatment (Fig. 8).

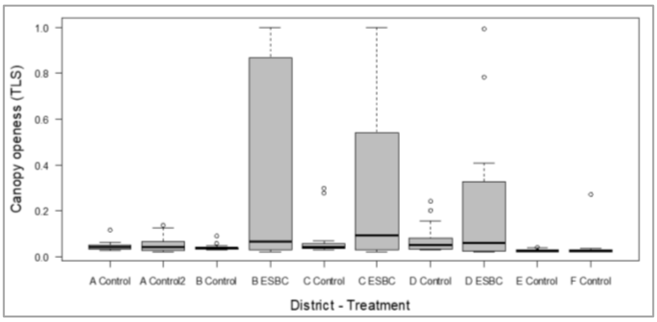


Fig. 8: Enhancement of structural β-complexity in the districts B, C and D show the enhancement of canopy openness among patches.

Preliminary results of the saproxylic beetle assemblage response from five districts with ESBC in the Bavarian Forest show that the community composition differs fundamentally between the climate regions (Region 2 and Region 3; Fig. 9). This was expected, but it became also evident that along the second axis, there is a systematic deviation of species compositions from control patches to areas with distributed interventions to aggregated interventions, as predicted by the ESBC treatment.

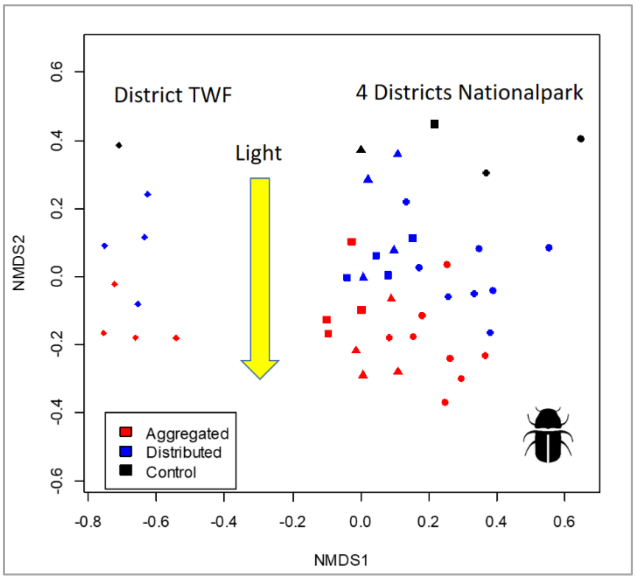


Fig. 9: Response of saproxylic communities to the ESBC treatments in five districts in South Eastern Germany. Different symbols indicate different blocks. Note that TWF is a district in lower elevations (Region 3, Fig. 1) with milder climate than the other four districts (Region 2). The consistent shift in communities along the second axis from control patches to distributed ones, and to aggregated interventions, underlines the potential of the ESBC interventions for creating abiotic heterogeneity that promotes the dissimilarity of species communities.

1.1 For a renewal proposal: Report on the progress to date

Not applicable

1.2 Project-related publication

1. Bae S, Levick S, Heidrich L, Magdon P, Leutner BF, Wöllauer S, Serebryanyk A, Nauss T, Krzystek P, Gossner MM, Schall P, Heibl C, **Bässler C**, Inken D, Schulze E-D, Krah F-S, Culmsee H, Jung K, Heurich M, Winter M-B, Fischer M, Seibold S, Thorn S, Gerlach T, **Hothorn T**, **Weisser WW, Müller J** (2019) Radar vision in the mapping of forest biodiversity from space. Nature Communications 10:4757
2. **Chao A**, Chiu C-H, Villeger S, Sun I-F, **Thorn S**, Lin Y-C, Chiang J-M, Sherwin WB (2019) An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecological Monographs 89:e01343.
3. **Eisenhauer N**, Schielzeth H, Barnes AD, Barry K, Bonn A, Brose U, Bruelheide H, Buchmann N, Buscot F, Ebeling A, Ferlian O, Freschet GT, Giling DP, Hättenschwiler S, Hillebrand H, Hines J, Isbell F, Koller-France E, König-Ries B, de Kroon H, Meyer ST, Milcu A, **Müller J**, Nock CA, Petermann JS, Roscher C, Scherber C, **Scherer-Lorenzen M**, Schmid B, Schnitzer SA, Schuldt A, Tscharntke T, Türke M, van Dam NM, **van der Plas F**, Vogel A, Wagg C, Wardle DA, Weigelt A, **Weisser WW**, Wirth C, Jochum M (2019) A multitrophic perspective on biodiversity–ecosystem functioning research. Advances in Ecological Research 61:1-54.
4. Heidrich L, Bae S, Levick S, Seibold S, Weisser W, Krzystek P, Magdon P, Nauss T, Schall P, Serebryanyk A, Wollauer S, **Ammer C**, Bassler C, Doerfler I, Fischer M, Gossner MM, Heurich M, **Hothorn T**, Jung K, Kreft H, Schulze ED, Simons N, **Thorn S, Muller J** (2020) Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests. Nature Ecology & Evolution 4:1431-1431.
5. **Peters MK**, Hemp A, Appelhans T, Becker JN, Behler C, **Classen A**, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Gerschlauer F, Gutlein A, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Kuhnel A, Mayr AV, Mwangomo E, Ngereza C, Njovu HK, Otte I, Pabst H, Renner M, Roder J, Rutten G, Costa DS, Sierra-Cornejo N, Vollstadt MGR, Dulle HI, Eardley CD, Howell KM, Keller A, Peters RS, Ssymank A, Kakengi V, Zhang J, Bogner C, Bohning-Gaese K, Brandl R, Hertel D, Huwe B, Kiese R, Kleyer M, Kuzyakov Y, Nauss T, Schleuning M, Tschapka M, Fischer M, **Steffan-Dewenter I** (2019) Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568:88-92.
6. Schall P, Gossner M, Heinrichs S, Fischer M, Boch S, Prati D, Jung K, Baumgartner V, Blaser S, Böhm S, Buscot F, Daniel R, Goldmann K, Kaiser K, Kahl T, Lange M, **Müller J**, Overmann J, Renner S, Schulze E, Sikorski J, Tschapka M, Türke M, **Weisser W**, Wemheuer B, Wubet T, **Ammer C** (2018) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of applied Ecology 55: 267-278.
7. Seibold S, Cadotte MW, MacIvor JS, **Thorn S, Müller J** (2018) The necessity of multi-tropic approaches in community ecology Trends in Ecology and Evolution 33:754-764.
8. Seibold S, Gossner MM, Simons NK, Blüthgen N, **Müller J**, Ambarli D, Ammer C, Bauhus J, Fischer M, Habel JC, Linsenmair KE, Nauss T, Penone C, Prati D, Schall P, Schulze E-D, Vogt J, Wöllauer S, **Weisser WW** (2019) Arthropod decline in grasslands and forests is associated with drivers at landscape level. Nature 574:671-674
9. Seibold S, Rammer W, **Hothorn T**, Seidl R, Ulyshen MD, Lorz J, **Cadotte M**, Lindemayer DB, Adhikari YP, Aragón R, Bae S, **Baldrian P**, Barimani Varandi H, Barlow J, **Bässler C**, Beauchêne J, Berenguer E, Bergamin RS, Birkemoe T, Boros G, Brandl R, Brustel: H, Burton PJ, Cakpo-Tossou YT, Castro J, Eugénie C, Cobb TP, Nina F, Fernández RD, Firn J, Gan KS, González G, Gossner MM, Habel JC, Christian H, Heibl C, Heikkala O, Hemp A, Hemp C, Hjältén J, Hotes S, Kouki J, Lachat T, Liu J, Liu Y, Luo Y-H, Macandog DM, Martina PE, Mukul SA, Nachin B, Nisbet K, O'Halloran J, Oxbrough A, Pandey JN, Pavlíček T, Pawson SM, Rakotondranary JS, Ramanamanjato J-B, Rossi L, Schmidl J, Schulze M, Seaton S, Stone MJ, Stork NE, Suran B, Sverdrup-Thygeson A, Thorn S, Thyagarajan G, Wardlaw TJ, Weisser WW, Yoon S, Zhang N, **Müller J** (2021) The contribution of insects to global forest deadwood decomposition. Nature 597:77–81
10. **Thorn S**, **Bässler C**, Bernhardt-Romermann M, Cadotte M, Heibl C, Schafer H, Seibold S, **Müller J** (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters 19:163-170.

2. Objectives and joint work programme

2.1 Objectives of the overall project and expected benefits of collaboration within the unit, incl. a description of the group composition and their project-specific qualifications

2.1.1 Objectives

Mission of the Research Unit

With our Research Unit (RU), we will improve the mechanistic understanding of anthropogenic homogenization of landscapes using forests as model system and to improve active-adaptive silvicultural management strategies and passive-adaptive disturbance management with the focus on biodiversity and multifunctionality. Therefore, we expand the ESC concept of Keeton (2006) to a spatially explicit **E**nhancing of **S**tructural **B**eta **C**omplexity (**ESBC**) approach, which aims to mimic the natural variation of successional stages between forest patches within a district. The district is defined as our landscape (γ-scale), characterized by the within-patch (α-) and between-patch (β-) diversity (see Fig. 6). This idea is not new (Puettmann et al. 2015). However, it is still unclear (A) whether this approach can successfully enhance the complexity of forests with respect to relevant abiotic factors, (B) whether and how biodiversity of multiple taxa respond, and (C) whether and how multifunctionality of a forest district can be enhanced by increasing β-diversity. Manipulative and replicated studies focusing on β-diversity are often seen as impossible (Isbell et al. 2017). This might be true for large landscapes, but it is certainly not true for the between-patch diversity of forest districts considered as a small forest landscape (see Fig. 5). Such districts are commonly manipulated in practice and in research projects (Hyvärinen et al. 2006; Work et al. 2004). Moreover, they are exactly the scale of decisions for forest managers during logging operations. Hence, forest districts and their patches provide a unique model system to study β-diversity and ecosystem functions at a scale highly relevant for forest managers. Such districts have the further advantage that species from the regional species pool of the forest, in which the districts are embedded, are able to colonize the patches if suitable, because dispersal limitations for most forest organism are low (below 1 km, Komonen and Müller 2018). Nevertheless, so far no experimental β-diversity study in forests exists (Mori et al. 2018).

Here we set up a cross-region experiment in managed forests to test the potential of an ESBC strategy for biodiversity and multifunctionality. We will sample the following 18 taxonomic groups from different trophic levels and several kingdoms as suggested for multitrophic studies by Seibold et al. (2018): mammals, birds, bats, spiders, beetles, Hymenopteran, Dipteran, true bugs, moths, springtails, nematodes, soil fungi, wood-inhabiting fungi, soil bacteria, bacteria in wood, vascular plants, bryophytes and lichens. As ecosystem functions, we will assess 21 of the major functions in temperate forests (Schuldt et al. 2018): microbial activity in soil, soil respiration, belowground secondary productivity, nutrient cycling, micro-climate regulation, aggregate stability, tree regeneration, leaf litter decomposition, wood decomposition, dung decomposition, carcass decomposition, primary productivity, below and above carbon sequestration, aboveground secondary productivity, pollination, seed dispersal, invertebrate herbivory resistance, vertebrate herbivory resistance, symbiosis, predation and parasitism.

This will be a unique comprehensive data set in BEF studies with biodiversity of different trophic levels combined with key ecosystem functions in forests, and approach only possible with the highly interdisciplinary collaboration of all subprojects. Simultaneously the RU will provide comparable data to forest inventories or IPBES to maximize transferability of the findings. All subprojects make essential contributions to ensure that the entire field of biodiversity and ecosystem function can be covered at the three spatial levels α, β and γ. SP1 provides the backbone of a forest ecosystem, the distribution and species composition of the trees, and the associated production function. SP2 provides the highly innovative structural component of the forest in the form of volatiles and the important function of pest insects. SP3 takes the step of quantifying the forest structures spatially and temporally at high resolution which is indispensable to track the temporal course over the years and also to be able to upscale the results to large areas. SP4 focuses on soil animals, which is particularly important in forests. Through the cooperation with our Mercator Fellow Baldrian the focus is expanded to soil fungi and bacteria. SP5 will focus on the important decomposition processes in litter, dung and carrion. These are core functions in the forest both for biodiversity and as a process. SP6 will focus on the interaction of plants and animals in dispersal with a focus on pollination and seed dispersal, two key functions in forests that are directly related to the diversity of animal species. SP7 focuses on deadwood and its microbes. Fungi and bacteria are the main recyclers here. At the same time, wood fungi represent an important part of biodiversity in forests. Thus, they directly influence the st,orage of carbon in the forest. SP8 will focus on the herb layer. In Central European forests, plants in the herb layer usually represent the largest plant diversity in forests and are very sensitive, especially to heterogeneity in succession stages. SP9 will fill comprehensively the gaps in the diversity of the higher trophic levels which have been missing in many BEF studies so far. Here various groups will be covered, from phytophagous insects to predators. SPZ will guarantee the synthesis towards BEF theory as well as towards forest management and provide all subprojects with appropriate analytical frameworks.

Our model forest type is a common mid-aged mixed Central European production forest district. Forest management (Fig. 1oA) has reduced the patch diversity at this scale over decades to centuries by silviculture homogenization. As a result, the light availability near the ground and the amount and diversity of deadwood features are more or less similar in all patches and heavily reduced compared to a natural forest (Fig. 10A). We have already established the experimental treatments to increase the spatial heterogeneity in districts by varying canopy cover and by creating deadwood features in experimental patches. Thereby, we have increased habitat diversity between patches that can be colonized by different species (Hilmers et al. 2018; Seibold et al. 2016). Moreover, the increase in deadwood diversity in space and time between patches is expected to increase the diversity of wood-associated species.

The way in which species colonize the different patches of heterogeneous landscapes follows deterministic and stochastic community assembly mechanisms (Fig. 10B). Succession theory predicts for various taxa that the community assembly of early successional stages is often characterized by stochastic processes. This of course is not true for all taxa. Particularly, tree communities regularly shift from density-dependent mortality with more deterministic processes in younger forests (Holzwarth et al. 2013), to density-independent mortality in older forests which can be stochastic (Franklin et al. 2002). Following the mathematical theory of stochasticity, community assembly is therefore not necessarily predictable. One important mechanism here is the so-called priority effect, which describes the order of early-arriving species and the prolonged impacts of early-colonizing species, affecting the community assembly and ecosystem functions over later years (Fukami et al. 2010; Weslien et al. 2011). A second process is ecological drift driven by the demographic stochasticity affecting communities (Chase 2010). Third, dispersal limitations are expected to affect the stochastic character of the community assembly in a specific patch (Wang and Loreau 2016).

In contrast, communities in late successional stages are predicted to be characterized more strongly by deterministic processes, such as habitat filtering or competition (Leibold et al. 2004; Mori et al. 2017). Concerning deadwood, for example, it has been shown that the chemical and physical characteristics of a dead tree at a specific stage filter a set of flying insects from the regional species pool, creating functionally more similar communities than would random sampling (Müller et al. 2014). Reciprocally, the removal of deadwood has been shown to alter the dominant assembly processes in different wood-inhabiting communities and is the current practice in most disturbed forests (Müller et al. 2019; Thorn et al. 2016). Hence, depending on taxonomic groups, we expect a shift in assembly processes from deterministic to stochastic processes or vice versa by our ESBC treatments (Fig. 10B).

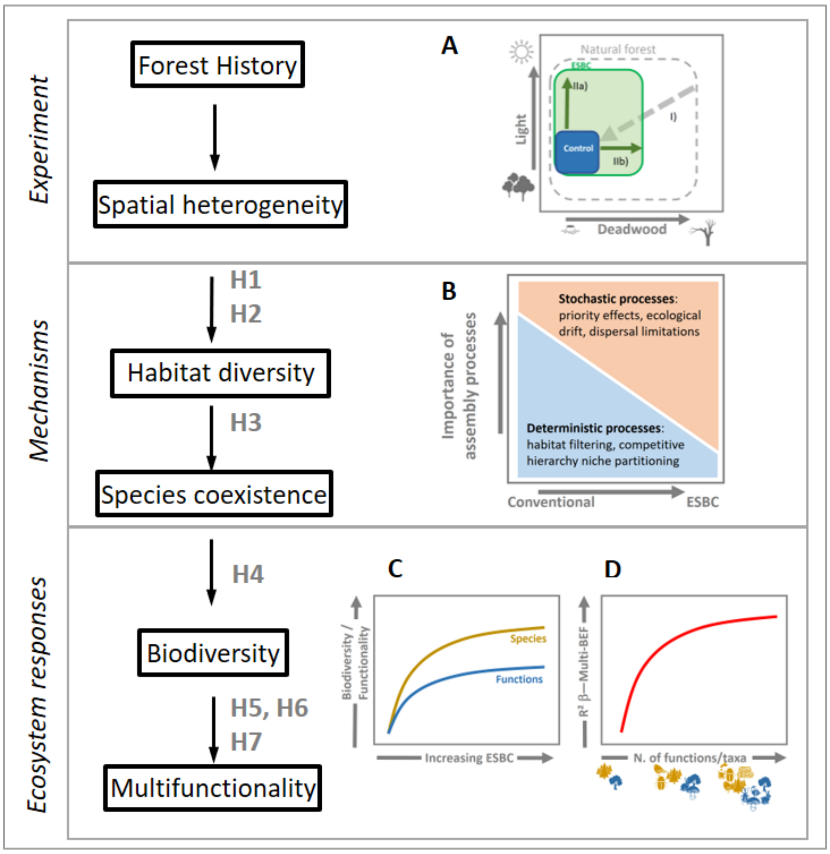


Fig. 10: Conceptual figure of the underlying hypotheses of our proposed RU. Due to management history, forest districts have been reduced in their niche space (blue area in A) compared to natural forests (dashed gray line), shown in A for two niche axes, light (IIa) and deadwood (IIb). Enhancement of Structural Beta Complexity (ESBC) is hypothesized to regain a substantial part of the niche space (green area in A) observed in natural forests, here referred to as "spatial heterogeneity" (H1). This intervention is expected to create an increase in habitat diversity among the patches (H2), which should translate into alterations of species coexistence, from stochastic to deterministic processes or vice versa (H3), e.g. by an increase of stochastic processes in early succession patches (B). An ESBC-based increase in species coexistence is expected to enhance β-diversity across trophic levels (H4). Based on BEF theory, this increase in biodiversity is hypothesized to enhance ecosystem functioning, but we expect stronger increase in biodiversity with increasing patch heterogeneity than functionality because of functional redundancy of species, here in specific of species-poor groups (H5) (C). The strength of the positive relationship between β-diversity and ecosystem multifunctionality is expected to increase with additional taxa and functions considered (D) (H6).

In addition to multitrophic community assembly processes in these landscapes, we are interested in how β-diversity enhancement influences multiple ecosystem functions (Mori et al. 2018; Mori et al. 2017). Because of functional redundancy of many species in forest ecosystems (e.g. fungi species decomposing wood or tree species increasing plant biomass; (Ammer 2019; Boddy and Watkinson 1995), we expect a stronger increase of β-diversity than of β-functionality with enhanced β structural complexity in a forest landscape (Fig. 10C). Moreover we assume that the lower the overall diversity of a species group (e.g. bats, birds), the more the few species that do exist are functional complementary to each other, whereas the bigger a group is (e.g. insects, fungi), the more species are functionally redundant with respect to each other. If β-diversity has similar effects on β-multifunctionality as observed for α-diversity, which is unknown so far, we can expect an increase in the strength of the biodiversity-multifunctionality relationship with the number of taxa and trophic levels included in a multitaxa diversity index (Schuldt et al. 2018; Soliveres et al. 2016). We also expect an increasing strength of the biodiversity-multifunctionality relationship with the number of functions included in a multifunctionality index (Fig. 10D, (Lefcheck et al. 2015; Meyer et al.

2018; Schuldt et al. 2018). The mechanisms, which determine multifunctionality, remain largely unclear, representing a serious knowledge gap (Gamfeldt and Roger 2017).

Frameworks to link statistically biodiversity and multifunctionality at different scales are still under debate. Van der Plas and colleagues (2016a) developed a new approach to partition biodiversity effects on multifunctionality at the α-scale into three mechanisms: First, species performing differently under different environmental conditions may lead to increased total resource use. This 'complementarity effect' (Loreau et al. 2001) might be linked to the species turnover component of β-diversity. Second, variation of dominance in species between communities, described as the nestedness component of β-diversity, might contribute to the multifunctional selection effect with dominant species driving major processes (Mori et al. 2018). Third, the averaging of individual species effects on ecosystem functions might relate biodiversity to multifunctionality. This mechanism has been described as the 'jack-of-all-trades'.

Also multiple approaches exist to quantify multifunctionality from the threshold approach assuming functions as fulfilled if being above a particular value (Byrnes et al. 2014), to averaging methods providing means across functions (Maestre et al. 2012) or weighing different functions according to their perceived relative contributions to ecosystem services (Allan et al. 2013). Here we plan to develop a new concept for β-diversity and β-multifunctionality along the Hill numbers, considering taxonomic, functional, and phylogenetic diversities (see Box 1, SPZ). Such a new framework improving the quantification of diversity measures and multifunctionality tested in an experimental approach will be of interest far beyond forest biodiversity research (Mori et al. 2018). Moreover, our results will guide managers of production forests and protected areas how they can best improve their active and passive strategies to increase biodiversity based on ecological principles.

Research questions and hypotheses

Our collaborative project combines forest science, ecology, remote sensing, chemical ecology and statistics. We focus on the cascading effects of an ESBC strategy enhancing the heterogeneity in forests, from habitat diversity between patches, to changes in species coexistence in heterogeneous forests, to multidiversity, and to multifunctionality. Our project will allow the identification of unknown mechanisms behind observed homogenization-diversity relationships and will reveal how these translate into multifunctionality. Moreover, it will help to quantify the potential for enhancing structural complexity using silvicultural approaches and improved management of disturbances in production forests, with potential benefits for β-diversity and thereby multifunctionality in temperate forests of Central Europe. Thereby, our project will address the following **general research question**:

Does silvicultural Enhancement of Structural Beta Complexity (ESBC) between forest patches increase biodiversity and multifunctionality in forests?

Section 1 (α-scale): The heterogeneity gradient by variations of canopy cover and deadwood availability (Fig. 10A)

The proposed RU will focus on the independent and shared contribution of canopy cover and different deadwood features to structural complexity. We expect shading by overstory trees as the dominant effect on species communities and functions (including soil communities; Mueller et al. 2016), followed by deadwood types (Seibold et al. 2016). Therefore, we will test two general hypotheses addressing shading and deadwood effects on biodiversity.

H1: **ESC** measures (**E**nhancement of **S**tructural **C**omplexity at the patch scale) increase light levels and variation of light, and thus enhances habitat diversity and biodiversity at the local scale (α-diversity).

H2: **ESC** measures increase the amount of deadwood and thus enhance habitat diversity and biodiversity at the local scale (α-diversity).

Section 2 (β-scale): Patch-heterogeneity and β-diversity of forest landscapes (Fig. 10B)

Here, we will focus on the community assembly at the landscape scale responding to the single patch treatments and the enhancement of structural complexity between forest patches. For the different taxa, trophic levels and spatial levels, we aim to identify the main drivers of environmental heterogeneity and the main assembly mechanisms. Unravelling how communities respond to variation in structural complexity on the landscape scale is crucial for understanding the impact of forest homogenization. More specifically, we will test if:

H3: **ESBC** increases β-diversity compared to conventionally managed forests.

H4: **ESBC** increases β-diversity by a shift in the assembly processes from deterministic to more stochastic community assembly processes (e.g. insects) or vice versa (e.g. trees) depending on the taxa.

Section 3: Patch-heterogeneity and ecosystem functions of forest landscapes (Fig. 10C, D, Fig. 2)

Here, we will focus on the effect of between-patch diversity on multiple ecosystem functions. We will analyse various functions on all patches. This will allow us to test different hypotheses addressing the question on how forest complexity drives β-multifunctionality and in which way homogenization of forest structure determines community processes and an expected reduction in ecosystem functions. We will test three general hypotheses to elucidate which mechanism dominates the increase of multifunctionality in forests following enhanced structural complexity. The three related hypotheses are:

H5: With increasing patch heterogeneity biodiversity increases faster than ecosystem functionality because of functional redundancy of species.

H6: The strength in the relationship between β-diversity and β-multifunctionality increases with the number of taxa and ecosystem functions included.

H7: **ESBC** shifts a forest from providing '*few functions everywhere*' mechanism to a forest dominated by functions provided by a '*all functions somewhere*' mechanism (Fig. 2).

2.1.2 Benefits of collaboration within the Research Unit

Establishment of the first real world β-diversity experiment in forests in Central Europe

In contrast to other areas in the world, interdisciplinary experimental forest biodiversity research in real world conditions is so far not well established in Germany. Using the opportunity of the University Forest Sailershausen, the forests of the Bavarian Forest Nationalpark connected to the University of Würzburg by the joint-Professorship of the speaker of the RU, as well as our collaboration partners in forest practice, we aim to demonstrate the attractiveness of such experimental sites for research and education even beyond the project. The high interest of researchers in the establishment phase of our project (see multiple pre-treatment investments by members of our research group) demonstrates the need for such collaborative work on the ground of a landowner supportive of science.

Interactions among the subprojects

The research questions of how β-diversity translates into multifunctionality of landscapes cannot be addressed in a single study, as too many aspects need to be included, i.e. different taxa, different functions, different scales, and new analysis frameworks. Therefore, our RU is a strongly interwoven net of different disciplines comprising all three components of diversity, namely structure, composition and functions (Noss 1990, Table 2). All subprojects provide data for synthesis approaches and for addressing the overarching hypotheses. All subprojects are connected by the central SPZ. Additionally, there are many close interconnections between single subprojects to answer specific research questions (Fig. 11). All SPs will collect data on species, structures or functions in all 234 patches, allowing for synthesis and comparisons across taxa, strata, trophic positions, processes and resulting functions following an “all-measurements-on-all-patches” philosophy. Subproject Z will take over responsibility for answering the overarching research questions, scientific coordination, dissemination of the results to forest practice, coordination of sampling campaigns, data storage and management, site management, standard microclimatic, soil and tree measurements, setting standards for analyses, and providing a general statistical framework with R codes for all subprojects. The Coordination Module (CM) will organize two retreats per year before and after field season with all participants at the Fieldstation Fabrikschleichach, in the Bavarian Forest National Park and in our additional study areas. The retreats will support the collaboration between the subprojects and allow exchanging views with international collaboration partners that are invited to these retreats, as learned from previous RUs (Eisenhauer et al. 2019a). Moreover, they will allow the PhD students to discuss their findings with forest practitioners. Thus, these meetings will not only support the PhD-students in scientific terms but will also allow them to establish their own network. Within the coordination module (CM) and SPZ, regular workshops along the main research fields of the RU will be organized. With the Fieldstation and the facilities of the Nationalpark Bavarian Forest two locations with meeting rooms and excellent retreat opportunities are available (Fig. 1d). Furthermore, we will use the experience of the national park in organizing international conferences on topics, such as forest dynamics, forest nature conservation and biodiversity, where the results of the RU could be presented at the end of the first phase. Near the Fieldstation, a regular national conference by the *Bayerische Staatsforsten* on research in forests will be used to present the results of the entire research group to the forestry practice.

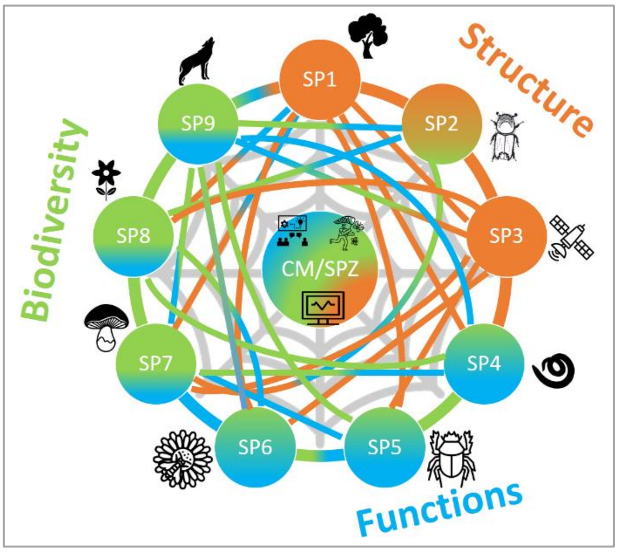


Fig. 11: Integration of the subprojects (SP) with highly complementary skills and knowledge (see icons) within the RU. The coordination module (CM) and the SPZ provide central scientific services and logistics to all subprojects (spider web). Green: subprojects providing biodiversity data, brown: subprojects that contribute data on forest structure, blue: subprojects that deliver data on ecosystem functions.

2.1.3 Qualification of participating researchers / working groups

N Eisenhauer, J Müller, M Scherer-Lorenzen, I Steffan-Dewenter, G von Oheimb, W Weisser, C Ammer and C Bässler have developed a broad experience in running experiments from object to district level in grasslands and forests (Baber et al. 2016; Baeten et al. 2013; Bruelheide et al. 2014; Ferlian et al. 2018; Gebhardt et al. 2014; Scherber et al. 2010; Seibold et al. 2016; Seibold et al. 2021). M Scherer-Lorenzen, N Eisenhauer, I Steffan-Dewenter and W Weisser have gained substantial experience in leading larger research groups (Baeten et al. 2013; Eisenhauer et al. 2019a; Peters et al. 2019; Weisser et al. 2017). C Ammer is the spokesperson of the DFG-funded Research Training Group 2300 on the enrichment of beech stands with conifers based on 40 plots and 11 collaborating subprojects. He and W Weisser are members of the steering committee of the Biodiversity Exploratories, a DFG-funded Infrastructure Priority Programme (SPP 1374). N Eisenhauer is speaker of the DFG Research Unit “The Jena Experiment” (FOR 5000), head of the iDiv Ecotron and the MyDiv tree diversity experiment. J Müller has coordinated the Bioklim Project in the Bavarian Forests, the interdisciplinary research team in the Bavarian Forest national park and the research group at the ecological Fieldstation Fabrikschleichach, altogether about 40 researchers. Moreover, he has initiated and coordinated several collaborative research teams in Europe (Friess et al. 2019; Hagge et al. 2019) and globally (Seibold et al. 2021) to answer overarching questions on forest ecosystems in a collaborative approach. J Müller and S Thorn gained substantial experience in developing and adapting statistical methods for different research questions in ecology (Chao et al. 2019b; Hofner et al. 2011; Hothorn et al. 2011; Kaldhusdal et al. 2015; Müller and Hothorn 2004). Relationships with leading mathematicians, statisticians and biostatisticians are institutionalised in the RU through Mercator fellowships and other collaborations.

The team consists of experts in several disciplines around forests, biodiversity, ecosystem functions and statistics. J Müller, C Ammer, M Scherer-Lorenzen, W Weisser, N Eisenhauer, G von Oheimb, P Biedermann, H Feldhaar, A Fichtner, B Schuldt and I Steffan-Dewenter have focused on different aspects of community ecology, biodiversity, biogeochemistry, structural diversity, BEF relationships and management in forests. J Müller, S Cesarz, H Feldhaar, A Claßen, C Bässler, S Thorn and M Peters complement the team by specific knowledge in the fields of the taxonomy and ecology of bats, birds, beetles, ants, bees, hoverflies, nematodes, fungi, seed dispersal, pollination, and decomposition functions. P Biedermann additionally contributes expertise in the interaction of insects and microbes together with his lab facilities in Freiburg. T Schmitt adds the chemical ecology expertise including his lab facilities in Würzburg. C Kuenzer and M Wegmann contribute their broad expertise in long-distance remote sensing in forest habitats. M Wegmann is also active in the GEO-BON Ecosystem Structure Working Group (focuses on the monitoring of the relevant *Essential Biodiversity Variables* and how they change in time). C Kuenzer, Professor at the remote sensing department in Würzburg and at the same time DLR department head, embedded in the Earth Observation Center, EOC of DLR, additionally ensures access to a large variety of resources on remote sensing. D Seidel will provide expertise in short distance remote sensing techniques and new approaches of quantifying structural complexity of forests.

Quantitative analyses of forest structures using terrestrial and airborne laser scanning in combination with ground-based measurements of trees have rapidly developed during the last decade. Three of the applicants (J Müller, C Ammer and D Seidel) have contributed substantially to an improved quantification of forest structures and their use in modelling communities and assembly patterns. Their original contribution involved the development of metrics for forest structure (Ehbrecht et al. 2017; Schall et al. 2018b), modelling a wide range of communities (fungi to vertebrates) in forests with structural variables from remote sensing (Bae et al. 2018; Müller and Brandl 2009; Peura et al. 2016; Vierling et al. 2011), and testing mechanisms in assembly processes (Müller et al. 2018; Müller et al. 2012). In the latter, the application of phylogenetic and functional diversity as well as their combination has been further developed for a number of forest taxa, including the creation of phylogenies and trait databases (Bässler et al. 2021; Bässler et al. 2014; Franke et al. 2020; Hagge et al. 2021; Thorn et al. 2016). By running large collaborative projects, M Scherer-Lorenzen gained much expertise in measuring functions in forests, including those based on rapid and proxy assessments (Baeten et al. 2019; van der Plas et al. 2018) as well as in cooperation with stakeholders (Dr. Forest Project). Thus, the selection of applicants is highly complementary in their taxonomic, methodological, and ecosystem-function expertise, allowing the project to cover the β-diversity response in a much broader way than by individual projects alone. The interdisciplinary approach in combination with a first real world β-diversity experiment is highly innovative, unique and novel. We will strengthen the team by working closely with the Mercator Fellows Prof. Petr Baldrian, Prof. Marc Cadotte, Prof. Torsten Hothorn, Prof. Akira Mori, Prof. Diana Six, Prof. Fons van der Plas, and will closely collaborate with Prof. A Chao. Here A Chao, M Cadotte and T Hothorn are leading experts in statistical frameworks in ecology.

2.1.4 Group composition

Applicant (PI / Co-PI)	**PhD**	**Current institution**	**Research area**
Prof. Dr. Christian **Ammer** (PI)	1996	University of Göttingen	Silviculture, Regeneration Ecology and Forest Dynamics
Prof. Dr. Claus **Bässler** (PI)	2008	University Frankfurt	Mycology, Forest Ecology, Conservation Biology
Prof. Dr. Peter **Biedermann** (PI)	2012	University of Freiburg	Bark Beetle Ecology, Insect-Microbes Interaction
Dr. Simone **Cesarz** (PI)	2012	iDiv, Leipzig University	Soil Zoology
Dr. Alice **Claßen** (PI)	2014	University of Würzburg	Ecosystem Functions and Services, Pollination, Biodiversity
Prof. Dr. Nico **Eisenhauer** (PI)	2008	iDiv, Leipzig University	Belowground Biodiversity, Ecosystem Functions
Prof. Dr. Heike **Feldhaar** (PI)	2003	University Bayreuth	Dispersal, Population Ecology
PD Dr. Andreas **Fichtner** (PI)	2009	Leuphana University Lüneburg	Forest Ecology
Prof. Dr. Claudia **Kuenzer** (PI)	2005	University of Würzburg	Remote Sensing
Prof. Dr. Jörg **Müller** (PI)	2005	University of Würzburg	Forest Ecology, Conservation Biology, Community Ecology, Biostatistics
Prof. Dr. Goddert **von Oheimb** (PI)	2002	TU Dresden	Forest Ecology, Ecosystem Functions, Plant Ecology
PD Dr. Marcell **Peters** (PI)	2008	University of Würzburg	Ecosystem Functions and Services, Decomposition, Climate Change
Prof. Dr. Michael **Scherer-Lorenzen** (PI)	1999	University of Freiburg	Plant Ecology, Ecosystem functions
Prof. Dr. Thomas **Schmitt** (PI)	2004	University of Würzburg	Chemical Ecology
Prof. Dr. Bernhard **Schuldt** (PI)	2010	University of Würzburg	Plant ecology, Ecophysiology
Dr. Dominik **Seidel** (PI)	2011	University of Göttingen	Forest Structure, Terrestrial Laser Scanning
Prof Dr. Ingolf **Steffan-Dewenter** (PI)	1997	University of Würzburg	Ecosystem Functions and Services, Pollination, Biodiversity
PD Dr. Simon **Thorn (PI)**	2016	University Würzburg	Biodiversity, Ecological Modelling, Forest Management
Dr. Martin **Wegmann** (Co-PI)	2009	University of Würzburg	Remote Sensing, Biodiversity
Prof. Dr. Wolfgang **Weisser** (Co-PI)	1994	TU München	Terrestrial Ecology

Applicants are principle investigators (PI) receiving project funding. Co-applicants (Co-PI) assume significant responsibility in the project but do not receive project funding. To evaluate and to improve workflows across the RU and to solve potential problems, we will form a steering committee (SC) that meets during annual assemblies, but also interacts regularly via a quarterly online meeting. The SC will set the rules of cooperation, publication, data management and exchange within the RU. The SC reports at each annual meeting and is elected every two years. Re-elections are possible. The SC consists of 4 PIs, a Postdoctoral researcher, a representative of the PhD-students and a technician. The SC members are elected by their respective groups. For the first two years, we will start with the following team: Jörg Müller (Speaker), Oliver Mitesser (Postdoc), Simone Cesarz (PI), Claudia Kuenzer (PI), Heike Feldhaar (PI), Nico Eisenhauer (PI), Representative of PhDs (to be elected), Technician (to be elected).

2.1.5 Road map and perspectives for Phase 2

In the first year, we plan to collect the comprehensive data on biodiversity and functions in the University Forest Sailershausen and the Bavarian Forest, where logistics are easier. We will then conduct a workshop to train all PhD students in interdisciplinary measurements to enable measurement by teams in different sites across disciplines. In the second year, we will perform comprehensive samplings at all remaining sites. Moreover, we will start with a well-elaborated subset of measures for biodiversity and functions as rapid assessment at 6 sites, each of them in one of the 6 climatic regions (for details see SPZ), to gather temporal data on biodiversity and ecosystem functions, to open the avenue for investigations on ESBC versus homogenous forests under climate warming and particularly extreme events in preparation of phase 2.

To support PhD students in their analyses, project Z (O Mitesser) will organize a workshop with our Mercator Fellows and further statistics collaborators after the first year. To synthesize and to transfer project findings to forest managers and other stakeholders and to get their feedback, the second Postdoc in SPZ/1 and the site manager from SPZ will organize an annual symposium of Biodiversity and Conservation in the Steigerwald Forest with presentations by PhD students, Postdoctoral researchers, PIs and with intensive discussion rounds. Moreover, SP1 and SPZ will establish a training course for forest and conservation managers. This will be based on the nature trail already established in the University Forest Sailershausen. The trail with the new information will be used by the many excursions, with students, practitioners and citizen scientists, visiting annually the University Forest. To reach the broad public, we will set up an interactive homepage with access to the most recent findings of the RU in English and German. We will further create corporate videos of the experiment, MinuteEarth style video clips (www.minuteearth.com) and podcasts for important messages resulting from our publications, and regular press releases and TV reports on major findings.

In the second funding phase, we aim to build on the insights of the first phase by additional measurements of biodiversity and functions as well as new manipulations of trees within the patches to enrich the variation of decomposition or to establish new patches if necessary. With our data from different climate zones and the time series over the years, we will then focus in-depth on the question how years with extreme weather conditions affect the overall findings. This will contribute unique data to the research on biodiversity and ecosystem functions under a changing climate. The first Postdoctoral researcher in Z (O Mitesser) will synthesize the findings on the effects of homogenization on β-diversity and mulitfunctionality in general, while the second Postdoc in Z/ SP1 will synthesize the findings towards improved silvicultural strategies and disturbance management, including economic aspects. Both will analyse how climate extremes affects our findings. In order to expand this, we are planning in the second phase two new subprojects, one focusing on tree growth and stand dynamics and one focusing on economic aspects of the ESBC. Both can be immediately fed with extensive data on tree growth and functions after the first phase. For this, we will include new partners in the second phase with complementary expertise.

Collecting long-term multi-taxa data across multiple years has been identified in several reviews as the major limitation in manipulative forest studies, e.g. deadwood, burning or salvage logging (Heikkala et al. 2016a; Seibold et al. 2015; Thorn et al. 2018). Here, the time span of the project of about a decade (3 years of preliminary studies, 4+4 years RU) opens promising opportunities to track the structural change of forest patches by regeneration and tree growth as well as decomposition of dead trees.

2.2 Joint work programme including proposed research methods

Study area and design

As described above, our final design will be a set of 11 pairs of districts of a size of 10-20 ha from Lübeck in the North, Saarland in the South West to the Bavarian Forest in the South East of Germany and the University Forest Sailershausen in the centre (Fig. 1). The sites vary in soil, climate and tree species composition: five montane acidic beech-spruce-fir mixed forests in the Bavarian Forest at different elevations covering two ownerships, two mixed beech-oak forests in Saarland and Lübeck, one beech-spruce forest in Hunsrück and three mixed forests in the University Forest Sailershausen (Tab. 1). Altogether, we will have 234 patches, which will be measured at least once. In a subset of three out of the 11 pairs, we established intensive sampling sites in the University Forest Sailershausen, which belongs to the Julius-Maximilian University of Würzburg. It offers ideal logistical conditions for intensive measurements and training of practitioners. Here, we refine the variation in structural heterogeneity by adding another six treatments that are relevant for silvicultural practice to the nine core treatments mentioned above (Fig. 12). The fact that a few years have already passed since the intervention took place is highly advantageous, since for example deadwood has already been colonized, and vegetation has responded (see SP8). In addition to our measurements, we will control for variation in the surrounding landscape (Le Provost et al. 2021) of each district by extraction of publically available remote sensing information on land use.

Our combined approach of intensive/extensive sites and rapid assessments over time will allow for an “all-measurements-on-all-patches” philosophy in time and space that will enable novel data syntheses (Weisser et al. 2017). For details on planning the harmonized sampling during growing season or in leaf-off-conditions see SPZ. To investigate the sensitivity of our findings to extreme climatic conditions, we will select one pair of the extensive patches in each of the six climate regions (see Fig. 1) for measurements of biodiversity, functions and important microclimate and stand properties every year. These data will be analysed with respect to climate extremes and variability in the second phase. Here, our preliminary work especially in 2018 and 2019, i.e. two years with exceptional drought, already provides considerable variation among years.

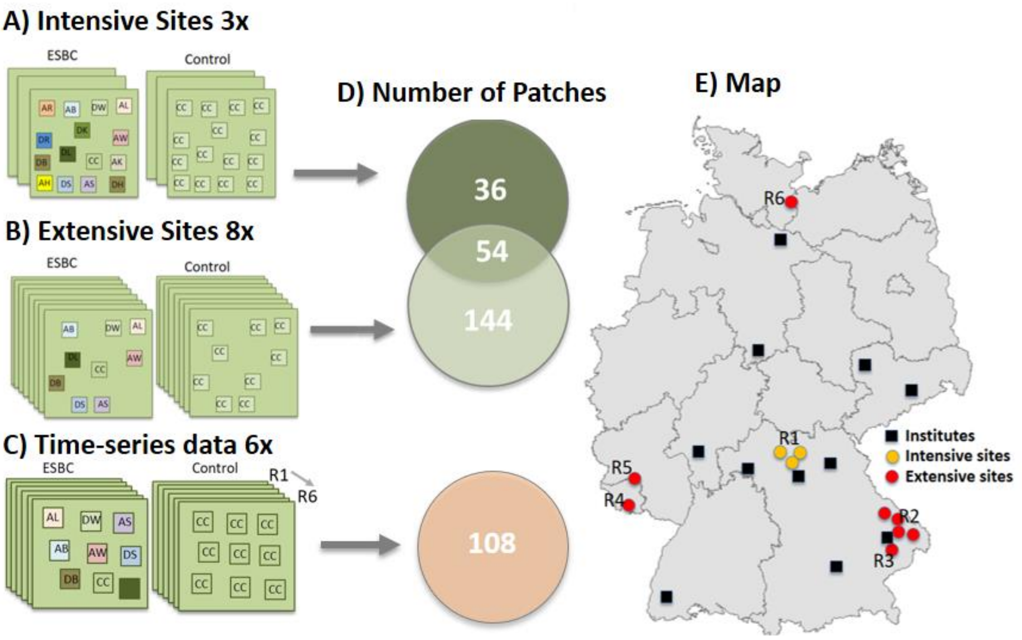


Fig. 12: Sampling design among sites: A) Intensive sampling comprises all ESBC treatments (see Fig. 5) on the 50x50m patches, while at the eight extensive sites (B) only a reduced set of nine treatments was realized (see Fig. 5). C) shows the design of the 6 sites for rapid assessment of time-series data. D) shows the number of patches investigated in the RU; note the patches sharing both intensities. E) Map of the 11 sites, the 6 climate regions, and the locations of collaborating institutes in this RU.

The very comprehensive measurements including microclimate and detailed forest structure on the intensive sites will further allow improving our mechanistic understanding of the link between β-diversity and multifunctionality. Our approach will benefit from the establishment of the treatments in different years, a sampling campaign of the pairs again in different years to control for year effects, as well as from repeated measurements.

Tab. 1: Overview of the forest characteristics in the 11 different districts with ESBC interventions. Tree age is the age of the dominant layer.

Abbreviation	**Elevation [m a.s.l.]**	**Tree species**	**Soil**	**Tree age [years]**
LUE	35	*Fagus-Quercus-Fraxinus-Larix*	Calcereous	120
SAR	308	*Fagus-Quercus-Carpinus*	Calcereous	60-70
SAC	373	*Fagus-Fraxinus-Quercus-Acer*	Calcereous	49-78
SAB	386	*Fagus- Quercus-Carpinus-Acer*	Calcereous	80
SAA	424	*Fraxinus- Carpinus- Acer-Pinus*	Calcereous	78-80
TUM	483	*Fagus-Picea-Abies-Pinus*	Acidic	70-100
HUN	725	*Fagus-Picea-Acer*	Acidic	120
GUG	837	*Fagus-Picea*	Acidic	80-110
KUH	852	*Fagus-Picea-Abies*	Acidic	90-121
JMH	857	*Fagus-Picea-Abies*	Acidic	90-120
TWF	1055	*Fagus-Picea-Abies*	Acidic	80-110

Methods to measure structural complexity: Forest structure, i.e. the 'stand physiognomy', will be assessed by a complementary combination of classical methods (field-mapping of trees including coordinates) with short- and long-distance remote sensing techniques (Terrestrial Laser Scanning, Airborne Laser Scanning, Hyperspectral, Sentinel 1 and Sentinel 2). To directly quantify treatments effects on microclimate conditions, we will use data loggers for temperature and moisture in all patches in all years (SPZ).

Biodiversity sampling: We will sample the following taxa in decreasing trophic order, covering all strata from belowground to soil surface to lower (shrub) layer up to the upper canopy by different methods, tackled by the respective subprojects in brackets: (1) **mammals**

(camera traps, lower layer) (SP 5, 9), (2) birds (breeding bird surveys by autonomous sound boxes) (SP 9), (3) **bats** (bat recorders, all layers) (SP 9), (4) **spiders** (pitfall traps, canopy fogging) (SP 9), (5) **beetles** (flight & pitfall traps, canopy fogging) (SP 2, 9), (6) **Hymenoptera** including bees, wasps, and ants (traps, nests, canopy fogging) (SP 6, 9), (7) **Diptera** (flight traps with top collector, canopy fogging) (SP 6, 9), (8) **true bugs** (flight traps, canopy fogging) (SP9), (9) **moths** (light traps, all layers) (SP 9), (10) **springtails** (pitfall traps, canopy fogging) (SP 9), (11) **nematodes** (below ground) (SP 4), (12) **soil fungi** (metabarcoding, belowground) (SP 7), (13) **wood-inhabiting fungi** (metabarcoding, lower layer) (SP2,7), (14) **soil bacteria** (metabarcoding, belowground) (SP 7), (15) **bacteria in wood** (metabarcoding, lower layer) (SP 7), (16) **vascular plants** (mapping, lower layer) (SP 8), (17) **bryophytes** (relevees, soil surface, lower layer) (SP 8), (18) **lichens** (relevees, soil surface, lower layer) (SP 8).

Ecosystem processes: We will measure 21 different functions including some key functions in temperate forests (respective subprojects in brackets): (1) **microbial activity in soil** (enzymes, O_2 consumption, carbon-use efficiency) (SP 4), (2) **soil respiration** (CO_2 efflux) (SP 4), (3) **belowground secondary productivity** (microbial biomass) (SP 4, 7,8), (4) **nutrient cycling** (nitrification rate) (SP 5), (5) **climate regulation** (temperature and precipitation data loggers) (Z), (6) **aggregate stability** (water stable soil aggregates) (SP 4), (7) **tree regeneration** (fenced and unfenced subplots, relevees) (SP 1, 8), (8) **leaf litter decomposition** (litterbags, tea bags) (SP 4, 5), (9) **wood decomposition** (enzyme activity in wood baits, wood bait mass loss, popsicle sticks) (SP 4, 5), (10) **dung decomposition** (mass loss of dung samples) (SP 5), (11) **carcass decomposition** (mass loss of rat carcasses) (SP 5), (12) **primary productivity** (basal area, stand volume, increment of woody plants, biomass increment of vascular plants, bryophytes and lichens) (SP 1, 8), (13) **carbon sequestration** (below and above ground) (SP 1, 4), (14) **aboveground secondary productivity** (weighted samples of moths) (SP9), (15) **pollination** (exclusion experiments on geophytes) (SP 6), (16) **seed dispersal** (exclusion experiments) (SP 6), (17) **invertebrate herbivory resistance** (canopy leafs, sapling leafs) (SP 9), (18) **vertebrate herbivory resistance** (ungulate exclusion fence) (SP 1), (19) **symbiosis** (bark beetle - fungus interactions) (SP 2), (20) **predation** (plastic caterpillars, predatory wasps/spider brood cells with caterpillar prey, standardized moth baits) (SP 6, 9), (21) **parasitism** (caterpillars occupied by parasitoids, parasitized brood cells of cavity nesting Hymenoptera) (SP 6). Key functions, such as growing stock and productivity, will provide data comparable to that obtained in national forest inventories (BWI) and IPBES approaches to maximize transferability of our results.

Rapid assessment over time: We will use our preliminary studies and the first-year comprehensive sampling in the University Forest Sailershausen to develop a reduced sampling campaign covering all taxonomic groups and functions mentioned above. This might involve a reduction in temporal resolution of assessments (e.g. only the three main months of activity for insect trapping), in resource replications (e.g. only one major dung or deadwood type for decomposition measures), or in using simpler proxy measures (e.g. structure for microclimate conditions). The simplification will include also the measurement of forest structures (e.g. only single scans with a terrestrial laser scanner per year) and the use of satellite radar data proven as similar powerful as high-resolution ALS data (Bae et al. 2019). After statistically-based selection of representative measurements for all sites, we will organize a training course in the different methods for all PhD students of the RU at the University Forest Sailershausen. Based on geographical locations of the participating universities, we will build teams to collect all data on all plots at the extensive sites. This concept of using rapid assessment and/or proxy measures, together with training on sampling methods, has already been very successfully adopted in other large-scale research projects (e.g. FunDivEUROPE, with participation of some researchers also included in this RU), resulting in a maximum of transdisciplinary and a minimum of logistic effort.

2.3 Research data and knowledge management

Data policy and repositories

Science and society require unprecedented access to ecological data across different spatial and temporal scales. Thus, proper data management plays a fundamental role. Nevertheless, principal challenges lie in the lack of data management knowledge among researchers including metadata standards, data repositories, data versioning, data citation and publication. This creates significant barriers in meta-analysis and data reuse. To address these challenges, we will develop a generic data management solution to guide our researchers through the entire data life cycle (Fig. 13), suitable and intuitively addressable also for future researchers.

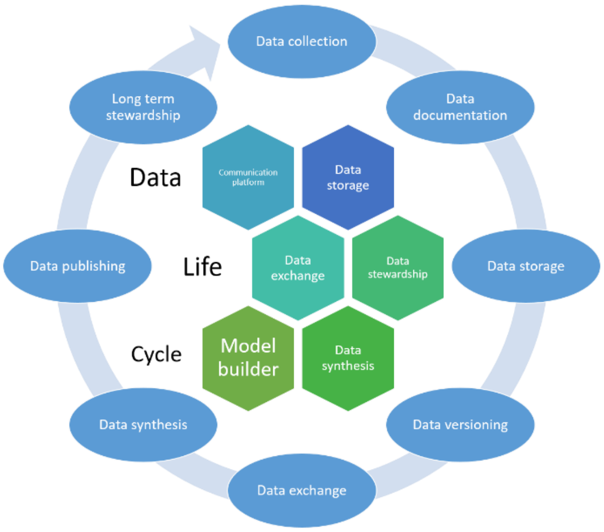


Fig. 13: Overview of the planned data management in the RU. For further explanations, please see text.

Data management will be headed by J Zhang who has gained substantial experience in the DFG Research Unit 1246 Kilimanjaro and is currently coordinating the data management in the collaborative Research Unit Landklif, and the EU projects UPSCALE and Safeguard, funded by the Horizon 2020 program. We aim for a data solution that supports metadata documentation, data storage, data backup and versioning, data exchange, online data analysis and visualization, as well as data publication and long-term stewardship. Our data solution will not only be a medium to store and query data, but also 1) a communication platform that regulates and documents data exchange and synthesis, 2) a safeguard of data stewardship beyond the life span of our project, and 3) a model builder that provides synthetic analysis techniques to efficiently explore and identify interesting patterns that otherwise would not be detected (data mining). It will fully follow the FAIR principles, findability, accessibility, interoperability and reusability. By full exploration of our data solution, research efficiency will be promoted. We will closely collaborate with and rely on technical standard solutions provided by the BExIS Experimental Data Management Platform (https://fusion.cs.uni-jena.de/fusion/projects/bexis/), and by Open Data Cube (https://www.opendatacube.org/), long-term data archive centers, such as PANGAEA (https://www.pangaea.de/) and NFDI4BioDiversity (https://www.nfdi4biodiversity.org/). To fully open this data pool for teaching of students at the University of Würzburg, the applied Earth Observation M.Sc. program EAGLE, headed by M Wegmann, will integrate the research project into its courses. Here, the project provides unique information on manipulated ground truth data and a diverse set of remote sensing data collected in the RU.

2.4 Potential impact on the research area and local research environment

Since our experimental plots were set up in very different forest tenures, a wide array of additional benefits can be expected. The University Forest, the Lübeck municipality forest and the study area in Saarland are regular excursion sites in the course of academic teaching. In the future, the results of the RU will be presented there regularly. This will lead to a broad establishment of BEF studies in forestry education. The two national parks Bavarian Forest and Hochwald-Hunsrück are regularly visited by nature conservation experts on field trips, which will lead to a regular exchange between the RU and nature conservation. The church forest of the diocese of Passau is a regular field trip destination for practitioners and private forest owners. As the cooperation partners are widely connected, the results of our RU will be disseminated.

As there are many other research activities going on in the University Forest and the Bavarian Forest National Park, the research group will have additional interactions with other research units, promising significant synergies among research projects. There is already vivid cooperation of the applicants with other institutes, for example, between research projects at the TU Munich by R Seidl and the Academy of Sciences in Prague (Czech Republic) via our Mercator Fellow P Baldrian. Research in the Bavarian Forest National Park has developed over the last 15 years in such a way that the National Park ranks as one of the leading research institutes in large protected areas worldwide. With the RU, this position could be further expanded, and it may serve as a blueprint for how top international research in the field of ecology and conservation biology can be carried out in other large-scale protected areas.

2.5 Measures to advance research careers

Measures to promote promising early career researchers

The speaker's working group has already had very good experiences with the atmosphere at the Fieldstation Fabrikschleichach and the Bavarian Forest National Park when it comes to retreats and workshops. During their visits, top-class scientists come to the two sites for a personal exchange face to face with young scientists. In addition, we will encourage the PhD students to visit our Mercator Fellows. Usually, this leads quickly to deep and fruitful cooperation, which has already resulted in many international publications. Due to the high level of interdisciplinarity of the RU, young scientists find even better opportunities to establish and expand their networks nationally and internationally.

To provide all participants of the RU with the best conditions for scientific success, we will ensure regular communication via an online platform, easy data access via data repositories and targeted collaboration between different institutions. The RU will also offer special training sessions by the PIs, the Mercator Fellows and other collaborators for the use of remote sensing data, the use of high-performance cluster computers, and various methods of biostatistics with a focus on β-diversity as well as ecosystem function approaches. Our team consists of excellent international scientists who have a great deal of experience in teaching and can inspire young scientists. Role model discussions will focus on the benefits of interdisciplinary and collaborative research for science and personal careers.

The regular workshops (2 per year) are especially important for PhD students to foster collaborations and new publications. Another workshop in the third year will specifically inform PhD students about career opportunities, including leadership positions and careers within and outside academia. This course will focus on addressing career perspectives related to graduate education. It will also be combined with a workshop specifically addressing career prospects for females in science. In the graduate programmes of several universities represented in the RU, doctoral students are generally encouraged to choose a mentor for their dissertation, who serves as an adviser and provides support beyond their main supervisor and their team. Candidates meet with their mentors at least twice a year to discuss work in progress, experiments, manuscript planning, and career prospects. Funded by the travel budgets of the individual projects, our early career scientists are enabled to present their research to the scientific community at national and international conferences. In addition, all PhD students in this project are strongly encouraged to network with each other, to share their views and experiences in an independent virtual discussion group of peers. Independent coordination of time slots and self-organised workshops exclusively for PhD students are also strongly encouraged, ideally prior to the annual conferences (see specific programme in the Networking Workshops module below).

In addition to the direct supervision of PhD students shared by the PIs in the consortium, and beyond the specific support in this RU, graduates can benefit from structured PhD programmes at the universities. Graduate schools and doctoral programmes complement each doctoral project with additional elements of support for candidates and supervisors. As part of such graduate programmes, candidates benefit from individual coaching and mentoring, counselling services, travel support, as well as gender- and diversity-oriented measures. Such graduate programmes are run at all universities, where candidates will be doing their doctorate within this RU.

Besides our PhD students and the Postdoctoral researchers, our collaboration will certainly enhance the scientific career of the following early to mid-career researchers in the RU: A Claaßen, S Cesarz, A Fichtner, M Peters and S Thorn. The RU will offer them an excellent platform to expand their research areas in an interdisciplinary framework, make their research more visible and expand their personal scientific network. In particular, the invitation of the international collaborators to the experimental sites will offer unique opportunities to discuss their research with international experts from different disciplines. In turn, they will serve as important mentors for the early career researchers.

Diversity and internationalisation in research careers

All institutions and graduate programmes involved in the application process recognise and promote the diversity and difference of doctoral researchers, in gender, nationality, religion and worldview, disability, age, ethnicity or sexual orientation. A wide range of counselling and service offers supports researchers in all life situations. The graduate schools at various universities and institutions of the RU offer a variety of mobility programmes and funding opportunities for international research stays, conference visits as well as the establishment of international networks. Internationalisation of science is a very important aspect of the funding programmes for early career scientists at different stages of their scientific education. Each of the participating universities has an International Office or a Welcome Centre and offers welcome services, intercultural workshops, social and cultural programmes or other services.

2.6 National and international cooperation and networking

National cooperation

Several of the PIs are leading or participating in other RU or collaborations funded by DFG, thematically linked to our RU, namely the Biodiversity Exploratories (DFG Priority Programme 1374), the Research Unit “Reassembly” (FOR5207) in Ecuadorian Forest, the Research Unit of the Jena Experiment (FOR 5000), the DFG-Research Training Group 2300 „Enrichment of European beech forests with conifers: impacts of functional traits on ecosystem functioning“, the International Research Training Group TreeDiversity Interactions (TreeDì, GRK 2324), and the DFG-Project Understanding the global freshwater system (GlobalCDA). C Bässler shares a GAČR-DFG Joint German-Czech Project Proposal with our Mercator Fellow P Baldrian. As Co-PI of an international project of Mercator Fellow P Baldrian, J Müller will participate in a project on "Effects of plant functional diversity on the ecosystem responses to forest harvesting" within the call “Facilities Integrating Collaborations for User Science Research (FICUS)” by the Joint Genome Institute and the Environmental Molecular Sciences Laboratory (proposal Nr. 60014). The project will use metagenomes, metatranscriptomes and genome sequencing and experimental plots of the RU among others. The collaboration will open an avenue to cutting edge microbiology methods in forest fungi and bacteria communities that can be used in the RU. N Eisenhauer, a member of the German Centre for Integrative Biodiversity Research (iDiv), will link the project directly with the DFG-funded Centre for Biodiversity. The regular exchange with the projects and consortia mentioned above will significantly increase the visibility of our work and enable us to use synergies beyond the proposed RU.

C Kuenzer's affiliation with the German Aerospace Center (DLR) will make additional resources available. As Professor at the Remote Sensing Department in Würzburg and at the same time being DLR department head of currently 55 scientists, she ensures unique access for the RU to a large variety of resources. These include, for example, tools for digital image processing, unrivalled data access to long time series of a wealth of sensors and geoinformation products, powerful in house parallel computing resources, an internship room with 12 work stations exclusive to the department, and access to a campaign bus, UAVs, a spectrometer, and a high-end thermal camera.

Similarly, J Müller's facilities will support the RU. As Professor at the Department of Animal Ecology and Tropical Biology in Würzburg and at the same time Bavarian Forest Nationalpark department head as well as deputy head of the Nationalpark with an own budget, he ensures unique access for the RU to study sites, rearing stations for insects, tree climbers, retreat accommodations and meeting rooms, conference halls, Minibusses, jeeps and a wide range of insect traps.

International collaboration

To strengthen international cooperation, we were able to recruit several high-profile researchers as Mercator Fellows (see 2.7). In addition, we have established a close cooperation with Prof A Chao's lab in Taiwan, one of the leading biostatistics labs worldwide. The speaker and his lab have already enjoyed several years of fruitful collaboration with A A Chao.

2.7 Collaboration with international cooperation partners

We will use the opportunity of the Mercator Fellowship to foster close cooperation with the following renowned international researchers throughout the RU:

- Dr Fons van der Plas, The Netherlands, is an Assistant Professor at Wageningen University with a strong expertise in relationships between biodiversity and ecosystem multifunctionality, particularly in (semi-) natural systems, and at both the scale of α, β and γ-diversity. He has ample experience with large, collaborative datasets, and also has expertise on plant traits, multitrophic interactions and theoretical models linking plant performance, biodiversity and ecosystem functioning. Through his expertise, we will help with further developing the theoretical / conceptual framework on landscape heterogeneity, forest (β) diversity and ecosystem multifunctionality, and he will also provide key input regarding the statistical synthesis of this project.

- Prof Marc Cadotte, Canada, is one of the leading scientists in the field of functional and phylogenetic diversity and-community ecology. He has developed several analytical approaches improving the field of ecology and biodiversity. Moreover, as editor in chief of Journal of Applied Ecology and Ecological Solutions and Evidence, he is in an excellent position to advise and to teach our doctoral students on their publication strategy.
- Dr Petr Baldrian, Czech Republic, is Associate Prof, heading a large lab in the Institute of Microbiology of the Czech Academy of Sciences in Prague. He has extensive analytical capacities but also the corresponding biostatistical knowledge. He is also one of the world's leading microbiologists in the field of fungal and bacterial communities. Through his expertise and the FICUS project mentioned above, the field of microbiology and the role of microbiome in the functioning in forest ecosystems in soil, tree and deadwood will be significantly strengthened within the RU.
- Prof Akira Mori, Japan, is an expert at the forefront of the field of biodiversity in terrestrial ecosystems with a special focus on β-diversity in forests. He is an active scientist not only in national activities, such as a member of the Science Council of Japan (SCJ), but also in international affairs including his contributions to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as a lead author. Through his expertise in β-diversity in forests he will significantly strengthen the RU.
- Prof Diana Six, US, is a leading expert in the interaction of microbes and beetles in forests. With deep understanding of the interactions and their impact on ecological processes, she will strengthen the RU in this important field of forest ecosystem functions. She is deeply involved in science communication at many levels. She works with a broad array of media and employs a variety of approaches including sci-art to reach varied audiences with the goal of increasing science literacy and supporting informed conservation policy, decisions, and actions. She also strives to provide a strong role model to young women and disadvantaged youth to motivate their participation in science and to increase the presence of women in leadership positions.
- Prof Torsten Hothorn, Switzerland, is statistician with a special expertise in statistical modelling in space and time. Besides clinical studies he has a long-term expertise in analyzing ecological data. He has developed numbers of important statistical methods broadly applied in ecology and available in the R framework. He will guarantee a high quality of final analyses in the RU testing the impact of different treatments in complex spatial and temporal frameworks. He will particularly support the SPZ in developing a common framework for analyses in the RU.

2.8 Description of the spokesperson’s qualifications

Jörg Müller is a forest and animal ecologist with long-term experience in field experiments in temperate biomes. He has already used this experience in several completed forestry experiments. In these research projects, but also in his former role as manager of a forestry enterprise, as well as in his role as manager of the oldest German national park, he is experienced in the management of large and interdisciplinary groups. In his research work, he has initiated several European research projects in beech forests, which led to numerous publications in internationally renowned scientific journals. The most recent collaborative project he initiated on six continents investigating the contribution of insects to the decomposition of wood has just been published in Nature (Seibold et al. 2021). To date, he his scientific results have been published in 220 articles in ISI journals, including Nature, Science, Trends in Ecology and Environment, Nature Ecology and Evolution, Nature Communications and Ecology Letters, most of them on temperate forest ecosystems.

Beside his expertise in project management and publication, Müller's broad interest and expertise may be the most important quality for his as spokesperson of this RU. With his large range of interests, he seems to be predestined for leading the RU and for successfully bringing together the various subprojects with different foci on biodiversity and ecosystem processes. He has published together with 10 of the PIs and Co-PIs as well as with four of the Mercator-Fellows listed above in various combinations, which promises a fruitful and productive collaboration also in the RU. However, the successful coordination of the subprojects is just one component of a prospering RU. The speaker's great practical experience in forest management and the related network have made it possible to initiate a forest experiment that is unique in Central Europe. Coordination

3. Coordination

3.1 Description of how joint objectives and the joint work programme will be implemented in the coordination project

The scientific coordination among subprojects, as well as the logistic organization and support on site, are the main responsibility of the core team organized in a coordination module (CM) and subproject SPZ (Fig. 14). According to DFG-suggestions, we established two postdoc positions. One will be the principal scientific coordinator (Postdoctoral researcher Oliver Mitesser) in the team of the spokesperson, J Müller. He will (i) develop the theoretical framework for the RU, (ii) the statistical framework to analyse the link of β diversity and multifunctionality, (iii) conduct the syntheses of the RU, (iv) and support and teach the PhD students in data analyses. A second postdoctoral researcher will be located in the team of C Ammer.

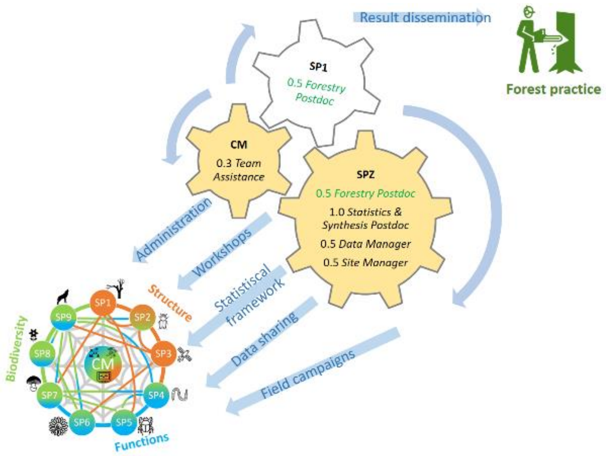


Fig. 14: Coordination concept for the RU consisting of CM module, SPZ and the link to SP1.

This postdoc will focus on deriving conclusions for forest management and the resulting linkages with forestry practice. Here, the results of the RU are regularly edited and then transferred, so that they can be considered in actual management. This will be done in regular exchange with forestry practitioners. In order to achieve maximum efficiency of the personnel resources used, 0.5 of this postdoctoral researcher was placed in the SPZ and 0.5 in SP1, the subproject with the greatest proximity to forestry practice, since it deals with forest structure, which is most prominently shaped by forest interventions. Another important part of the coordination is to ensure consistent data management, highly available short- as well as accessible long-term storage, and annotation by meta-data as essential requisite for the success of the RU. We will manage this with a 0.5 highly experienced data manager (Jie Zhang) in the team of the spokesperson. A 0.5 site manager is necessary for the duration of the RU. His task will be to take care of all sites, patches and infrastructure installed to provide basic data for all SPs. A forest scientist with many years of experience (Michael Junginger) in the team of J Müller will fill this position. He will supervise permanent measurements on all plots, organise cooperation with the landowners as well as joint field campaigns. The RU will cause considerable additional organisational work for the spokesperson's team. Since the university supplies the speaker with a 0.5 full-time equivalent administration assistant, only the current team assistant (Hermine Wohlpart) position should increase by another 0.3 full-time equivalent. Ms Wohlpart is highly experienced in project and financial management.

Tab. 2: Data exchange within the RU.

Subproject	**Provides**	**Receives**
SPZ: Scientific coordination, site management, knowledge transfer, background data, data management, statistics	Overall coordination, access to data, storage of data, tree measurements, soil data, microclimate data, statistical methods for all subprojects	Multiple data on diversity and functions for syntheses
SP1: Forest structure and micro-climate	3D forest structure from below canopy, structural complexity of all patches, canopy openness and understory complexity of all patches, high-resolution micro-climatic data on soil moisture and vertical profiles of temperature and air humidity, regeneration inventory	Forest structure information on plot and landscape level, herb layer assemblages, microbiome composition, animal diversity data
SP2: Volatilome and symbiosis	Diversity data on volatiles (VOCs) and on saproxylic beetles, bark and ambrosia beetles (BABs), invasive and pest BABs, natural enemies of BABs and fungal symbionts of specific pest BABs. Functions on specific pest BAB-fungus symbioses.	Data on flying-insect diversity, plant diversity, forest structure and deadwood microbial diversity
SP3: Novel Earth Observation techniques for forest structure analysis and multi-scale characterization	forest structure information (on patch and landscape level)	diversity data of higher trophic levels, forest structure data on tree level, tree species and inventory-like data
SP4: Soil biodiversity and functioning	Nematode diversity (taxonomic, functional), microbial respiration, microbial biomass, carbon use efficiency, PLFA/NLFA data (for microbial community composition and fungal and bacterial biomass), soil-aggregate stability, soil water content	forest structure, vegetation data, decomposition data and material, microclimate, soil CN, soil pH

SP5: After life – decomposition	Data on the diversity of macrodetritivores and decomposition rates of 10 types of organic matter; data on nutrient fluxes, leaf litter and seed rain production	Data on microclimate, leaf litter production, amount of dead wood, forest structure and data on mammal, microorganisms and invertebrate detritivore communities
SP6: Plant-animal interactions - pollination, parasitism, and seed dispersal	Diversity and trait data on ants, bees, wasps, hoverflies. Quantitative data on seed removal and seed predation (including gastropods and vertebrates), seed sets (pollination), plant-pollinator interaction rates, parasitism rates	Data on forest structure on multiple scales, data on plant diversity (especially of understorey plant assemblages) and primary productivity, diversity data of higher trophic levels
SP7: Dead wood microbial diversity	Dead –wood fungal and bacterial diversity data, dead-wood microbial biomass data, dead-wood physical and chemical properties, dead-wood decomposition measures	Data on microclimate conditions and dead-wood structures (e.g., amount, diversity)
SP8: Understorey plant assemblages and primary production	Diversity and biomass data on non-tree vascular plants, terricolous bryophytes and lichens, trait data on herbaceous plants, diversity data on wood-dependent bryophytes and liches, understorey primary aboveground and belowground productivity, PAR data	Forest structure, microclimate and soil data, understory complexity, data on soil biodiversity and dead-wood fungal and bacterial diversity, diversity data of higher trophic levels, the functions pollination, seed dispersal, decomposition
SP9: Multifunctionality and higher trophic level diversity	Diversity data on groups of trophic levels 2a, 2b, predators, Functions above ground secondary productivity, invertebrate herbivory resistance, predation and parasitism.	Data on plant diversity, forest structure and the functions primary productivity, below ground secondary productivity, pollination, seed dispersal

3.2 Requested modules

3.2.1 Coordination Module

The principal tasks of the coordination module (CM) consist of administrative work packages, such as:

- assisting subprojects in research activities
- maintaining project infrastructure including accommodation, and storage.
- facilitating field work planning, accommodation and transport for all subprojects and collaborators
- ensuring equal opportunities to all project participants including gender balance and integration of people from distinct cultural and societal backgrounds (3.2.4 Gender Equality Measures in Research Networks Module)
- preparing and organizing workshops (see 3.2.7 Module Project Specific Workshops).

3.2.2 Module Network Funds (Funding for Staff, Direct Project Costs and Instrumentation)

Funding of CM will be allocated to the University of Würzburg and administered by the speaker and his group (Module 1).

3.2.3 Module Start-Up Funding

Not applicable.

3.2.4 Module Standard Allowance for Gender Equality Measures

In our RU, female scientists of different levels within their professional careers are well represented among the principal investigators with four out of 20 (20%) of our PIs being female, which mirrors well the gender distribution in forest ecology. These applicants can clearly serve as role models for successful female scientists in a still largely male-dominated community. In addition, we will actively involve our scientifically renowned international female cooperation partners and Mercator fellows (A Chao, D Six) in scientific workshops with an additional opportunity for female early career scientists to gain very personal insights into their respective career pathways (see “Einblicke” below), enabling them to develop their own scientific network.

We aim to consider as many women of scientific excellence, as possible in our RU, e.g. as invited guests for seminars and in our collaborations. The different levels of experience of participating women open an excellent opportunity to build up sustainable support of young female scientists by experienced female academics. For early career female PhD students, we start building a network for women in science within the RU, but also by encouraging them to attend international meetings and actively introducing them to international colleagues.

We will aim for balanced gender proportion when recruiting junior researchers. To attract as many female PhD students as possible, we will start active recruitment of females (see below). The same is true for the Postdoctoral researcher in SPZ/1. In addition to the internal workshop on gender equality and internationalization in research careers (see below), junior female scientists are strongly encouraged to participate in other mentoring programmes and workshops of the participating universities that are tailored to the specific challenges of women in science. The University of Bayreuth, for example, has developed the "Einblicke" programme, in which female professors are invited to explain their personal career paths in science to young academics and to advise them on questions regarding the compatibility of work and family. H Feldhaar has hosted several of these “Einblicke” events before and will co-organize such workshops within the RU. Another example is the University of Göttingen, where all PhD-students have to be enrolled in a Graduate school, offers courses and workshops on career development exclusively for female students.

Our team also comprises of several PIs (male and female) who are parents of young children. Their function as mentors and participation in workshops on gender equality and scientific careers will provide our graduate students with the unique opportunity to exchange with scientists, who have successfully managed to combine family life with a scientific career. Given that children are still a major reason, in particular for women to decide against a scientific career, we intensify the personal exchange of experiences and advise a highly important and unique opportunity for supporting future leaders in science (both males and females) provided by our RU. Especially for early career female researchers with children (but also for males when required), we will organize childcare to enable participation of workshops and meetings. Dates and times of assemblages and meetings will be arranged family-friendly. Especially female early career scientists with children will be supported with student helpers, which will be guaranteed by all PIs.

We will continue to increase the proportion of women among PIs in future phases of the RU. For PhD positions, we will promote initiative applications of women and, in general, the diversity of students, not only in terms of gender equality but also in terms of cultural background and ethnicity. To encourage female scientists to apply for positions all PIs will actively ask colleagues in their respective field (nationally and internationally) to forward the advertisements for positions to excellent female young scientists (e.g. former or current Master students). All PIs will ensure equal opportunities and consistently tackle all forms of discrimination and underrepresentation. In order to sensitize the PIs to these issues, we will include a section on gender, diversity and anti-discrimination measures already in the kick-off meeting. We will provide the PIs with a guide (prepared by the University of Bayreuth) on how to identify problems and take appropriate countermeasures. In addition, we will hold a special workshop on gender equality in academic careers in an intercultural context. Finally, an ombudsperson will be elected who can be contacted confidentially in cases of misconduct, sexual harassment or any other kind of discrimination.

All participating universities are committed to attracting female students, graduates and academic staff and to promoting internationalization and diversity in academia. Several participating institutions have taken measures to improve family-friendly working conditions, e.g. family rooms with office space. We will provide all team members with information about such institutional support measures and the corresponding offices in the participating institutions. J Zhang from China as data manager and envisioned collaborations with scientists from Taiwan, Japan and US will enhance the European-Asian-North American scientific interaction.

Funding is requested for short-term support for flexible childcare. For longer supervision tasks, e.g. pregnancy or family care responsibilities, which require temporary support for the PhD students, the PIs of the subprojects will approach the DFG for individual support programmes. We will organize a central workshop for the research group dealing with the career perspectives of female scientists in forest ecology. During this workshop, we will discuss in depth the existing qualification concepts for the advancement of female scientists and actively contribute to breaking down barriers that still need to be overcome. This two-day workshop is planned in conjunction with the third annual meeting (see 3.2.7 Project-specific workshop module), i.e. at a stage when post-doctoral career prospects are becoming an increasingly important topic for our female PhD students.

Overall, the Gender Equality Measures will thus comprise two tasks:

- Support of flexible childcare (or elder care) and home office supplies
- Workshop on gender equality in scientific careers in an intercultural context

3.2.5 Module Professorships

Not applicable.

3.2.6 Module Temporary Substitute for Clinicians

Not applicable.

3.2.7 Module Project-Specific Workshops

The RU will take advantage of the excellent conditions for workshops, conferences and retreats at the Fieldstation Fabrikschleichach and the Bavarian Forest National Park. The respective facilities are of high quality and affordable. In addition, the RU will use the broad expertise of the Mercator Fellows as top-class scientists to convey various aspects in the workshops.

LIST OF WORKSHOPS:

Date	Type	Location	Description
April 2022	Kick-off meeting	Fieldstation Fabrikschleichach	First general meeting (day 1). Workshop on **data collection** (day 2). Workshop on **good scientific practice** and **equal opportunities** for women and across participants (day 3). H Feldhaar, D Six, C Ammer, N Eisenhauer, M Scherer-Lorenzen, J Müller. Excursion University Forest Sailershausen.
October 2022	Annual meeting	Bavarian Forest Nationalpark	Workshop **data management** /d**ata repository** (day 1). Workshop **statistical analyses** (day 2). Workshop on **statistical framework for beta diversity and multifunctionality** SPZ & T Hothorn, A Chao, F van der Plas (day 3). Excursion Bavarian Forest Nationalpark.
March 2023	Workshop	Fieldstation Fabrikschleichach	Workshop **temperate forests** (day 1); **Beta diversity and ecosystem functions** (day 2); C Ammer, J Müller, S Thorn, F van der Plas, M Scherer-Lorenzen, N Eisenhauer
October 2023	Workshop and Annual meeting	Bavarian Forest Nationalpark	Workshop on **functional and phylogenetic diversity** – (day 1); **Methods and applications for bacterial and fungi communities** in forests (day 2); M Cadotte, A Chao, P Baldrian, C Bässler. Introduction of including sequencing methods in forests. Excursion church forest of the diocese of Passau.
April 2024	Workshop	Fieldstation Fabrikschleichach	Workshop **Statistical modelling with focus on first data** (day 1); Introduction into **scientific writing** (day 2); Workshop on **gender equality in scientific careers** in an intercultural context (day 3); O Mitesser, T Hothorn, A Chao, M Scherer-Lorenzen, M Cadotte, D Six.; A Chao, D Six, A Mori, H Feldhaar, invited speaker).
October 2024	Annual meeting	Bavarian Forest Nationalpark	Synthesis workshop led by SPZ: Analysing cross subproject data on biodiversity and ecosystem functions (J Müller, N Eisenhauer, T Hothorn), Forests under climate change (invited speaker) - day 1. **Career opportunities**, including leadership positions and careers within and outside academia (day 2 PIs and Mercator Fellows) – **Career perspectives for women in science only for females** organized by Heike Feldhaar and Diana Six (invited speaker) day 2.
March 2025	Workshop	Lübeck	Workshop with all PIs day 1: **Conclusion and preparation** for Phase 2 (lead organizers Jörg Müller, Christian Ammer, Nico Eisenhauer, Heike Feldhaar). Focus on overarching research questions (day 2; PIs, Mercator Fellows and collaborators). Day 2 – Visit of the municipality forest Lübeck.
October 2025	Annual meeting	Saarland	Workshop on **synthesis** papers (day 1; lead organizer Jörg Müller, Nico Eisenhauer, C Ammer, M Scherer-Lorenzen). Day 2 – Visit of the state forestry Saarland

3.2.8 Module Mercator Fellows

We have been able to recruit several top-class scientists as Mercator Fellows for our RU. This will strengthen the RU with their specific expertise (see above) and will provide an exceptional opportunity for the PhD students to discuss and also to publish their findings with leading scientists. At least once a year, Mercator Fellows are scheduled to participate in meetings of the RU.

Name	Location
Cadotte Marc	Toronto, Canada
Mori Akira	Yokohama, Japan
Six Diana	Missoula, US
Baldrian Petr	Prague, Czech Republic
Hothorn Torsten	Zurich, Switzerland
van der Plas Fons	Wageningen, Netherlands

3.2.9 Module Public Relations

As a first point of contact and unified communication channel, we will set up a website in English and German, which integrates and collects all dissemination measures. We expect a substantial interest, both from within the scientific community as well as in forest practice and the public, including policymakers and non-governmental organizations – particularly since forests are gaining increased attention due to the visible impact climate change on forest health. Here, our homepage will serve as a platform to link biodiversity and ecosystem functions approaches with forest management with a biodiversity focus. In the first two years, we will present the general background and motivation of our work with a lecture series on "Forest biodiversity and ecosystem functions", presented by the PIs and the Mercator Fellows. In parallel, PhD students and postdocs will report brief updates from their fieldwork via corporate videos. In the further course of the RU, we will use MinuteEarth-style video clips (www.minuteearth.com) and podcasts published via social media channels, to disseminate important messages from our publication. To maximize the attractiveness of the videos, we will collaborate with the multiple award-winning nature filmmaker Jan Haft, expert for macro-videos. We will hire a professional to ensure a functional and attractive website that increases the visibility of the RU. We will ensure that the homepage is attractive by employing visual media, e.g. updated wildlife videos, live webcam and sound streams. We will also embed and maintain a Twitter channel (English and German) for regular updates and highlights, and to link relevant channels with similar scope. We will use a licensed version of DeepL.com to manage the website translation and to provide information and news in both languages most effectively.

References

Allan E, Bossdorf O, Dormann CF, Prati D, Gossner MM, Tscharntke T, Bluthgen N, Bellach M, Birkhofer K, Boch S, Bohm S, Borschig C, Chatzinotas A, Christ S, Daniel R, Diekotter T, Fischer C, Friedl T, Glaser K, Hallmann C, Hodac L, Holzel N, Jung K, Klein AM, Klaus VH, Kleinebecker T, Krauss J, Lange M, Morris EK, Muller J, Nacke H, Pasalic E, Rillig MC, Rothenwohrer C, Schally P, Scherber C, Schulze W, Socher SA, Steckel J, Steffan-Dewenter I, Turke M, Weiner CN, Werner M, Westphal C, Wolters V, Wubet T, Gockel S, Gorke M, Hemp A, Renner SC, Schoning I, Pfeiffer S, Konig-Ries B, Buscot F, Linsenmair KE, Schulze ED, Weisser WW, Fischer M (2014) Interannual variation in land-use intensity enhances grassland multidiversity. Proceedings of the National Academy of Science, USA 111:308-313.

Allan E, Weisser WW, Fischer M, Schulze ED, Weigelt A, Roscher C, Baade J, Barnard RL, Bessler H, Buchmann N, Ebeling A, Eisenhauer N, Engels C, Fergus AJF, Gleixner G, Gubsch M, Halle S, Klein AM, Kertscher I, Kuu A, Lange M, Le Roux X, Meyer ST, Migunova VD, Milcu A, Niklaus PA, Oelmann Y, Pasalic E, Petermann JS, Poly F, Rottstock T, Sabais ACW, Scherber C, Scherer-Lorenzen M, Scheu S, Steinbeiss S, Schwichtenberg G, Temperton V, Tscharntke T, Voigt W, Wilcke W, Wirth C, Schmid B (2013) A comparison of the strength of biodiversity effects across multiple functions. Oecologia 173:223-237.

Ammer C (2019) Diversity and forest productivity in a changing climate. New Phytologist 221:50-66.

Anderson MJ, Crist TO, Chase JM, Vellend M, Inouye BD, Freestone AL, Sanders NJ, Cornell HV, Comita LS, Davies KF, Harrison SP, Kraft NJB, Stegen JC, Swenson NG (2011) Navigating the multiple meanings of beta diversity: a roadmap for the practicing ecologist. Ecology Letters 14:19-28.

Baber K, Otto P, Kahl T, Gossner MM, Wirth C, Gminder A, Bassler C (2016) Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi. Forest Ecology and Management 377:161-169.

Bae S, Levick S, Heidrich L, Magdon P, Leutner BF, Wöllauer S, Serebryanyk A, Nauss T, Krzystek P, Gossner MM, Schall P, Heibl C, Bässler C, Inken D, Schulze E-D, Krah F-S, Culmsee H, Jung K, Heurich M, Winter M-B, Fischer M, Seibold S, Thorn S, Gerlach T, Hothorn T, Weisser WW, Müller J (2019) Radar vision in the mapping of forest biodiversity from space. Nature Communications 10:4757

Bae S, Müller J, Lee D, Vierling KT, Vogeler JC, Vierling LA, Hudak AT, Latifi H, Thorn S (2018) Taxonomic, functional, and phylogenetic diversity of bird assemblages are oppositely associated to productivity and heterogeneity in temperate forests. Remote Sensing of Environment 215:145-156.

Bae S, Müller J, Förster B, Hilmers T, Hochrein S, Jacobs M, Leroy BML, Pretzsch H, Weisser WW, Mitesser O (2021) Tracking the temporal dynamics of insect defoliation by high-resolution radar satellite data. Methods in Ecology and Evolution, in press, DOI: 10.1111/2041-210X.13726.

Baeten L, Bruelheide H, van der Plas F, Kambach S, Ratcliffe S, Jucker T, Allan E, Ampoorter E, Barbaro L, Bastias CC, Bauhus J, Benavides R, Bonal D, Bouriaud O, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Checko E, Coomes DA, Dahlgren J, Dawud SM, De Wandeler H, Domisch T, Finer L, Fischer M, Fotelli M, Gessler A, Grossiord C, Guyot V, Hattenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Koricheva J, Lehtonen A, Muller S, Muys B, Nguyen D, Pollastrini M, Radoglou K, Raulund-Rasmussen K, Ruiz-Benito P, Selvi F, Stenlid J, Valladares F, Vesterdal L, Verheyen K, Wirth C, Zavala MA, Scherer-Lorenzen M (2019) Identifying the tree species compositions that maximize ecosystem functioning in European forests. Journal of Applied Ecology 56:733-744.

Baeten L, Verheyen K, Wirth C, Bruelheide H, Bussotti F, Finer L, Jaroszewicz B, Selvi F, Valladaresh F, Allan E, Ampoorter E, Auge H, Avacariei D, Barbaro L, Barnoaiea I, Bastias CC, Bauhus J, Beinhoff C, Benavides R, Benneter A, Berger S, Berthold F, Boberg J, Bonal D, Braggernann W, Carnol M, Castagneyrol B, Charbonnier Y, Checko E, Coomess D, Coppi A, Dalmaris E, Danila G, Dawud SM, de Vries W, De Wandeler H, Deconchat M, Domisch T, Duduman G, Fischer M, Fotelli M, Gessler A, Gimeno TE, Granier A, Grossiord C, Guyot V, Hantsch L, Hattenschwiler S, Hector A, Hermy M, Holland V, Jactel H, Joly FX, Jucker T, Kolb S, Koricheva J, Lexer MJ, Liebergesell M, Milligan H, Muller S, Muys B, Nguyen D, Nichiforel L, Pollastrini M, Proulx R, Rabasa S, Radoglou K, Ratcliffe S, Raulund-Rasmussen K, Seiferling I, Stenlid J, Vesterdal L, von Wilpert K, Zavala MA, Zielinski D, Scherer-Lorenzen M (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. Perspectives in Plant Ecology Evolution and Systematics 15:281-291.

Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA (2011) Has the Earth's sixth mass extinction already arrived? Nature 471:51.

Baselga A (2010) Partitioning the turnover and nestedness components of beta diversity. Global Ecology and Biogeography 19:134-143.

Baselga A (2012) The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. Global Ecology and Biogeography 21:1223-1232.

Bässler C, Brandl R, Müller J, Krah F, Reinelt A, Halbwachs H (2021) Global analysis reveals an environmentally driven latitudinal pattern in mushroom size across fungal species. Ecology Letters 24:658-667

Bässler C, Ernst R, Cadotte M, Heibl C, Müller J (2014) Near-to-nature logging influences fungal community assembly processes in a temperate forest. Journal of Applied Ecology 51:939-948

Bauhus J, Puettmann K, Messier C (2009) Silviculture for old-growth attributes. Forest Ecology and Management 258:525-537.

Begehold H, Rzanny M, Flade M (2015) Forest development phases as an integrating tool to describe habitat preferences of breeding birds in lowland beech forests. Journal of Ornithology 156:19-29.

Blüthgen N, Simons NK, Jung K, Prati D, Renner SC, Boch S, Fischer M, Hölzel N, Klaus VH, Kleinebecker T, Tschapka M, Weisser WW, Gossner MM (2016) Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. Nature Communications 7:10697. doi: 10.1038/ncomms10697

Boddy L, Watkinson SC (1995) Wood decomposition, higher fungi, and their role in the nutrient redistribution. Canadian Journal of Botany 73:1377-1383

Bruelheide H, Nadrowski K, Assmann T, Bauhus J, Both S, Buscot F, Chen XY, Ding BY, Durka W, Erfmeier A, Gutknecht JLM, Guo DL, Guo LD, Hardtle W, He JS, Klein AM, Kuhn P, Liang Y, Liu XJ, Michalski S, Niklaus PA, Pei KQ, Scherer-Lorenzen M, Scholten T, Schuldt A, Seidler G, Trogisch S, von Oheimb G, Welk E, Wirth C, Wubet T, Yang XF, Yu MJ, Zhang SR, Zhou HZ, Fischer M, Ma KP, Schmid B (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. Methods in Ecology and Evolution 5:74-89.

Burley HM, Mokany K, Ferrier S, Laffan SW, Williams KJ, Harwood TD (2016) Primary productivity is weakly related to floristic alpha and beta diversity across Australia. Global Ecology and Biogeography 25:1294-1307.

Bussler H, Fuchs H, Schmidl J, Thorn S (2020) „Urwaldreliktarten“ und bedeutende Standorte der Arten in Bayern (Insecta: Coleoptera: Xylobionta). Beiträge zur bayerischen Entomofaunistik 20:71–89

Byrnes JEK, Gamfeldt L, Isbell F, Lefcheck JS, Griffin JN, Hector A, Cardinale BJ, Hooper DU, Dee LE, Duffy JE (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods in Ecology and Evolution 5:111-124.

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. Nature 486:59-67.

Cavalli R, Mason F (2003) Techniques for re-establishment of dead wood for saproxylic fauna conservation. LIFE Nature project NAT/IT/99/6245 "Bosco della Fontana" (Mantova, Italy). National Centre for the Study and Conservation of Forest Biodiversity, Mantova, p 105

Chao A, Chiu C-H, Villeger S, Sun I-F, Thorn S, Lin Y-C, Chiang J-M, Sherwin WB (2019a) An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecological Monographs 89, e01343.

Chao A, Chiu CH (2016) Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiation measures. Methods in Ecology and Evolution 7:919-928

Chao A, Colwell RK, Gotelli NJ, Thorn S (2019b) Proportional mixture of two rarefaction/extrapolation curves to forecast biodiversity changes under landscape transformation. Ecology Letters 22:1913-1922.

Chao AN, Chiu CH, Wu SH, Huang CL, Lin YC (2019c) Comparing two classes of alpha diversities and their corresponding beta and (dis)similarity measures, with an application to the Formosan sika deer Cervus nippon taiouanus reintroduction programme. Methods in Ecology and Evolution 10:1286-1297.

Chase JM (2010) Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. Science 328:1388-1391.

Craven D, Eisenhauer N, Pearse WD, Hautier Y, Isbell F, Roscher C, Bahn M, Beierkuhnlein C, Bonisch G, Buchmann N, Byun C, Catford JA, Cerabolini BEL, Cornelissen JHC, Craine JM, De Luca E, Ebeling A, Griffin JN, Hector A, Hines J, Jentsch A, Kattge J, Kreyling J, Lanta V, Lemoine N, Meyer ST, Minden V, Onipchenko V, Polley HW, Reich PB, van Ruijven J, Schamp B, Smith MD, Soudzilovskaia NA, Tilman D, Weigelt A, Wilsey B, Manning P (2018) Multiple facets of biodiversity drive the diversity-stability relationship. Nature Ecology & Evolution 2:1579-1587.

Crutzen PJ (2002) Geology of mankind. Nature 415:23-23.

De Frenne P, Zellweger F, Rodríguez-Sánchez F, Scheffers BR, Hylander K, Luoto M, Vellend M, Verheyen K, Lenoir J (2019) Global buffering of temperatures under forest canopies. Nature Ecology & Evolution 3:744–749

Donato DC, Campbell JL, Franklin JF (2012) Multiple successional pathways and precocity in forest development: can some forests be born complex? Journal of Vegetation Science 23:576-584.

Dörfler I, Mueller J, Weisser W, Gossner MM, Seibold S (2018) Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests Biological Conservation 228:70-78.

Dörfler I, Müller J, Gossner MM, Hofner B, Weisser WW (2017) Success of deadwood enrichment strategy in production forests depends on stand type and management intensity. Forest Ecology and Management 400:607-620.

Duffy JE, Godwin CM, Cardinale BJ (2017) Biodiversity effects in the wild are common and as strong as key drivers of productivity. Nature 549:261-+.

Ebeling A, Lind EW, Meyer ST, Barnes AD, Borer ET, Eisenhauer N, Weisser WW (2020) Contrasting effects of plant diversity on beta- and gamma-diversity of grassland invertebrates. Ecology 101.

Eckelt A, Müller J, Bense U, Brustel H, Bußler H, Chittaro Y, Cizek L, Frei A, Holzer E, Kadej M, Kahlen M, Köhler F, Möller G, Mühle H, Sanchez A, Schaffrath U, Schmidl J, Smolis A, Szallies A, Németh T, Wurst C, Thorn S, Christensen RHB, Seibold S (2018) “Primeval forest relict beetles” of Central Europe: a set of 168 umbrella species for the protection of primeval forest remnants. Journal of Insect Conservation 22:15-28.

Ehbrecht M, Schall P, Ammer C, Fischer M, Seidel D (2019) Effects of structural heterogeneity on the diurnal temperature range in temperate forest ecosystems. Forest Ecology and Management 432:860-867.

Ehbrecht M, Schall P, Ammer C, Seidel D (2017) Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agricultural and Forest Meteorology 242:1-9. doi: 10.1016/j.agrformet.2017.04.012

Eisenhauer N, Bonkowski M, Brose U, Buscot F, Durka W, Ebeling A, Fischer M, Gleixner G, Heintz-Buschart A, Hines J, Jesch A, Lange M, Meyer S, Roscher C, Scheu S, Schielzeth H, Schloter M, Schulz S, Unsicker S, van Dam N, Weigelt A, Weisser W, Wirth C, Wolf J, Schmid B (2019a) Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity–ecosystem functioning relationships. Research Ideas and Outcomes 5:e47042

Eisenhauer N, Dobies T, Cesarz S, Hobbie SE, Meyer RJ, Worm K, Reich PB (2013) Plant diversity effects on soil food webs are stronger than those of elevated CO2 and N deposition in a long-term grassland experiment. Proceedings of the National Academy of Science USA 110:6889-6894.

Eisenhauer N, Schielzeth H, Barnes AD, Barry K, Bonn A, Brose U, Bruelheide H, Buchmann N, Buscot F, Ebeling A, Ferlian O, Freschet GT, Giling DP, Hättenschwiler S, Hillebrand H, Hines J, Isbell F, Koller-France E, König-Ries B, de Kroon H, Meyer ST, Milcu A, Müller J, Nock CA, Petermann JS, Roscher C, Scherber C, Scherer-Lorenzen M, Schmid B, Schnitzer SA, Schuldt A, Tscharntke T, Türke M, van Dam NM, van der Plas F, Vogel A, Wagg C, Wardle DA, Weigelt A, Weisser WW, Wirth C, Jochum M (2019b) A multitrophic perspective on biodiversity–ecosystem functioning research. Advances in Ecological Research 61:1-54

Ellison AM (2010) Partitioning diversity. Ecology 91:1962-1963

Endres G (1929) Die Eichen des Spessarts II. Forstwissenschaftliches Centralblatt 51:277–289

Fahrig L (2019) Habitat fragmentation: A long and tangled tale. Global Ecology and Biogeography 28:33-41.

Ferlian O, Cesarz S, Craven D, Hines J, Barry KE, Bruelheide H, Buscot F, Haider S, Heklau H, Herrmann S, Kuhn P, Pruschitzki U, Schadler M, Wagg C, Weigelt A, Wubet T, Eisenhauer N (2018) Mycorrhiza in tree diversity-ecosystem function relationships: conceptual framework and experimental implementation. Ecosphere 9:e02226.

Franke S, Brandl R, Heibl C, Mattivi A, Muller J, Pinkert S, Thorn S (2020) Predicting regional hotspots of phylogenetic diversity across multiple species groups. Diversity and Distributions 26:1305-1314.

Franklin JF, Cromack K, Denison W (1981) Ecological characteristics of old-growth Douglas-fir forests. . In: Service UF (ed) General Technical Report PNW, vol. 118. Pacific Northwest Forest and Range Experiment Station, Portland, Oregon

Franklin JF, Spies TA, Van Pelt R, Carey AB, Thornburgh DA, Berg DR, Lindenmayer DB, Harmon ME, Keeton WS, Shaw DC, Bible K, Chen JQ (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. Forest Ecology and Management 155:399-423.

Friess N, Muller JC, Aramendi P, Bassler C, Brandle M, Bouget C, Brin A, Bussler H, Georgiev KB, Gil R, Gossner MM, Heilmann-Clausen J, Isacsson G, Kristin A, Lachat T, Larrieu L, Magnanou E, Maringer A, Mergner U, Mikolas M, Opgenoorth L, Schmidl J, Svoboda M, Thorn S, Vandekerkhove K, Vrezec A, Wagner T, Winter MB, Zapponi L, Brandl R, Seibold S (2019) Arthropod communities in fungal fruitbodies are weakly structured by climate and biogeography across European beech forests. Diversity and Distributions 25:783-796.

Fujii S, Mori AS, Koide D, Makoto K, Matsuoka S, Osono T, Isbell F (2017) Disentangling relationships between plant diversity and decomposition processes under forest restoration. Journal of Applied Ecology 54:80-90.

Fukami T, Dickie IA, Wilkie JP, Paulus BC, Park D, Roberts A, Buchanan PK, Allen RB (2010) Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecology Letters 13:675-684

Gamfeldt L, Roger F (2017) Revisiting the biodiversity-ecosystem multifunctionality relationship. Nature Ecology & Evolution 1:0168.

Gebhardt T, Häberle KH, Matyssek R, Schulz C, Ammer C (2014) The more, the better? Water relations of Norway spruce stands after progressive thinning. Agricultural and Forest Meteorology 197:235-243

Gossner MM, Lewinsohn TM, Kahl T, Grassein F, Boch S, Prati D, Birkhofer K, Renner SC, Sikorski J, Wubet T, Arndt H, Baumgartner V, Blaser S, Bluthgen N, Borschig C, Buscot F, Diekotter T, Jorge LR, Jung K, Keyel AC, Klein AM, Klemmer S, Krauss J, Lange M, Muller J, Overmann J, Pasalic E, Penone C, Perovic DJ, Purschke O, Schall P, Socher SA, Sonnemann I, Tschapka M, Tscharntke T, Turke M, Venter PC, Weiner CN, Werner M, Wolters V, Wurst S, Westphal C, Fischer M, Weisser WW, Allan E (2016) Land-use intensification causes multitrophic homogenization of grassland communities. Nature 540:266-+.

Grman E, Zirbel CR, Bassett T, Brudvig LA (2018) Ecosystem multifunctionality increases with beta diversity in restored prairies. Oecologia 188:837-848.

Grove SJ (2002) Saproxylic insect ecology and the sustainable management of forests. Annual Review in Ecology and Systematics 33:1-23

Hagge J, Abrego N, Bassler C, Bouget C, Brin A, Brustel H, Christensen M, Gossner MM, Heilmann-Clausen J, Horak A, Gruppe A, Isacsson G, Kohler F, Lachat T, Larrieu L, Schlaghamersky J, Thorn S, Zapponi L, Muller J (2019) Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. Journal of Biogeography 46:1054-1065.

Hagge J, Müller J, Birkemoe T, Buse J, Christensen RHB, Gossner MM, Gruppe A, Heibl C, Jarzabek-Müller A, Seibold S, Siitonen J, Soutinho JG, Thygeson AS, Thorn S, Drag L (2021) What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. Journal of Animal Ecology 90:1934-1947

Hammill E, Hawkins CP, Greig HS, Kratina P, Shurin JB, Atwood TB (2018) Landscape heterogeneity strengthens the relationship between beta-diversity and ecosystem function. Ecology 99:2467-2475.

Hartig GL (1808) Anweisung zur Holzzucht für Förster. Neue Akademische Buchhandlung, Marburg

Hautier Y, Isbell F, Borer ET, Seabloom EW, Harpole WS, Lind EM, MacDougall AS, Stevens CJ, Adler PB, Alberti J, Bakker JD, Brudvig LA, Buckley YM, Cadotte M, Caldeira MC, Chaneton EJ, Chu CJ, Daleo P, Dickman CR, Dwyer JM, Eskelinen A, Fay PA, Firn J, Hagenah N, Hillebrand H, Iribarne O, Kirkman KP, Knops JMH, La Pierre KJ, McCulley RL, Morgan JW, Partel M, Pascual J, Price JN, Prober SM, Risch AC, Sankaran M, Schuetz M, Standish RJ, Virtanen R, Wardle GM, Yahdjian L, Hector A (2018) Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. Nature Ecology & Evolution 2:50-56.

Hautier Y, Zhang PF, Loreau M, Wilcox KR, Seabloom EW, Borer ET, Byrnes JEK, Koerner SE, Komatsu KJ, Lefcheck JS, Hector A, Adler PB, Alberti J, Arnillas CA, Bakker JD, Brudvig LA, Bugalho MN, Cadotte M, Caldeira MC, Carroll O, Crawley M, Collins SL, Daleo P, Dee LE, Eisenhauer N, Eskelinen A, Fay PA, Gilbert B, Hansar A, Isbell F, Knops JMH, MacDougall AS, McCulley RL, Moore JL, Morgan JW, Mori AS, Peri PL, Pos ET, Power SA, Price JN, Reich PB, Risch AC, Roscher C, Sankaran M, Schutz M, Smith M, Stevens C, Tognetti PM, Virtanen R, Wardle GM, Wilfahrt PA, Wang SP (2020) General destabilizing effects of eutrophication on grassland productivity at multiple spatial scales. Nature Communications 11:5375.

Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. Nature 448:188-U186.

Heidrich L, Bae S, Levick S, Seibold S, Weisser W, Krzystek P, Magdon P, Nauss T, Schall P, Serebryanyk A, Wollauer S, Ammer C, Bassler C, Doerfler I, Fischer M, Gossner MM, Heurich M, Hothorn T, Jung K, Kreft H, Schulze ED, Simons N, Thorn S, Muller J (2020) Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests. Nature Ecology & Evolution 4:1431-1431.

Heikkala O, Martikainen P, Kouki J (2016a) Decadal effects of emulating natural disturbances in forest management on saproxylic beetle assemblages. Biological Conservation 194:39-47.

Heikkala O, Sebastian S, Koivula M, Martikainen P, Müller J, Thorn S, Kouki J (2016b) Retention forestry and prescribed burning result in functionally different saproxylic beetle assemblages than clear-cutting. Forest Ecology and Management 359 51-58.

Hill M (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427-432.

Hilmers T, Friess N, Bässler C, Heurich M, Brandl R, Pretzsch H, Seidl R, Müller J (2018) Biodiversity along temperate forest succession. Journal of Applied Ecology 55:2756-2766.

Hofner B, Müller J, Hothorn T (2011) Monotonicity-Constrained Species Distribution Models. Ecology 92 1895-1901.

Holzwarth F, Kahl A, Bauhus J, Wirth C (2013) Many ways to die - partitioning tree mortality dynamics in a near-natural mixed deciduous forest. Journal of Ecology 101:220-230.

Hothorn T, Müller J, Schröder B, Kneib T, Brandl R (2011) Decomposing environmental, spatial, and spatiotemporal components of species distributions. Ecological Monographs 81:329-347

Hyvärinen E, Kouki J, Martikainen P (2006) Fire and green-tree retention in conservation of red-listed and rare deadwood-dependent beetles in finnish boreal forests. Conservation Biology 20:1711-1719.

Isbell F, Calcagno V, Hector A, Connolly J, Harpole WS, Reich PB, Scherer-Lorenzen M, Schmid B, Tilman D, van Ruijven J, Weigelt A, Wilsey BJ, Zavaleta ES, Loreau M (2011) High plant diversity is needed to maintain ecosystem services. Nature 477:199-U196.

Isbell F, Gonzalez A, Loreau M, Cowles J, Diaz S, Hector A, Mace GM, Wardle DA, O'Connor MI, Duffy JE, Turnbull LA, Thompson PL, Larigauderie A (2017) Linking the influence and dependence of people on biodiversity across scales. Nature 546:65-72.

Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88:2427-2439

Jost L (2010) Independence of alpha and beta diversities. Ecology 91:1969-1974

Jost L, Chao A, Chazdon RL (2011) Compositional similarity and beta diversity. In: Magurran A, McGill B (eds) Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press, Oxford, pp 66-84

Jucker T, Bouriaud O, Avacaritei D, Coomes DA (2014) Stabilizing effects of diversity on aboveground wood production in forest ecosystems: linking patterns and processes. Ecology Letters 17:1560–1569

Jurasinski G, Retzer V, Beierkuhnlein C (2009) Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. Oecologia 159:15-26.

Kaldhusdal A, Brandl R, Müller J, Möst L, Hothorn T (2015) Spatio-Phylogenetic Multi-Species Distribution Models. Methods in Ecology and Evolution 6:187-197.

Keeton WS (2006) Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. Forest Ecology and Management 235:129-142.

Knoke T (2003) Predicting red heartwood formation in beech trees (*Fagus sylvatica* L.). Ecological Modelling 169:295-312.

Komonen A, Müller J (2018) Dispersal ecology of dead wood organisms: implications for connectivity conservation. Conservation Biology 32:535–545.

Kortmann M, Roth N, Buse J, Hilszczański J, Jaworski T, Morinière J, Seidl R, Thorn S, Müller JC (2021) Arthropod dark taxa provide new insights into diversity responses to bark beetle infestations. Ecological Applications accepted

Krah FS, Seibold S, Brandl R, Baldrian P, Muller J, Bassler C (2018) Independent effects of host and environment on the diversity of wood-inhabiting fungi. Journal of Ecology 106:1428-1442.

Laliberte E, Wells JA, DeClerck F, Metcalfe DJ, Catterall CP, Queiroz C, Aubin I, Bonser SP, Ding Y, Fraterrigo JM, McNamara S, Morgan JW, Merlos DS, Vesk PA, Mayfield MM (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. Ecology Letters 13:76-86. d

Larrieu L, Cabanettes A (2012) Species, live status, and diameter are important tree features for diversity and abundance of tree microhabitats in subnatural montane beech-fir forests. Canadian Journal of Forest Research 42:1433-1445.

Larrieu L, Cabanettes A, Gouix N, Burnel L, Bouget C, Deconchat M (2017) Development over time of the tree-related microhabitat profile: the case of lowland beech-oak coppice-with-standards set-aside stands in France. European Journal of Forest Research 136:37-49.

Le Provost G, Thiele J, Westphal C, Penone C, Allan E, Neyret M, van der Plas F, Ayasse M, Bardgett RD, Birkhofer K, Boch S, Bonkowski M, Buscot F, Feldhaar H, Gaulton R, Goldmann K, Gossner MM, Klaus VH, Kleinebecker T, Krauss J, Renner S, Scherreiks P, Sikorski J, Baulechner D, Bluthgen N, Bolliger R, Borschig C, Busch V, Chiste M, Fiore-Donno AM, Fischer M, Arndt H, Hoelzel N, John K, Jung K, Lange M, Marzini C, Overmann J, Pasalic E, Perovic DJ, Prati D, Schafer D, Schoning I, Schrumpf M, Sonnemann I, Steffan-Dewenter I, Tschapka M, Turke M, Vogt J, Wehner K, Weiner C, Weisser W, Wells K, Werner M, Wolters V, Wubet T, Wurst S, Zaitsev AS, Manning P (2021) Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. Nature Communications 12: 3918.

Lefcheck JS, Byrnes JEK, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, Hensel MJS, Hector A, Cardinale BJ, Duffy JE (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature Communications 6: 6936.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A (2004) The metacommunity concept: a framework for multi-scale community ecology. Ecology Letters 7:601-613

Leroy BML, Lemme H, Braumiller P, Hilmers T, Jacobs M, Hochrein S, Kienlein S, Müller J, Pretzsch H, Stimm K, Seibold S, Jaworek J, Hahn WA, Weisser WW (2021) Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems – an experimental approach. Ecological Solutions and Evidence 2:e12045

Lindenmayer DB, Franklin JF, Lohmus A, Baker SC, Bauhus J, Beese W, Brodie A, Kiehl B, Kouki J, Pastur GM, Messier C, Neyland M, Palik B, Sverdrup-Thygeson A, Volney J, Wayne A, Gustafsson L (2012) A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. Conservation Letters 5:421-431.

Loreau M, Barbier M, Filotas E, Gravel D, Isbell F, Miller SJ, Montoya JM, Wang SP, Aussenac R, Germain R, Thompson PL, Gonzalez A, Dee LE (2021) Biodiversity as insurance: from concept to measurement and application. Biological Reviews early access.

Loreau M, Mouquet N, Gonzalez A (2003) Biodiversity as spatial insurance in heterogeneous landscapes. Proc. Natl. Acad. Sci. U. S. A. 100:12765-12770.

Loreau M, Naeem S, Inchausti P, Bengtsson J, Grime JP, Hector A, Hooper DU, Huston MA, Raffaelli D, Schmid B, Tilman D, Wardle DA (2001) Ecology - Biodiversity and ecosystem functioning: Current knowledge and future challenges. Science 294:804-808

Maestre FT, Quero JL, Gotelli NJ, Escudero A, Ochoa V, Delgado-Baquerizo M, Garcia-Gomez M, Bowker MA, Soliveres S, Escolar C, Garcia-Palacios P, Berdugo M, Valencia E, Gozalo B, Gallardo A, Aguilera L, Arredondo T, Blones J, Boeken B, Bran D, Conceicao AA, Cabrera O, Chaieb M, Derak M, Eldridge DJ, Espinosa CI, Florentino A, Gaitan J, Gatica MG, Ghiloufi W, Gomez-Gonzalez S, Gutierrez JR, Hernandez RM, Huang XW, Huber-Sannwald E, Jankju M, Miriti M, Monerris J, Mau RL, Morici E, Naseri K, Ospina A, Polo V, Prina A, Pucheta E, Ramirez-Collantes DA, Romao R, Tighe M, Torres-Diaz C, Val J, Veiga JP, Wang DL, Zaady E (2012) Plant Species Richness and Ecosystem Multifunctionality in Global Drylands. Science 335:214-218.

Manning P, Loos J, Barnes AD, Batary P, Bianchi F, Buchmann N, De Deyn GB, Ebeling A, Eisenhauer N, Fischer M, Frund J, Grass I, Isselstein J, Jochum M, Klein AM, Klingenberg EOF, Landis DA, Leps J, Lindborg R, Meyer ST, Temperton VM, Westphal C, Tscharntke T (2019) Transferring biodiversity-ecosystem function research to the management of 'real-world' ecosystems. In: Eisenhauer N, Bohan DA, Dumbrell AJ (eds) Mechanisms Underlying the Relationship between Biodiversity and Ecosystem Function, vol 61, pp 323-356.

Maxwell S, Fuller RA, Brooks TM, Watson JEM (2016) The ravages of guns, nets and bulldozers. Nature 536:143-145.

McGill BJ, Dornelas M, Gotelli NJ, Magurran AE (2015) Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution 30:104-113.

Messier C, Bauhus J, Sousa-Silva R, Auge H, Baeten L, Barsoum N, Bruelheide H, Caldwell B, Cavender-Bares J, Dhiedt E, Eisenhauer N, Ganade G, Gravel D, Guillemot J, Hall JS, Hector A, Herault B, Jactel H, Koricheva J, Kreft H, Mereu S, Muys B, Nock CA, Paquette A, Parker JD, Perring MP, Ponette Q, Potvin C, Reich PB, Scherer-Lorenzen M, Schnabel F, Verheyen K, Weih M, Wollni M, Zemp DC (2021) For the sake of resilience and multifunctionality, let's diversify planted forests! Conservation Letters online first.

Meyer ST, Ptacnik R, Hillebrand H, Bessler H, Buchmann N, Ebeling A, Eisenhauer N, Engels C, Fischer M, Halle S, Klein AM, Oelmann Y, Roscher C, Rottstock T, Scherber C, Scheu S, Schmid B, Schulze ED, Temperton VM, Tscharntke T, Voigt W, Weigelt A, Wilcke W, Weisser WW (2018) Biodiversity-multifunctionality relationships depend on identity and number of measured functions. Nature Ecology & Evolution 2:44-49.

Miklin J, Sebek P, Hauck D, Konvicka O, Cizek L (2018) Past levels of canopy closure affect the occurrence of veteran trees and flagship saproxylic beetles. Diversity and Distributions 24:208-218.

Moning C, Müller J (2009) Critical forest age thresholds for diversity of lichens, molluscs and birds in temperate beech (Fagus sylvatica L.) plant communities. Ecological Indicators 9:922–932

Mori AS, Isbell F, Seidl R (2018) b-Diversity, Community Assembly, and Ecosystem Functioning. Trends Ecol Evol 33:549-564

Mori AS, Osono T, Cornelissen JHC, Craine J, Uchida M (2017) Biodiversity-ecosystem function relationships change through primary succession. Oikos 126:1637-1649.

Mori AS, Ota AT, Fujii S, Seino T, Kabeya D, Okamoto T, Ito MT, Kaneko N, Hasegawa M (2015) Concordance and discordance between taxonomic and functional homogenization: responses of soil mite assemblages to forest conversion. Oecologia 179:527-535.

Mori AS, Shiono T, Koide D, Kitagawa R, Ota AT, Mizumachi E (2013) Community assembly processes shape an altitudinal gradient of forest biodiversity. Global Ecology and Biogeography 22:878-888.

Morin X, Fahse L, de Mazancourt C, Scherer-Lorenzen M, Bugmann H (2014) Temporal stability in forest productivity increases with tree diversity due to asynchrony in species dynamics. Ecology Letters 17:1526-1535.

Mueller KE, Eisenhauer N, Reich PB, Hobbie SE, Chadwick OA, Chorover J, Dobies T, Hale CM, Jagodzinski AM, Kalucka I, Kasprowicz M, Kieliszewska-Rokicka B, Modrzynski J, Rozen A, Skorupski M, Sobczyk L, Stasinska M, Trocha LK, Weiner J, Wierzbicka A, Oleksyn J (2016) Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species. Soil Biology & Biochemistry 92:184-198.

Müller J, Brandl R (2009) Assessing biodiversity by remote sensing and ground survey in montainous terrain: the potential of LiDAR to predict forest beetle assemblages. Journal of Applied Ecology 46:897–905.

Müller J, Brandl R, Brändle M, Förster B, De Araujo BC, Gossner MM, Ladas A, Wagner M, Maraun M, Schall P, Schmidt S, Heurich M, Thorn S, Seibold S (2018) LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127:814-824. d

Müller J, Bütler R (2010) A review of habitat thresholds for dead wood: a baseline for management recommendations. European Journal of Forest Research 129:981-992.

Müller J, Hothorn T (2004) Maximally selected two-sample statistics as a new tool for the identification and assessment of habitat factors with an application to breeding-bird communities in oak forests. European Journal of Forest Research 123:219-228.

Müller J, Jarzabek-Müller A, Bussler H, Gossner MM (2014) Hollow beech trees identified as keystone structures by analyses of functional and phylogenetic diversity of saproxylic beetles. Animal Conservation 17:154-162.

Müller J, Mehr M, Bässler C, Fenton MB, Hothorn T, Pretzsch H, Klemmt H-J, Brandl R (2012) Aggregative response in bats: prey abundance versus habitat. Oecologia 169:673-684

Müller J, Noss RF, Thorn S, Bässler C, Leverkus AB, Lindenmayer D (2019) Increasing disturbance demands new policies to conserve intact forest. Conservation Letters 12:e12449

Naeem S, Duffy JE, Zavaleta E (2012) The Functions of Biological Diversity in an Age of Extinction. Science 336:1401-1406.

Newbold T, Hudson LN, Hill SLL, Contu S, Lysenko I, Senior RA, Borger L, Bennett DJ, Choimes A, Collen B, Day J, De Palma A, Diaz S, Echeverria-Londono S, Edgar MJ, Feldman A, Garon M, Harrison MLK, Alhusseini T, Ingram DJ, Itescu Y, Kattge J, Kemp V, Kirkpatrick L, Kleyer M, Correia DLP, Martin CD, Meiri S, Novosolov M, Pan Y, Phillips HRP, Purves DW, Robinson A, Simpson J, Tuck SL, Weiher E, White HJ, Ewers RM, Mace GM, Scharlemann JPW, Purvis A (2015) Global effects of land use on local terrestrial biodiversity. Nature 520:45-+.

Noss RF, Dinerstein EB, Gilbert M, Gilpin B, Miller R, Terborgh J, Trombulak S (1999) Core areas: where nature reigns. In: Soulé ME, Terborgh J (eds) Continental conservation: scientific foundations of regional reserve networks. Island Press, Washington, D.C.

Ódor P, Heilmann-Clausen J, Christensen M, Aude E, Dort vKW, Piltaver A, Siller I, Veerkamp MT, Standovár T, Hees vAFM, Kosec J, Matocec N, Kraigher H, Grebenc T (2006) Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation 131:58-71.

Olden JD, Comte L, Giam X (2016) Biotic Homogenisation. In: eLS. John Wiley & Sons LC (ed)

Paillet Y, Debaive N, Archaux F, Cateau E, Gilg O, Guilbert E (2019) Nothing else matters? Tree diameter and living status have more effects than biogeoclimatic context on microhabitat number and occurrence: An analysis in French forest reserves. Plos One 14:e0216500.

Peters MK, Hemp A, Appelhans T, Becker JN, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Gerschlauer F, Gutlein A, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Kuhnel A, Mayr AV, Mwangomo E, Ngereza C, Njovu HK, Otte I, Pabst H, Renner M, Roder J, Rutten G, Costa DS, Sierra-Cornejo N, Vollstadt MGR, Dulle HI, Eardley CD, Howell KM, Keller A, Peters RS, Ssymank A, Kakengi V, Zhang J, Bogner C, Bohning-Gaese K, Brandl R, Hertel D, Huwe B, Kiese R, Kleyer M, Kuzyakov Y, Nauss T, Schleuning M, Tschapka M, Fischer M, Steffan-Dewenter I (2019) Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568:88-+.

Peura M, Gonzalez RS, Müller J, Heurich M, Vierling LA, Mönkkönen M, Bässler C (2016) Mapping a ‘cryptic kingdom’: Performance of lidar derived environmental variables in modelling the occurrence of forest fungi. Remote Sens. Environ. 186 428-438.

Pommerening A, Murphy ST (2004) A review of the history, definitions and methods of continuous cover forestry with special attention to afforestation and restocking. Forestry 77:27-44.

Puettmann KJ, Wilson SM, Baker SC, Donoso PJ, Drossler L, Amente G, Harvey BD, Knoke T, Lu YC, Nocentini S, Putz FE, Yoshida T, Bauhus J (2015) Silvicultural alternatives to conventional even-aged forest management - what limits global adoption? For. Ecosyst. 2:16.

Rackham O (2008) Ancient woodlands: modern threats. The New Phytologist 180:571–586.

Radkau J (2007) Holz - Wie ein Naturstoff Geschichte schreibt. . Oekom Verlag, München

Ratcliffe S, Wirth C, Jucker T, van der Plas F, Scherer-Lorenzen M, Verheyen K, Allan E, Benavides R, Bruelheide H, Ohse B, Paquette A, Ampoorter E, Bastias CC, Bauhus J, Bonal D, Bouriaud O, Bussotti F, Carnol M, Castagneyrol B, Checko E, Dawud SM, De Wandeler H, Domisch T, Finer L, Fischer M, Fotelli M, Gessler A, Granier A, Grossiord C, Guyot V, Haase J, Hattenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Kambach S, Kolb S, Koricheva J, Liebersgesell M, Milligan H, Muller S, Muys B, Nguyen D, Nock C, Pollastrini M, Purschke O, Radoglou K, Raulund-Rasmussen K, Roger F, Ruiz-Benito P, Seidl R, Selvi F, Seiferling I, Stenlid J, Valladares F, Vesterdal L, Baeten L (2017) Biodiversity and ecosystem functioning relations in European forests depend on environmental context. Ecology Letters 20:1414-1426.

Roth N, Doerfler I, Bussler H, Blaschke M, Bässler C, Gossner MM, Heideroth A, Thorn S, W. Weisser W, Müller J (2019) Decadal effects of landscape-wide enrichment of dead wood on saproxylic organisms in beech forests of different historic management intensity Diversity and Distributions 25:430-441

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH (2000) Biodiversity - Global biodiversity scenarios for the year 2100. Science 287:1770-1774.

Sandström J, Bernes C, Junninen K, Lõhmus A, Macdonald E, Müller J, Jonsson BG (2019) Impacts of dead-wood manipulation on the biodiversity of temperate and boreal forests - A systematic review. Journal of Applied Ecology 56:1770-1781.

Schall P, Gossner M, Heinrichs S, Fischer M, Boch S, Prati D, Jung K, Baumgartner V, Blaser S, Böhm S, Buscot F, Daniel R, Goldmann K, Kaiser K, Kahl T, Lange M, Müller J, Overmann J, Renner S, Schulze E, Sikorski J, Tschapka M, Türke M, Weisser W, Wemheuer B, Wubet T, Ammer C (2018a) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of applied Ecology 55 267–278.

Schall P, Schulze ED, Fischer M, Ayasse M, Ammer C (2018b) Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology 32:39-52.

Schelhaas MJ, Nabuurs GJ, Schuck A (2003) Natural disturbances in the European forests in the 19th and 20th centuries. Global Change Biology 9:1620-1633

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze ED, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein AM, Koller R, Konig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Muller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556.

Scherer-Lorenzen M (2014) The functional role of biodiversity in the context of global change. In: Burslem D, Coomes D, Simonson WD (eds) Forests and Global Change. Cambridge University Press, Cambridge, pp 195-238

Schuldt A, Assmann T, Brezzi M, Buscot F, Eichenberg D, Gutknecht J, Hardtle W, He JS, Klein AM, Kuhn P, Liu XJ, Ma KP, Niklaus PA, Pietsch KA, Purahong W, Scherer-Lorenzen M, Schmid B, Scholten T, Staab M, Tang ZY, Trogisch S, von Oheimb G, Wirth C, Wubet T, Zhu CD, Bruelheide H (2018) Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications 9:10.

Schuldt A, Bruelheide H, Durka W, Michalski SG, Purschke O, Assmann T (2014) Tree diversity promotes functional dissimilarity and maintains functional richness despite species loss in predator assemblages. Oecologia 174:533-543.

Schuldt A, Ebeling A, Kunz M, Staab M, Guimaraes-Steinicke C, Bachmann D, Buchmann N, Durka W, Fichtner A, Fornoff F, Hardtle W, Hertzog LR, Klein AM, Roscher C, Schaller J, von Oheimb G, Weigelt A, Weisser W, Wirth C, Zhang JY, Bruelheide H, Eisenhauer N (2019) Multiple plant diversity components drive consumer communities across ecosystems. Nature Communications 10:1460.

Schwenk WS, Donovan TM, Keeton WS, Nunery JS (2012) Carbon storage, timber production, and biodiversity: comparing ecosystem services with multi-criteria decision analysis. Ecological Applications 22:1612-1627

Sebek P, Altman J, Platek M, Cizek L (2013) Is active management the key to the conservation of saproxylic biodiversity? Pollarding promotes the formation of tree hollows. PlosOne 8:e60456

Seibold S, Bässler C, Brandl R, Büche B, Szallies A, Thorn S, Ulyshen M, Müller J (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood Journal of Applied Ecology 53:934–943.

Seibold S, Bässler C, Brandl R, Gossner MM, Thorn S, Ulyshen MD, Müller J (2015) Experimental studies of dead-wood biodiversity - a review identifying global gaps in knowledge. Biological Conservation 191:139-149.

Seibold S, Cadotte MW, MacIvor JS, Thorn S, Müller J (2018) The necessity of multi-tropic approaches in community ecology Trends in Ecology and Evolution 33:754-764.

Seibold S, Rammer W, Hothorn T, Seidl R, Ulyshen MD, Lorz J, Cadotte M, Lindemayer DB, Adhikari YP, Aragón R, Bae S, Baldrian P, Barimani Varandi H, Barlow J, Bässler C, Beauchêne J, Berenguer E, Bergamin RS, Birkemoe T, Boros G, Brandl R, Brustel: H, Burton PJ, Cakpo-Tossou YT, Castro J, Eugénie C, Cobb TP, Nina F, Fernández RD, Firn J, Gan KS, González G, Gossner MM, Habel JC, Christian H, Heibl C, Heikkala O, Hemp A, Hemp C, Hjältén J, Hotes S, Kouki J, Lachat T, Liu J, Liu Y, Luo Y-H, Macandog DM, Martina PE, Mukul SA, Nachin B, Nisbet K, O'Halloran J, Oxbrough A, Pandey JN, Pavlíček T, Pawson SM, Rakotondranary JS, Ramanamanjato J-B, Rossi L, Schmidl J, Schulze M, Seaton S, Stone MJ, Stork NE, Suran B, Sverdrup-Thygeson A, Thorn S, Thyagarajan G, Wardlaw TJ, Weisser WW, Yoon S, Zhang N, Müller J (2021) The contribution of insects to global forest deadwood decomposition. Nature 597:77–81.

Seidl R, Schelhaas M-J, Rammer W, Verkerk PJ (2014) Increasing forest disturbances in Europe and their impact on carbon storage. Nature Climate Change 4 806–810.

Senf C, Mori A, Müller J, Seidl R (2020) The response of canopy height diversity to natural disturbances in two temperate forest landscapes. Landscape Ecology 35:2101–2112.

Senf C, Müller J, Seidl R (2019) Post-disturbance recovery of forest cover and tree height differ with management in Central Europe. Landscape Ecology 34:2837–2850

Simons NK, Felipe-Lucia MR, Schall P, Ammer C, Bauhus J, Blüthgen N, Boch S, Buscot F, Fischer M, Goldmann K, Gossner MM, Hänsel F, Jung K, Manning P, Nauss T, Oelmann Y, Pena R, Polle A, Renner SC, Schloter M, Schöning I, Schulze E-D, Solly EF, Sorkau E, Stempfhuber B, Wubet T, Müller J, Seibold S, Weisser WW (2021) National Forest Inventories capture the multifunctionality of managed forests in Germany. For. Ecosyst. 8:5.

Simons NK, Felipe-Lucia MRF, Schall P, Ammer C, Bauhus J, Blüthgen N, Boch S, Buscot F, Fischer M, Goldmann K, Gossner MM, Hänsel F, Jung K, Manning P, Nauss T, Oelmann Y, Pena R, Polle A, Renner SC, Schloter M, Schöning I, Schulze E-D, Solly EF, Sorkau E, Stempfhuber B, Wubet T, Müller J, Seibold S, Weisser WW (2020) National Forest Inventories capture the multifunctionality of managed forests in Germany. Forest Ecosystems 8:5.

Sirami C, Gross N, Baillod AB, Bertrand C, Carrie R, Hass A, Henckel L, Miguet P, Vuillot C, Alignier A, Girard J, Batary P, Clough Y, Violle C, Giralt D, Bota G, Badenhausser I, Lefebvre G, Gauffre B, Vialatte A, Calatayud F, Gil-Tena A, Tischendorf L, Mitchell S, Lindsay K, Georges R, Hilaire S, Recasens J, Sole-Senan XO, Robleno I, Bosch J, Barrientos JA, Ricarte A, Marcos-Garcia MA, Minano J, Mathevet R, Gibon A, Baudry J, Balent G, Poulin B, Burel F, Tscharntke T, Bretagnolle V, Siriwardena G, Ouin A, Brotons L, Martin JL, Fahrig L (2019) Increasing crop heterogeneity enhances multitrophic diversity across agricultural regions. Proc. Natl. Acad. Sci. U. S. A. 116:16442-16447. doi: 10.1073/pnas.1906419116

Soares C, Sampaio MB, Santos FS, Martins FR, dos Santos FAM (2020) Patterns of species diversity in different spatial scales and spatial heterogeneity on beta diversity. Acta Botanica Brasilica 34:9-16.

Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, Alt F, Arndt H, Baumgartner V, Binkenstein J, Birkhofer K, Blaser S, Bluthgen N, Boch S, Bohm S, Borschig C, Buscot F, Diekotter T, Heinze J, Holzel N, Jung K, Klaus VH, Kleinebecker T, Klemmer S, Krauss J, Lange M, Morris EK, Muller J, Oelmann Y, Overmann J, Pasalic E, Rillig MC, Schaefer HM, Schloter M, Schmitt B, Schoning I, Schrumpf M, Sikorski J, Socher SA, Solly EF, Sonnemann I, Sorkau E, Steckel J, Steffan-Dewenter I, Stempfhuber B, Tschapka M, Turke M, Venter PC, Weiner CN, Weisser WW, Werner M, Westphal C, Wilcke W, Wolters V, Wubet T, Wurst S, Fischer M, Allan E (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456-+.

Sommerfeld A, Senf C, Buma B, D'Amato AW, Després T, Díaz-Hormazábal I, Fraver S, Frelich LE, Gutiérrez ÁG, Hart SJ, Harvey BJ, He HS, Hlásny T, Holz A, Kitzberger T, Kulakowski D, Lindenmayer D, Mori AS, Müller J, Paritsis J, Perry GLW, Stephens SL, Svoboda M, Turner MG, Veblen TT, Seidl R (2018) Patterns and drivers of recent disturbances across the temperate forest biome. Nature Communications 9:4355

Speight MCD (1989) Saproxylic invertebrates and their conservation. Council of Europe, Nature and environment series 42:1-79

Spence JR (2001) The new boreal forestry: adjusting timber management to accommodate biodiversity. Trends in Ecology & Evolution 16:591-593.

Swanson FJ, Franklin JF (1992) New forestry principles from ecosystem analysis of Pacific-Northwest Forests. Ecological Applications 2:262-274.

Swanson ME, Franklin JF, Beschta RL, Crisafulli CM, Dellasala DA, Hutto RL, Lindenmayer DB, Swanson FJ (2011) The forgotten stage of forest succession: early-successional ecosystems on forest sites. Frontiers in Ecology and the Environment 9:117-125

Thorn S, Bassler C, Bernhardt-Romermann M, Cadotte M, Heibl C, Schafer H, Seibold S, Muller J (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters 19:163-170.

Thorn S, Bässler C, Brandl R, Burton PJ, Cahall R, Campbell JL, Castro J, Choi C-Y, Cobb T, Donato DC, Durska E, Fontaine JB, Gauthier S, Hebert C, Hothorn T, Hutto RL, Lee E-J, Leverkus AB, Lindenmayer DB, Obrist MK, Rost J, Seibold S, Seidl R, Thom D, Waldron K, Wermelinger B, Winter M-B, Zmihorski M, Müller J (2018) Impacts of salvage logging on biodiversity – a meta-analysis. Journal of Applied Ecology 55:279–289

Thorn S, Chao A, Georgiev KB, Müller J, Bässler C, Campbell JL, Castro J, Chen Y-H, Choi C-Y, Cobb TP, Donato DC, Durska E, Macdonald E, Feldhaar H, Fontaine JB, Fornwalt PJ, Hernández RM, Hutto RL, Koivula M, Lee E-J, Lindenmayer D, Mikusiński G, Obrist MK, Perlík M, Rost J, Waldron K, Wermelinger B, Weiß I, Żmihorski M, Leverkus AB (2020) Estimating retention benchmarks for salvage logging to protect biodiversity. Nature Communications 11:4762.

Tilman D, Lehman CL, Thomson KT (1997) Plant diversity and ecosystem productivity: Theoretical considerations. Proc. Natl. Acad. Sci. U. S. A. 94:1857-1861.

Tilman D, Reich PB, Knops J, Wedin D, Mielke T, Lehmann C (2001) Diversity and productivity in a long term grassland experiment. Science 294:843-845.

Tscharntke T, Grass I, Wanger TC, Westphal C, Batáry P (2021) Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends in Ecology & Evolution online first.

Turner MG, Romme WH, Tinker DB (2003) Surprises and lessons from the 1988 Yellowstone fires. Frontiers in Ecology and the Environment 1:351-358.

van der Plas F (2019) Biodiversity and ecosystem functioning in naturally assembled communities. Biological Reviews 94:1220-1245.

van der Plas F (2021) Beta diversity Experiment, www.fonsvanderplas.nl/projects/

van der Plas F, Allan E, Fischer M, Alt F, Arndt H, Binkenstein J, Blaser S, Bluthgen N, Bohm S, Holzel N, Klaus VH, Kleinebecker T, Morris K, Oelmann Y, Prati D, Renner SC, Rillig MC, Schaefer HM, Schloter M, Schmitt B, Schoning I, Schrumpf M, Solly EF, Sorkau E, Steckel J, Steffan-Dewenter I, Stempfhuber B, Tschapka M, Weiner CN, Weisser WW, Werner M, Westphal C, Wilcke W, Manning P (2019) Towards the development of general rules describing landscape heterogeneity-multifunctionality relationships. Journal of Applied Ecology 56:168-179.

van der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Hector A, Ampoorter E, Baeten L, Barbaro L, Bauhus J, Benavides R, Benneter A, Berthold F, Bonal D, Bouriaud O, Bruelheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Coomes D, Coppi A, Bastias CC, Dawud SM, De Wandeler H, Domisch T, Finer L, Gessler A, Granier A, Grossiord C, Guyot V, Hattenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Jucker T, Koricheva J, Milligan H, Muller S, Muys B, Nguyen D, Pollastrini M, Raulund-Rasmussen K, Selvi F, Stenlid J, Valladares F, Vesterdal L, Zielinski D, Fischer M (2016a) Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nature Communications 7:11109.

van der Plas F, Manning P, Soliveres S, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Ampoorter E, Baeten L, Barbaro L, Bauhus J, Benavides R, Benneter A, Bonal D, Bouriaud O, Bruelheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Coomes DA, Coppi A, Bastias CC, Dawud SM, De Wandeler H, Domisch T, Finer L, Gessler A, Granier A, Grossiord C, Guyot V, Hattenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Jucker T, Koricheva J, Milligan H, Mueller S, Muys B, Nguyen D, Pollastrini M, Ratcliffe S, Raulund-Rasmussen K, Selvi F, Stenlid J, Valladares F, Vesterdal L, Zielinski D, Fischer M (2016b) Biotic homogenization can decrease landscape-scale forest multifunctionality (vol 113, pg 3557, 2016). Proc. Natl. Acad. Sci. U. S. A. 113:E2549-E2549.

van der Plas F, Ratcliffe S, Ruiz-Benito P, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Ampoorter E, Baeten L, Barbaro L, Bastias CC, Bauhus J, Benavides R, Benneter A, Bonal D, Bouriaud O, Bruelheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Cornelissen JHC, Dahlgren J, Checko E, Coppi A, Dawud SM, Deconchat M, De Smedt P, De Wandeler H, Domisch T, Finer L, Fotelli M, Gessler A, Granier A, Grossiord C, Guyot V, Haase J, Haettenschwiler S, Jactel H, Jaroszewicz B, Joly F-X, Jucker T, Kambach S, Kaendler G, Kattge J, Koricheva J, Kunstler G, Lehtonen A, Liebergesell M, Manning P, Milligan H, Mueller S, Muys B, Nguyen D, Nock C, Ohse B, Paquette A, Penuelas J, Pollastrini M, Radoglou K, Raulund-Rasmussen K, Roger F, Seidl R, Selvi F, Stenlid J, Valladares F, van Keer J, Vesterdal L, Fischer M, Gamfeldt L, Allan E (2018) Continental mapping of forest ecosystem functions reveals a high but unrealised potential for forest multifunctionality. Ecology Letters 21:31-42.

Veech J, Crist TO (2010a) Toward a unified view of diversity partitioning. Ecology 91:1988-1992

Veech JA, Crist TO (2010b) Diversity partitioning without statistical independence of alpha and beta. Ecology 91:1964–1969.

Vierling KT, Bässler C, Brandl B, Vierling LA, Weiß I, Müller J (2011) Spinning a laser web: predicting spider distributions using lidar Ecological Applications 21:577-588

Wang S, Brose U, van Nouhuys S, Holt RD, Loreau M (2021) Metapopulation capacity determines food chain length in fragmented landscapes. Proceedings of the National Acadamey of Science USA 118:e2102733118.

Wang SP, Loreau M (2016) Biodiversity and ecosystem stability across scales in metacommunities. Ecology Letters 19:510-518.

Weisser WW, Roscher C, Meyer ST, Ebeling A, Luo GJ, Allan E, Besser H, Barnard RL, Buchmann N, Buscot F, Engels C, Fischer C, Fischer M, Gessler A, Gleixner G, Halle S, Hildebrandt A, Hillebrand H, de Kroon H, Lange M, Leimer S, Le Roux X, Milcu A, Mommer L, Niklaus PA, Oelmann Y, Proulx R, Roy J, Scherber C, Scherer-Lorenzen M, Scheu S, Tscharntke T, Wachendorf M, Wagg C, Weigelt A, Wilcke W, Wirth C, Schulze ED, Schmid B, Eisenhauer N (2017) Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. Basic and Applied Ecology 23:1-73.

Weslien J, Djupström LB, Schroeder M, Widenfalk O (2011) Long-term priority effects among insects and fungi colonizing decaying wood. Journal of Animal Ecology 80:1155-1162.

Whittaker RH (1960) Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs 30:279-338

Whittaker RH (1972) Evolution and measurement of species diversity. Taxon 2121:213–251.

Work TT, Shorthouse DP, Spence JR, Volney WJA, Langor D (2004) Stand composition and structure of the boreal mixedwood and epigaeic arthropods of the Ecosystem Management Emulating Natural Disturbance (EMEND) landbase in northwestern Alberta. Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere 34:417-430.

Subprojects

Project Description – Project Proposals

Jörg Müller, Würzburg
Christian Ammer, Göttingen
Nico Eisenhauer, Leipzig
Michael Scherer-Lorenzen, Freiburg

SPZ Scientific coordination, synthesis, site and data management

---

Project Description

1 Starting Point

General importance of joint central coordination of the Research Unit (RU)

Experience from large integrated projects shows that they can only be successful if central tasks and responsibilities are taken over by a dedicated subproject that coordinates the whole RU, specifically in terms of developing common analyses frameworks, coordinated field campaigns, protocols, data curation and dissemination of results (Bässler et al. 2008; Eisenhauer et al. 2019a; Fischer et al. 2010; Weisser et al. 2017). These activities are indispensable for the provision of infrastructure for everyone working in long-term experiments, enable the sustainable use of experimental plots and are the prerequisite for synthesis analyses.

1.1 State of the art and preliminary work

An experimental study on enhancing the structural diversity between patches for improving multidiversity and multifunctionality in production forests can build on existing knowledge regarding the effects of different forest structures at patch level on both biodiversity and ecosystem functions (Heidrich et al. 2020; Simons et al. 2020). In the last few decades in particular, various methods have been developed for standardized biodiversity surveys in forests in all strata, as well as for animals, plants, fungi and bacteria, including barcoding and autonomous recordings of vocalization. Methods such as metabarcoding have opened up completely new possibilities, even for species groups that are very cryptic but also very important for forest functions, e.g. fungi. However, as many of these methods have only recently become available for large sample sizes, there are hardly any coordinated measurement campaigns across the different strata of a forest as well as different groups of organisms and trophic levels (Penone et al. 2019), although this would be very promising for biodiversity–ecosystem functioning (BEF) studies (Seibold et al. 2018). Our group has tested different methods in forests from below ground to the canopy for their efficiency to measure different aspects of biodiversity, trophic levels and ecosystem functions, some of them will be provided by the SPZ for all plots.

One of the basic pieces of information in forests is forest structure (Ehbrecht et al. 2021). This is primarily defined by the number, size, type and distribution of trees in a forest, but also by their vertical structural diversity and vitality of these structures. Their vitality determines whether trees are healthy, have first signs of senescence or are dead. The leaves of a tree are habitat and resource for a diverse folivorous community (Brändle and Brandl 2001). This habitat is determined by the identity of a tree, the chemical composition of the leaves, the microclimate within the tree crown, as well as by the phylogenetic distance from neighboring trees (Valdés-Correcher et al. 2020; Yguel et al. 2011). After their death, dead trees provide habitat for a diverse and multitrophic decomposer community (Stokland et al. 2012). Further, small structures on dead or alive tree stems and branches form so-called tree-related microhabitats that provide essential substrates or habitats for species, which can also be assessed by standardized sampling methods (Larrieu et al. 2018). Hence, many studies on biodiversity and ecosystem functions are based on a solid inventory of dead and alive trees in a forest (Dörfler et al. 2017; Schall et al. 2018; Simons et al. 2020). So far, in preparation of this proposed RU, we have already recorded such information on trees in the three districts with an Enhancement of Structural Beta Complexity (ESBC) in the University Forest as well as in the five districts with ESBC in the Bavarian Forest.

Similar to tree species and structure, soil is an important control variable for biodiversity and ecosystem functions (Delgado-Baquerizo et al. 2016; Scherber et al. 2010; Schuldt et al. 2019; Soliveres et al. 2016). Nutrient and water availability are key drivers of vegetation, which in turn is an important driver of species communities below and above ground (Sulikowska-Drozd and Horsák 2007). In recent years, it has become apparent that microclimatic factors like temperature and moisture can also play a major role in species composition and ecosystem processes (Gottschall et al. 2019; Griffiths et al. 2021; Seibold et al. 2016). Therefore, information on soil chemistry, texture, water balance and microclimate in soil and on the soil surface is of great importance in forest experiments and gives basic and crucial information for all proposed subprojects. For some of the patches (for the design see main proposal), we have already shown how basic microclimatic measured are affected by the treatments (Thom et al. 2020). Based on survey data, we have successfully tested the potential of canopy cover as a strong surrogate for microclimate (De Frenne et al. 2019) on diversity and composition of many taxa of different trophic levels (Bässler et al. 2010; Greve et al. 2018; Mueller et al. 2016; Seibold et al. 2016). Moreover, we have shown that this might also affect the assembly processes of communities, e.g. in fungi (Bässler et al. 2016) or the response of predators to prey (Müller et al. 2012). This highlights the need to collect basic microclimatic data as it will be done by SPZ for more mechanistic insights along with remote sensing data for upscaling on large forest landscapes.

The structures of a forest form the template for biodiversity at different scales. However, the connection of different scales of diversity (α, β, γ), different aspects of biodiversity (taxonomic, functional, phylogenetic, structural) and their connection to ecosystem functions, again on the different scales α, β and γ, is an unsolved problem in biostatistics (Mori et al. 2018). Here, we already developed the idea for a general statistical framework for our RU, together with our cooperation partners in statistics Prof. Anne Chao (National Tsing Hua University, Taiwan), Prof. Chun-Huo Chiu (National Taiwan University, Taiwan), Dr. Fons van der Plas (University of Leipzig) and Prof. Torsten Hothorn (University of Zürich, Switzerland). In the following, we review a unified biodiversity approach to quantify biodiversity and its partitioning (α-, β-, γ-diversities) in our data. In work package 5 (2.3), we describe the idea for a novel framework that generalizes the conventional concept of multifunctionality.

How to quantify and compare biodiversity across assemblages was once one of the most controversial issues in ecology (Magurran and McGill 2011). In his pioneering paper, Hill (1973) integrated species richness and abundance into a class of diversity measures that later came to be known as Hill numbers (or the effective number of equally abundant species), parameterized by a diversity order q ≥ 0 (Hill 1973) with the weight of the most abundant species increasing with order q. There is a growing consensus that Hill numbers convey all the information in a species abundance distribution and completely characterize taxonomic/species diversity in an assemblage; see a multi-author *Ecology* forum (Ellison (2010) and papers following it). Hill numbers of all orders are in units of "species equivalents" and include the three most widely used species diversity measures: (1) species richness, which treats species equally and thus is sensitive to individuals of rare species for q = 0; (2) the Hill number of order q = 1 reduces to the exponential of Shannon diversity, which treats individuals equally and thus is sensitive to common species; and (3) the Hill number of order q = 2 reduces to the inverse of the Simpson concentration index, which is sensitive to dominant species. Therefore, the role of rare, common and dominant species for any diversity measure (including taxonomic and functional diversities, see below) can be assessed based on this framework. We believe that Hill numbers are particularly useful in our BEF approach, because dominant species often drive major ecosystem functions. A main advantage of using Hill numbers is that they obey the replication principle (Hill 1973) and can thus be partitioned into independent components of α- and β-diversity (Chao and Chiu 2016; Legendre and De Cáceres 2013). In general, the multiplicative β- (ratio of γ- and α-) diversity quantifies the effective number of study plots; it has a minimum value of one (when all plots are identical in species abundance distributions) and a maximum value of the number of plots (when there are no shared species among plots). Thus, the range of beta diversity depends on the number of plots. For example, the β value for a stand with 9 plots is in the range of [1; 9], whereas the β value for a stand with 15 plots is in the range of [1; 15]. Thus, β values with different numbers of plots cannot be compared directly due to differences in their ranges; they should be monotonically transformed to obtain dissimilarity measures in the range of [0; 1], so that the resulting dissimilarity measures can be compared. Chao and Chiu (2016) proved that two major approaches to β diversity, i.e., diversity decomposition and the variance approach (Legendre and De Cáceres 2013) converge to the same classes of Jaccard- and Sørensen-type dissimilarity measures in the range of [0; 1]. These two classes of taxonomic measures include most of the commonly used dissimilarity indices as special cases, i.e., the classical richness-based Jaccard and Sørensen index, information based Horn dissimilarity, and the frequency-based Morisita-Horn index.

Another considerable advantage of using Hill numbers is that the framework provides a unified approach to include species differences with respect to species' evolutionary history (i.e., phylogenetic trees) or species traits (see Chao et al. 2014a; 2019). Thus, three major dimensions of biodiversity can be compared meaningfully: taxonomic diversity (the effective number of equally abundant species), phylogenetic diversity (the effective number of equally divergent lineages) and functional diversity (the effective number of equally distinct virtual functional groups). This unified framework also led to Jaccard- and Sørensen-type phylogenetic and functional dissimilarity indices.

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. **Eisenhauer N**, Schielzeth H, Barnes AD, Barry K, Bonn A, Brose U, Bruelheide H, Buchmann N, Buscot F, Ebeling A, Ferlian O, Freschet GT, Giling DP, Hättenschwiler S, Hillebrand H, Hines J, Isbell F, Koller-France E, König-Ries B, de Kroon H, Meyer ST, Milcu A, **Müller J**, Nock CA, Petermann JS, Roscher C,

Scherber C, **Scherer-Lorenzen M**, Schmid B, Schnitzer SA, Schuldt A, Tscharntke T, Türke M, van Dam NM, van der Plas F, Vogel A, Wagg C, Wardle DA, Weigelt A, Weisser WW, Wirth C, Jochum M (2019) A multitrophic perspective on biodiversity–ecosystem functioning research. Advances in Ecological Research 61:1-54.

2. Seibold S, Cadotte MW, MacIvor JS, Thorn S, **Müller J** (2018) The necessity of multi-tropic approaches in community ecology. Trends in Ecology and Evolution 33:754-764.
3. Simons NK, Felipe-Lucia MR, Schall P, Ammer C, Bauhus J, Blüthgen N, Boch S, Buscot F, Fischer M, Goldmann K, Gossner MM, Hänsel F, Jung K, Manning P, Nauss T, Oelmann Y, Pena R, Polle A, Renner SC, Schloter M, Schöning I, Schulze E-D, Solly EF, Sorkau E, Stempfhuber B, Wubet T, **Müller J**, Seibold S, Weisser WW (2021) National Forest Inventories capture the multifunctionality of managed forests in Germany. Forest Ecosystems 8:5.
4. Thorn S, Bassler C, Bernhardt-Romermann M, Cadotte M, Heibl C, Schafer H, Seibold S, **Müller J** (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters 19:163-170.
5. **Eisenhauer** N, Bonkowski M, Brose U, Buscot F, Durka W, Ebeling A, Fischer M, Gleixner G, Heintz-Buschart A, Hines J, Jesch A, Lange M, Meyer S, Roscher C, Scheu S, Schielzeth H, Schloter M, Schulz S, Unsicker S, van Dam N, Weigelt A, Weisser W, Wirth C, Wolf J, Schmid B (2019) Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity–ecosystem functioning relationships. Research Ideas and Outcomes 5:e47042.
6. Schuldt A, Ebeling A, Kunz M, Staab M, Guimaraes-Steinicke C, Bachmann D, Buchmann N, Durka W, Fichtner A, Fornoff F, Hardtle W, Hertzog LR, Klein AM, Roscher C, Schaller J, von Oheimb G, Weigelt A, Weisser W, Wirth C, Zhang JY, Bruelheide H, **Eisenhauer** N (2019) Multiple plant diversity components drive consumer communities across ecosystems. Nature Communications 10:1460.
7. Weisser WW, Roscher C, Meyer ST, Ebeling A, Luo GJ, Allan E, Besser H, Barnard RL, Buchmann N, Buscot F, Engels C, Fischer C, Fischer M, Gessler A, Gleixner G, Halle S, Hildebrandt A, Hillebrand H, de Kroon H, Lange M, Leimer S, Le Roux X, Milcu A, Mommer L, Niklaus PA, Oelmann Y, Proulx R, Roy J, Scherber C, **Scherer-Lorenzen** M, Scheu S, Tscharntke T, Wachendorf M, Wagg C, Weigelt A, Wilcke W, Wirth C, Schulze ED, Schmid B, **Eisenhauer** N (2017) Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. Basic and Applied Ecology 23:1-73.
8. Schuldt, A., Assmann, T., Brezzi, M., Buscot, F., Eichenberg, D., Gutknecht, J., Härdtle, W., He, J.-S., Klein, A.-M., Kühn, P., Liu, X., Ma, K., Niklaus, P.A., Pietsch, K.A., Purahong, W., **Scherer-Lorenzen**, M., Schmid, B., Scholten, T., Staab, M., Tang, Z., Trogisch, S., von Oheimb, G., Wirth, C., Wubet, T., Zhu, C.-D., Bruelheide, H. (2018). Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications 9:2989.
9. Glatthorn J, Annighöfer P, Balkenhol N, Leuschner C, Polle A, Scheu S, Schuldt A, Schuldt B, **Ammer C** (2021) An interdisciplinary framework to describe and evaluate the functioning of forest ecosystems. Basic and Applied Ecology 52:1-14.
10. Schall P, Heinrichs S, **Ammer C**, Ayasse M, Boch S, Buscot F, Fischer M, Goldmann K, Overmann Jörg, Schulze E-D, Sikorski J, Weisser W, Wubet T, Gossner M M (2020) Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems?' Journal of Applied Ecology 57:1363–1375.

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.2.3 Patents

Not applicable

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

Four years

2.2 Objectives

The coordination project SPZ has six main coordination objectives: the organization of coordinated sampling campaigns across locations (WP1), collection and provisioning of central data on tree cover (WP2) and background data on soil and abiotic environment (WP3), the organization of data storage and curation (WP4), the development of a statistical framework for β-diversity and multifunctionality and the testing of the main hypotheses described in the Coordination Project (WP5), and the synthesis of the findings for forestry practice (WP6). The organization of coordinated sampling campaigns includes the temporal coordination of joint collection of data at the plots across SPs, the arrangements with the landowners and the organization of local contractors to support the measurements on the districts distributed across Germany. The collection of central data on soil properties and dead and alive trees includes standardized measurements on all plots by the SPZ team. The organization of data management includes the provision of a central database, training in the use of data protocols and making the data publicly available. Furthermore, SPZ has the scientific objective to develop a new statistical framework for linking β -diversity and multifunctionality, to perform synthesis analyses based on the overall data, and to perform syntheses for forest management.

2.3 Work programme including proposed research methods

All tasks listed in WP1, WP4 and WP5 will be coordinated by the speaker J Müller. He will be supported by the requested *statistics & synthesis postdoc*, the *site manager* and the *data manager*. The coordination of sampling across the six regions and 234 patches (see Fig. 13 main proposal) requires an experienced person with long-lasting experience in organizing field campaigns in forests. Here, we will hire M Junginger (0.5) as the *site manager*, a forest scientist with expertise in sampling biodiversity and ecosystem functions in forests. The sampling of trees (WP2) requires field experience and knowledge on tree species, particularly when it comes to the identification of living trees and standing or lying deadwood. This will be conducted by A Parth and S Bondzio under the supervision of C Ammer, financed by the University Göttingen and further supported by student helpers. The soil measurements (WP3) require considerable lab capacities. This will be supervised by N Eisenhauer and M Scherer-Lorenzen and conducted by technicians (applied in SP5 and permanent staff in their labs) with support of student helpers. Data management (WP4) also requires an experienced person. The *data manager* will support the standardized storage and sharing of the data. Here, we will hire J Zhang (0.5) with long term experience in data management of research units (Peters et al. 2019; Redlich et al. 2021, see 7.1.1). For the statistical framework and the synthesis (WP5), a person with statistical and modelling skills is necessary. Here, we will hire O Mitesser as the *statistics & synthesis postdoc*, trained as a mathematician and physicist with a PhD in biology and many years of experience in statistical modelling and analysis of big data (Mitesser et al. 2015; Uhler et al. 2021). To synthesize the results of the RU for forest management (WP6), we will hire a *forestry postdoc* (with a background in forestry), which will be supervised by C Ammer with 0.5 in SPZ and 0.5 jointly by SP1.

WP1: Coordinated sampling campaigns across regions

1. Set up of all plots for the RU

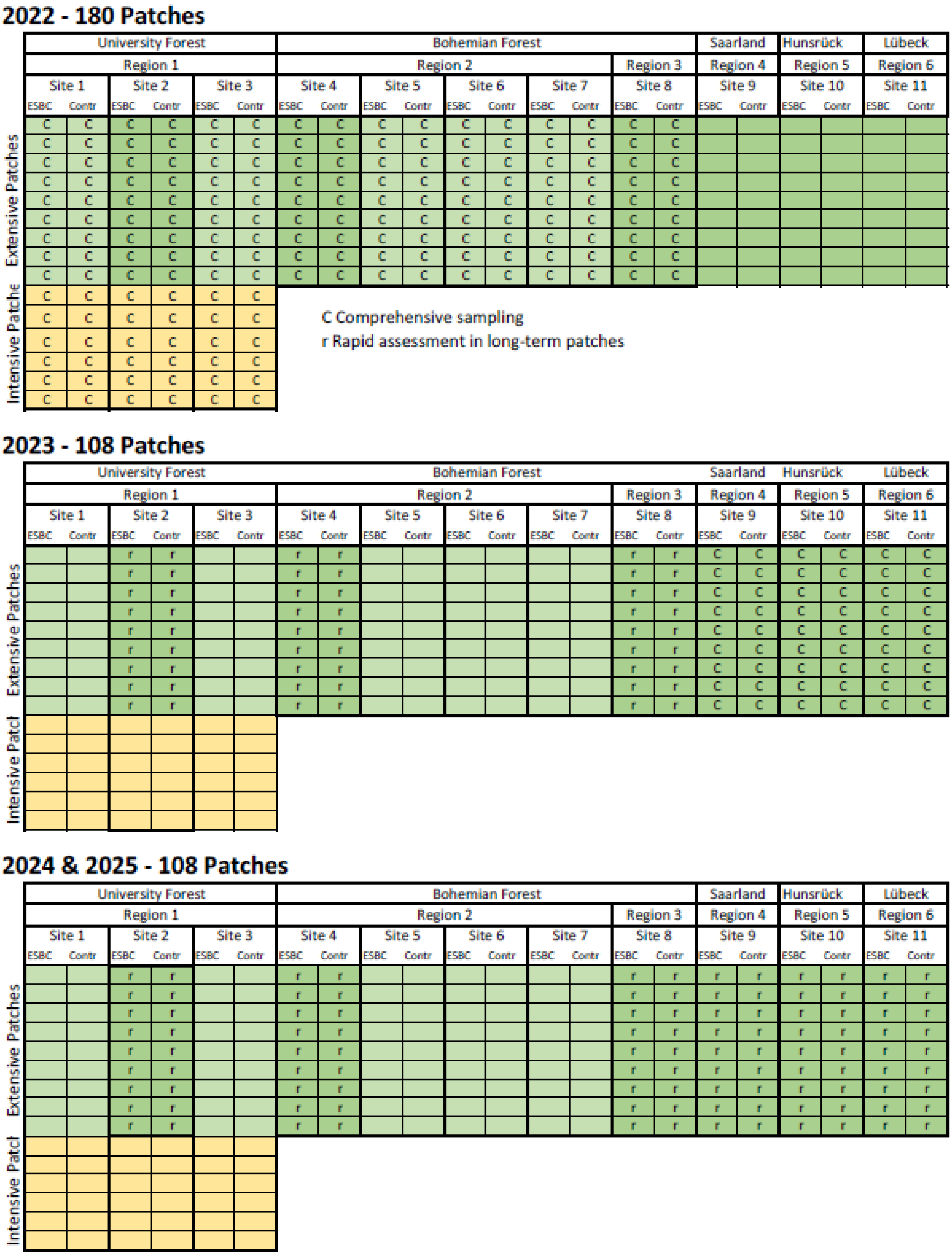
This task includes the selection of control districts in all regions (note that the treatment districts have already been selected, see main proposal), the final set up and marking of the patch center and the edges. It also includes the maintenance of the existing patches as well as creating maps and gpx files for easy access for all researchers of the RU. This will all be done by the site manager with support of student helpers.

2. Coordination of all field campaigns

In this task we will coordinate the collection following different time schemes and methods, which have to be conducted on the research plots according to Fig. 1. Here, the site manager will coordinate the field campaigns in a way to increase efficiency by combining campaigns as much as possible and by hiring local free-lancers to reduce travel distances. An online, virtual field-book will be an important tool to coordinate and monitor all activities on the plots.

3. Communication with the landowners

This task focus on a regular exchange with landowners, to inform them about all field activities. Wherever necessary, the *site manager* shall seek solutions to potential conflicts between RU and landowners. He is supported by the *forestry postdoc*, C Ammer and the speaker of the RU.



2022 - 180 Patches

	University Forest						Bohemian Forest										Saarland		Hunsrück		Lübeck	
	Region 1						Region 2								Region 3		Region 4		Region 5		Region 6	
	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		Site 7		Site 8		Site 9		Site 10		Site 11	
	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr
Extensive Patches	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C						
Intensive Patche	C	C	C	C	C	C																
	C	C	C	C	C	C																
	C	C	C	C	C	C																
	C	C	C	C	C	C																
	C	C	C	C	C	C																
	C	C	C	C	C	C																

C Comprehensive sampling
r Rapid assessment in long-term patches

2023 - 108 Patches

	University Forest						Bohemian Forest										Saarland		Hunsrück		Lübeck	
	Region 1						Region 2								Region 3		Region 4		Region 5		Region 6	
	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		Site 7		Site 8		Site 9		Site 10		Site 11	
	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr
Extensive Patches			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
			r	r			r	r							r	r	C	C	C	C	C	C
Intensive Patc																						

2024 & 2025 - 108 Patches

	University Forest						Bohemian Forest										Saarland		Hunsrück		Lübeck	
	Region 1						Region 2								Region 3		Region 4		Region 5		Region 6	
	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		Site 7		Site 8		Site 9		Site 10		Site 11	
	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr	ESBC	Contr
Extensive Patches			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
			r	r			r	r							r	r	r	r	r	r	r	r
Intensive Patc																						

Fig. 1: Sampling plan for the coordinated field sampling of the Research Unit, including one comprehensive (see C) sampling in all patches and a continuous rapid assessment (see r) for time series.

<u>Output:</u> A coordinated sampling campaign across sites and subprojects.

WP2: Tree measurements

1. Mapping trees

This task includes the measurement of diameter at breast height (dbh) of all living and dead trees including deadwood pieces >20 cm (diameter at breast height) using field map software. This will all be done by the technicians A Parth and S Bondzio with support of the *forestry* *postdoc* and with support of student helpers. It will serve as important supporting information for all other subprojects and can be used for calculating aboveground biomass production data when repeated.

2. Creating maps for all patches

In this task we will analyse all tree characteristics for the patches, including basal area, volume and spatial arrangement of the trees, as a baseline for further analyses of all subprojects and tree growth simulation in the second phase. This will be conducted by the *forestry postdoc*.

Output: A database with each tree, dbh, vitality and spatial position within the 50x50 patches for all 234 patches.

WP 3: Basic abiotic and soil measurements

1. Chemical analyses

This task involves taking soil cores and analysing them with regard to chemical soil properties, to be done twice during the first phase of the RU and during the rapid assessment campaigns. It serves to document treatment-related changes in soils and to provide baseline data for other subprojects. This will be done by two technicians (à 25%) that will be supported by student helpers. The following parameters (see table below) will be measured for the different soil layers; samples will be pooled at the extensive sites, but analysed separately at the intensive sites to obtain a measure of within-patch heterogeneity. Michael Scherer-Lorenzen (MSL); Nico Eisenhauer (NE).

Tab. 1: Soil and litter measurements.

Soil layer	Measurements	Spatial scale	Who
0 - 10 cm	C, N Soil	9 samples/plot	MSL
Litter layer	C, N Litter via elemental analyser		
0 – 10 cm	pH	9 samples/plot	NE
0 – 10 cm	Soil texture (sand, silt, clay)	9 samples/plot	NE
0 – 10 cm	Microelements via ICP-OES	9 samples/plot	MSL
Litter traps	Litter fall (g)	5 traps/plot	MSL

In the lab of M Scherer-Lorenzen, an elemental analyser for C and N analysis (Elementar vario EL cube) and an inductively coupled plasma optical emission spectrometer (ICP-OES Spectroblue EOP TI, axial and radial plasma viewing) will be available for the RU. The latter is able to measure up to 60 chemical elements (e.g. phosphorus, alcaline and alcaline earth elements, heavy metals). This allows determining detailed information on chemical characteristics of soils, plant and animal samples in the RU, in close collaboration with all other subprojects. N Eisenhauer’s lab is equipped to analyse soil pH and texture for the RU. Soil texture will be analysed using an automated system that calculates the particle size distribution by Stokes’ law (Durner and Iden, 2021). Soil pH will be measured using an Orion Star™ A211 pH meter.

2. Basic microclimatic data

To provide basic information on the abiotic environment below and above ground, soil moisture, temperature and air humidity will be monitored in the centre of all patches. Air temperature and air humidity readings at 1.3 m height aboveground (Easylog) will be supported by soil moisture, soil temperature and air temperature measurements within the herbaceous layer (TMS-4, Tomst, Czech Republic). This recently developed Temperature-Moisture-

Sensor (TMS) mimics a small herbaceous plant (Wild et al. 2019). In the intensively-studied patches in Sailershausen, three TMS-4 sensors will be operated in order assess within-plot heterogeneity. These will be installed and supervised by N Eisenhauer.

Output: A database with standardized information on soil characteristics and below and above ground microclimate for all 234 patches.

WP 4: Organization of data storage and curation

1. Data storage

We will develop a data solution that supports metadata documentation, data storage, data backup and versioning, data exchange, online data analysis and visualization, as well as data publication and long-term stewardship. This will be done by the *data manager* J Zhang, an expert in data management. To maximize exchange options with the other DFG-funded research collaborations, we will closely collaborate with the BExIS Experiment Data Management Platform (https://fusion.cs.uni-jena.de/fusion/projects/bexis/), Open Data Cube (https://www.opendatacube.org/), and long-term data archive centres, such as PANGAEA (https://www.pangaea.de/) and NFDI4BioDiversity (https://www.nfdi4biodiversity.org/)

2. Integrating the data into teaching

To fully open this unique data pool for teaching of students, the *data manager* will open the data with support of M Wegmann (University of Würzburg) and student helpers for courses such as the applied Earth Observation M.Sc. program EAGLE. We will also make data from the RU available to the Data Crunch Cup Würzburg, which is a data analysing competition for students organized by the Center for Computational and Theoretical Biology. Students of all subjects are invited to analyse data and complete tasks as part of the competition. This will increase the popularity of the RU throughout the University of Würzburg and beyond and attract students to conduct their Bachelor or Master theses with us in the context of the RU.

Output: A data storage and management system, which integrates all data collected in the RU and provides common information for all participants.

WP 5: Statistical Framework and synthesis

1. Developing a statistical framework for beta diversity and multifunctionality

This task includes several steps to develop a new framework for biodiversity and multifunctionality of landscapes as well as to test the effect of the treatments on different aspects of biodiversity and ecosystem processes at the patch scale. For a fair comparison of biodiversity across scales (patches or districts), a standardization approach via size- and coverage-based rarefaction and extrapolation will be applied (Chao et al. 2014). This approach aims to compare biodiversity estimates for equally large or equally complete samples. Here, “coverage” is an objective measure of sample completeness (Chao and Jost 2012). After considering all these facets of biodiversity measurements, we will analyse taxon-, functional- and phylogenetic diversities. Moreover, we will use our biodiversity measurements on α- and β-diversity scales in a multi-taxon-diversity framework. Such a framework to combine diversity measurements of many taxa with variation in species numbers by a proportional weighting was developed by Allan et al. (2014). To describe the difference in assembly mechanisms, i.e. how species assemble in local communities, we will test different measures, such as for instance mean pair-wise distances of species dissimilarities compared to a Null model in distance matrices (Thorn et al. 2016). To compensate for unequal knowledge on traits in different taxa, we plan to integrate the method of Cadotte et al. (2013) combining information from measured traits and from phylogenies.

To quantify multifunctionality, we will first test the established threshold approach on patch and district level, which assumes that a function is fulfilled if it exceeds a certain threshold (Byrnes et al. 2014; van der Plas et al. 2016). Here, patches above and below the respective threshold are coded as 1 and 0. Hence, this approach is conceptually similar to presence-absence based biodiversity quantifications (e.g. species richness), in the sense that those functions are considered analogous to species and therefore either considered 'present' (provided above a threshold that reflects minimum desirable levels) or 'absent' (not provided above the given threshold). Second, we will also quantify ecosystem multifunctionality based on a 'threshold-plus approach' (Manning et al. 2018), whereby functions are considered absent (value of 0) when not exceeding a minimum threshold, or provide any possible level higher than zero if exceeding a minimum threshold. This way, ecosystem multifunctionality is quantified conceptually similar to abundance-based biodiversity quantifications (e.g. Shannon or Simpson diversity), in the sense that functions either have values of zero, low values or high values. By doing so, we seek to expand the concept of multifunctionality towards the framework of Hill numbers for quantifying biodiversity. Since we will include Hill-based multifunctionality quantifications to the order of q=1 (exponential of Shannon multifunctionality) and q=2 (inverse of the Simpson concentration index of multifunctionality), this opens the avenue to examine the effects of biodiversity on dominant or rare/infrequent functions and to partition multifunctionality in α- and β-components. We will then extend this concept similarly as above to a multifunctional β-approach. We will compare this novel approach with the functional diversity (the effective number of equally distinct virtual functional groups) described above. This task will be conducted by the *statistics & synthesis postdoc* (O Mitesser) under the supervision of J Müller and in close collaboration with our collaborator A Chao and the Mercator Fellows T Hothorn, M Cadotte and F van der Plas.

To test the relation of our diversity measures, single functions and multifunctionality (as response variables) on the patch scale to environmental variables or any covariates (as predictors), we will apply generalized additive mixed (GAM) models, which are more general formulations of generalized linear models (GLM) and also can represent survival analysis of decay processes. Fitting and implementation of GAM models can be performed using the mgcv package in R. Predictors in the GAM models can be parametric (as in the usual GLM) or linked by many non-parametric smooth functions (e.g., splines or kernel-type smoothers). The GAM model is thus very flexible with less assumptions and can be used to model many different kinds of non-linear patterns or trends. Moreover, in the GAM model, predictors can be fixed effects and random effects. We thus can treat blocks as random factors, while canopy openness and interactions to further treatments are regarded as fixed factors. This allows our framework to take repeated measures and non-linear relations into account. Finally, to test the effect of α- and β-diversity as well as confounding environmental variables on multifunctionality of the stands, we will explore structured equation models (Shipley 2009). This task will be developed by our *statistics & synthesis postdoc* in collaboration with our Mercator Fellow T Hothorn. In addition, this approach is well suited to disentangle direct effects of treatments on multifunctionality via changes in the abiotic environment from indirect effects via biodiversity and can also analyse interaction paths between different taxonomic groups (Giling et al. 2019). Such a combination of food web and community ecology approaches across trophic levels seems very promising in BEF studies (Eisenhauer et al. 2013; Eisenhauer et al. 2019b; Seibold et al. 2018).

2. Syntheses on multifunctionality

To synthesize the data on biodiversity and ecosystem functions, we will first test our analysis with simulated data. In a second approach, we will apply the framework to all data collected by the RU testing the seven main hypotheses described in the Coordination Project for the whole data set of diversity and functions. This will be done by the *statistics & synthesis postdoc* under the supervision of J Müller, N Eisenhauer and M Scherer-Lorenzen.

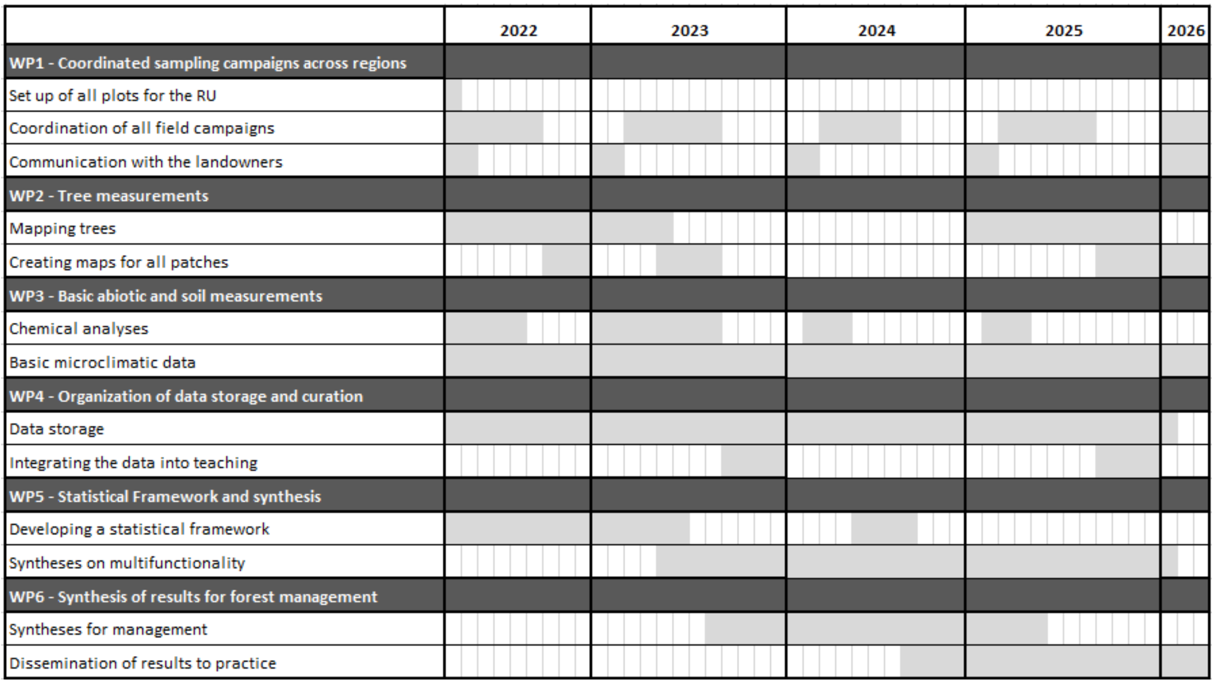
Output: A first manuscript presenting the new statistical framework for analyzing biodiversity and multifunctionality at different scales and along the Hill numbers in a conceptual ecological journal, as Ecology Letters. A second manuscript presenting synthesis analyses from the whole research unit for a general ecological journal such as Nature Ecology and Evolution.

WP6: Synthesis of results for forest management

The task of this work package is to analyse the relationship between biodiversity and ecosystem functions as response to different silvicultural and conservation-oriented interventions. After statistical analysis, the effect of various combinations of interventions not present in the experimental setting can be simulated by feeding alternative scenarios into the models. This will be done by the *forestry postdoc* under supervision of C Ammer and J Müller. The task includes a comprehensive literature review of existing knowledge on how different interventions affect structure, biodiversity and functions in forests, the analysis of data from the RU and the discussion of the results with forestry practitioners. Finally, recommendations for action are to be developed.

Output: A synthesis manuscript presenting the major implications for silvicultural management based on the findings of the RU in a applied ecological or forestry journal as Journal of Applied Ecology or Forest Ecology and Management. A practical guideline for practitioners summarizing the main findings.

Table 2: Time table of the work program by month.



3 Bibliography concerning the state of the art, the research objectives, and the work programme

Allan E, Bossdorf O, Dormann CF, Prati D, Gossner MM, Tscharntke T, Bluthgen N, Bellach M, Birkhofer K, Boch S, Bohm S, Borschig C, Chatzinotas A, Christ S, Daniel R, Diekotter T, Fischer C, Friedl T, Glaser K, Hallmann C, Hodac L, Holzel N, Jung K, Klein AM, Klaus VH, Kleinebecker T, Krauss J, Lange M, Morris EK, Muller J, Nacke H, Pasalic E, Rillig MC, Rothenwohrer C, Schally P, Scherber C, Schulze W, Socher SA, Steckel J, Steffan-Dewenter I, Turke M, Weiner CN, Werner M, Westphal C, Wolters V, Wubet T, Gockel S, Gorke M, Hemp A, Renner SC, Schoning I, Pfeiffer S, Konig-Ries B, Buscot F, Linsenmair KE, Schulze ED, Weisser WW, Fischer M (2014) Interannual variation in land-use intensity enhances grassland multidiversity. Proc. Natl. Acad. Sci. U. S. A. 111:308-313.

Bässler C, Förster B, Moning C, Müller J (2008) The BIOKLIM-Project: Biodiversity Research between Climate Change and Wilding in a temperate montane forest – The conceptual framework. Waldökologie, Landschaftsforschung und Naturschutz 7:21-33.

Bässler C, Müller J, Cadotte MW, Heibl C, Bradtka JH, Thorn S, Halbwachs H (2016) Functional response of lignicolous fungal guilds to bark beetle deforestation. Ecological Indicators 65:149-160.

Bässler C, Müller J, Dziock F, Brandl R (2010) Microclimate and especially resource availability are more important than macroclimate for assemblages of wood-inhabiting fungi Journal of Ecology 98:822-832.

Brändle M, Brandl R (2001) Species richness of insects and mites on trees: expanding Southwood. J. Animal Ecology 70:491-504

Byrnes JEK, Gamfeldt L, Isbell F, Lefcheck JS, Griffin JN, Hector A, Cardinale BJ, Hooper DU, Dee LE, Duffy JE (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods in Ecology and Evolution 5:111-124.

Cadotte M, Cecile HA, Walker SC (2013) The ecology of differences: assessing community assembly with trait and evolutionary distances. Ecology Letters 16:1234-1244.

Chao A, Gotelli NG, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species biodiversity studies. Ecological Monographs 84:45-67.

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completness rather than size. Ecology 93:2533-2547.

De Frenne P, Zellweger F, Rodríguez-Sánchez F, Scheffers BR, Hylander K, Luoto M, Vellend M, Verheyen K, Lenoir J (2019) Global buffering of temperatures under forest canopies. Nature Ecology & Evolution 3:744–749.

Delgado-Baquerizo M, Maestre FT, Reich PB, Jeffries TC, Gaitan JJ, Encinar D, Berdugo M, Campbell CD, Singh BK (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. Nature Communications 7:10541.

Dörfler I, Müller J, Gossner MM, Hofner B, Weisser WW (2017) Success of deadwood enrichment strategy in production forests depends on stand type and management intensity. Forest Ecology and Management 400:607-620.

Ehbrecht M, Seidel D, Annighofer P, Kreft H, Kohler M, Zemp DC, Puettmann K, Nilus R, Babweteera F, Willim K, Stiers M, Soto D, Boehmer HJ, Fisichelli N, Burnett M, Juday G, Stephens SL, Ammer C (2021) Global patterns and climatic controls of forest structural complexity. Nature Communications 12:519.

Eisenhauer N, Bonkowski M, Brose U, Buscot F, Durka W, Ebeling A, Fischer M, Gleixner G, Heintz-Buschart A, Hines J, Jesch A, Lange M, Meyer S, Roscher C, Scheu S, Schielzeth H, Schloter M, Schulz S, Unsicker S, van Dam N, Weigelt A, Weisser W, Wirth C, Wolf J, Schmid B (2019a) Biotic interactions, community assembly, and eco-evolutionary dynamics as drivers of long-term biodiversity–ecosystem functioning relationships. Research Ideas and Outcomes 5:e47042

Eisenhauer N, Dobies T, Cesarz S, Hobbie SE, Meyer RJ, Worm K, Reich PB (2013) Plant diversity effects on soil food webs are stronger than those of elevated CO2 and N deposition in a long-term grassland experiment. Proc. Natl. Acad. Sci. U. S. A. 110:6889-6894.

Eisenhauer N, Schielzeth H, Barnes AD, Barry K, Bonn A, Brose U, Bruelheide H, Buchmann N, Buscot F, Ebeling A, Ferlian O, Freschet GT, Giling DP, Hättenschwiler S, Hillebrand H, Hines J, Isbell F, Koller-France E, König-Ries B, de Kroon H, Meyer ST, Milcu A, Müller J, Nock CA, Petermann JS, Roscher C, Scherber C, Scherer-Lorenzen M, Schmid B, Schnitzer SA, Schuldt A, Tscharntke T, Türke M, van Dam NM, van der Plas F, Vogel A, Wagg C, Wardle DA, Weigelt A, Weisser WW, Wirth C, Jochum M (2019b) A multitrophic perspective on biodiversity–ecosystem functioning research. Advances in Ecological Research 61:1-54.

Ellison AM (2010) Partitioning diversity. Ecology 91:1962-1963.

Fischer M, Bossdorf O, Gockel S, Hansel F, Hemp A, Hessenmoller D, Korte G, Nieschulze J, Pfeiffer S, Prati D, Renner S, Schoning I, Schumacher U, Wells K, Buscot F, Kalko EKV, Linsenmair KE, Schulze ED, Weisser WW (2010) Implementing large-scale and long-term functional biodiversity research: The Biodiversity Exploratories. Basic and Applied Ecology 11:473-485.

Giling DP, Beaumelle L, Phillips HRP, Cesarz S, Eisenhauer N, Ferlian O, Gottschall F, Guerra C, Hines J, Sendek A, Siebert J, Thakur MP, Barnes AD (2019) A niche for ecosystem multifunctionality in global change research. Global Change Biology 25:763-774.

Gottschall F, Davids S, Newiger-Dous TE, Auge H, Cesarz S, Eisenhauer N (2019) Tree species identity determines wood decomposition via microclimatic effects. Ecology and Evolution 9:12113-12127. doi: 10.1002/ece3.5665

Greve ME, Hager J, Weisser WW, Schall P, Gossner MM, Feldhaar H (2018) Effect of forest management on temperate ant communities. Ecosphere 9:2303.

Griffiths HM, Eggleton P, Hemming-Schroeder N, Swinfield T, Woon JS, Allison SD, Coomes DA, Ashton LA, Parr CL (2021) Carbon flux and forest dynamics: Increased deadwood decomposition in tropical rainforest tree-fall canopy gaps. Global Change Biology 27:1601-1613.

Heidrich L, Bae S, Levick S, Seibold S, Weisser W, Krzystek P, Magdon P, Nauss T, Schall P, Serebryanyk A, Wollauer S, Ammer C, Bassler C, Doerfler I, Fischer M, Gossner MM, Heurich M, Hothorn T, Jung K, Kreft H, Schulze ED, Simons N, Thorn S, Muller J (2020) Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests. Nature Ecology & Evolution 4:1431-1431. doi: 10.1038/s41559-020-01292-0

Hill M (1973) Diversity and evenness: a unifying notation and its consequences. Ecology 54:427-432.

Larrieu L, Paillet Y, Winter S, Bütler R, Kraus D, Krumm F, Lachat T, Michel AK, Regnery B, Vandekerkhove K (2018) Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. Ecological Indicators 84:194-207.

Magurran AE, McGill BJ (2011) Biological Diversity: Frontiers in Measurement and Assessment. Oxford University Press, Oxford

Manning P, van der Plas F, Soliveres S, Allan E, Maestre FT, Mace G, Whittingham MJ, Fischer M (2018) Redefining ecosystem multifunctionality (vol 2, pg 427, 2018). Nature Ecology & Evolution 2:1515.

Mitesser O, Koeroesi A, Möhringer P, Bohn G (2015) 3D Flight Path Tracking of Butterflies by Image Processing. International Journal of Electrical and Computer Engineering Systems 6:29–31.

Mori AS, Isbell F, Seidl R (2018) b-Diversity, Community Assembly, and Ecosystem Functioning. Trends in Ecology and Evolution 33:549-564.

Mueller KE, Eisenhauer N, Reich PB, Hobbie SE, Chadwick OA, Chorover J, Dobies T, Hale CM, Jagodzinski AM, Kalucka I, Kasprowicz M, Kieliszewska-Rokicka B, Modrzynski J, Rozen A, Skorupski M, Sobczyk L, Stasinska M, Trocha LK, Weiner J, Wierzbicka A, Oleksyn J (2016) Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species. Soil Biology & Biochemistry 92:184-198.

Müller J, Mehr M, Bässler C, Fenton MB, Hothorn T, Pretzsch H, Klemmt H-J, Brandl R (2012) Aggregative response in bats: prey abundance versus habitat. Oecologia 169:673-684.

Penone C, Allan E, Soliveres S, Felipe-Lucia M, Gossner M, Seibold S, Simons N, Schall P, van der Plas F, Manning P, Manzanedo R, Boch S, Prati D, Ammer C, Bauhus J, Buscot F, Ehbrecht M, Goldmann K, Jung K, Müller J, Müller J, Pena R, Polle A, Renner S, Ruess L, Schöning I, Schrumpf M, Solly E, Tschapka M, Weisser W, Wubet T, Fischer M (2019) Specialisation and diversity of multiple trophic groups are promoted by different forest features. Ecology Letters 22:170–180.

Peters MK, Hemp A, Appelhans T, Becker JN, Behler C, Classen A, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Gerschlauer F, Gutlein A, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Kuhnel A, Mayr AV, Mwangomo E, Ngereza C, Njovu HK, Otte I, Pabst H, Renner M, Roder J, Rutten G, Costa DS, Sierra-Cornejo N, Vollstadt MGR, Dulle HI, Eardley CD, Howell KM, Keller A, Peters RS, Ssymank A, Kakengi V, Zhang J, Bogner C, Bohning-Gaese K, Brandl R, Hertel D, Huwe B, Kiese R, Kleyer M, Kuzyakov Y, Nauss T, Schleuning M, Tschapka M, Fischer M, Steffan-Dewenter I (2019) Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. Nature 568:88-92.

Redlich S, Zhang J, Benjamin C, Dhillon MS, Englmeier J, Ewald J, Fricke U, Ganuza C, Haensel M, Hovestadt T, Kollmann J, Koellner T, Kübert-Flock C, Kunstmann H, Menzel A, Moning C, Peters W, Riebl R, Rummler T, Botero SR, Tobisch C, Uhler J, Uphus L, Müller J, Steffan-Dewenter I (2021) Disentangling effects of climate and land use on biodiversity and ecosystem services – a multi-scale experimental design. bioRxiv:2021.2003.2005.434036.

Schall P, Schulze ED, Fischer M, Ayasse M, Ammer C (2018) Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology 32:39-52.

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze ED, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein AM, Koller R, Konig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Muller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556.

Schuldt A, Ebeling A, Kunz M, Staab M, Guimaraes-Steinicke C, Bachmann D, Buchmann N, Durka W, Fichtner A, Fornoff F, Hardtle W, Hertzog LR, Klein AM, Roscher C, Schaller J, von Oheimb G, Weigelt A, Weisser W, Wirth C, Zhang JY, Bruelheide H, Eisenhauer N (2019) Multiple plant diversity components drive consumer communities across ecosystems. Nature Communications 10:1460.

Seibold S, Bässler C, Brandl R, Büche B, Szallies A, Thorn S, Ulyshen M, Müller J (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood Journal of Applied Ecology 53:934–943

Seibold S, Cadotte MW, MacIvor JS, Thorn S, Müller J (2018) The necessity of multi-tropic approaches in community ecology Trends in Ecology and Evolution 33:754-764

Shipley B (2009) Confirmatory path analysis in a generalized multilevel context. Ecology 90:363-368.

Simons NK, Felipe-Lucia MRF, Schall P, Ammer C, Bauhus J, Blüthgen N, Boch S, Buscot F, Fischer M, Goldmann K, Gossner MM, Hänsel F, Jung K, Manning P, Nauss T, Oelmann Y, Pena R, Polle A, Renner SC, Schloter M, Schöning I, Schulze E-D, Solly EF, Sorkau E, Stempfhuber B, Wubet T, Müller J, Seibold S, Weisser WW (2020) National Forest Inventories capture the multifunctionality of managed forests in Germany. For. Ecosyst.

Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, Alt F, Arndt H, Baumgartner V, Binkenstein J, Birkhofer K, Blaser S, Bluthgen N, Boch S, Bohm S, Borschig C, Buscot F, Diekotter T, Heinze J, Holzel N, Jung K, Klaus VH, Kleinebecker T, Klemmer S, Krauss J, Lange M, Morris EK, Muller J, Oelmann Y, Overmann J, Pasalic E, Rillig MC, Schaefer HM, Schloter M, Schmitt B, Schoning I, Schrumpf M, Sikorski J, Socher SA, Solly EF, Sonnemann I, Sorkau E, Steckel J, Steffan-Dewenter I, Stempfhuber B, Tschapka M, Turke M, Venter PC, Weiner CN, Weisser WW, Werner M, Westphal C, Wilcke W, Wolters V, Wubet T, Wurst S, Fischer M, Allan E (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459.

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, Cambridge

Sulikowska-Drozd, Horsák M (2007) Woodland mollusc communities along environmental gradients in the East Carpathians. Biologia, Bratislava 62:201-209.

Thom D, Sommerfeld A, Sebald J, Hagge J, Müller J, Seidl R (2020) Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agricultural and Forest Meteorology 291:108066.

Thorn S, Bassler C, Bernhardt-Romermann M, Cadotte M, Heibl C, Schafer H, Seibold S, Muller J (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters 19:163-170.

Durner W, Iden SC (2021) The improved integral suspension pressure method (ISP+) for precise particle size analysis of soil and sedimentary materials. Soil and Tillage Research 213:105086.

Uhler J, Redlich S, Zhang J, Hothorn T, Tobisch C, Ewald J, Thorn S, Seibold S, Mitesser O, Morinière J, Bozicevic V, Benjamin CS, Englmeier J, Fricke U, Ganuza C, Haensel

M, Riebl R, Botero SR, Rummler T, Uphus L, Schmidt S, Steffan-Dewenter I, Müller J (2021) Relationship of insect biomass and richness with land use along a climate gradient. Nature Communications, accepted

Valdés-Correcher E, Moreira X, Augusto L, Barbaro L, Bouget C, Bouriaud O, Branco M, Centenaro G, Csóka G, Damestoy T, Dobrosavljević J, Duduman M-L, Dulaurent A-M, Eötvös CB, Faticov M, Ferrante M, Fürjes-Mikó Á, Galmán A, Gossner MM, Hampe A, Harvey D, Howe AG, Kadiri Y, Kaennel-Dobbertin M, Koricheva J, Kozel A, Kozlov MV, Löveï GL, Lupaştean D, Milanović S, Mrazova A, Opgennoorth L, Pitkänen J-M, Popova A, Popović M, Prinzing A, Queloz V, Roslin T, Sallé A, Sam K, Scherer-Lorenzen M, Schuldt A, Selikhovkin A, Suominen L, Tack AJM, Tahadlova M, Thomas R, Castagneyrol B (2020) Search for top-down and bottom-up drivers of latitudinal trends in insect herbivory in oak trees in Europe. bioRxiv 2020.2002.2025.964213

van der Plas F, Manning P, Allan E, Scherer-Lorenzen M, Verheyen K, Wirth C, Zavala MA, Hector A, Ampoorter E, Baeten L, Barbaro L, Bauhus J, Benavides R, Benneter A, Berthold F, Bonal D, Bouriaud O, Bruelheide H, Bussotti F, Carnol M, Castagneyrol B, Charbonnier Y, Coomes D, Coppi A, Bastias CC, Dawud SM, De Wandeler H, Domisch T, Finer L, Gessler A, Granier A, Grossiord C, Guyot V, Hattenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Jucker T, Koricheva J, Milligan H, Muller S, Muys B, Nguyen D, Pollastrini M, Raulund-Rasmussen K, Selvi F, Stenlid J, Valladares F, Vesterdal L, Zielinski D, Fischer M (2016) Jack-of-all-trades effects drive biodiversity-ecosystem multifunctionality relationships in European forests. Nature Communications 7:11109

Weisser WW, Roscher C, Meyer ST, Ebeling A, Luo GJ, Allan E, Besser H, Barnard RL, Buchmann N, Buscot F, Engels C, Fischer C, Fischer M, Gessler A, Gleixner G, Halle S, Hildebrandt A, Hillebrand H, de Kroon H, Lange M, Leimer S, Le Roux X, Milcu A, Mommer L, Niklaus PA, Oelmann Y, Proulx R, Roy J, Scherber C, Scherer-Lorenzen M, Scheu S, Tscharntke T, Wachendorf M, Wagg C, Weigelt A, Wilcke W, Wirth C, Schulze ED, Schmid B, Eisenhauer N (2017) Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. Basic and Applied Ecology 23:1-73.

Wild J, Kopecky M, Macek M, Sanda M, Jankovec J, Haase T (2019) Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. Agricultural and Forest Meteorology 268:40-47.

Yguel B, Bailey R, Tosh ND, Vialatte A, Vasseur C, Vitrac X, Jean F, Prinzing A (2011) Phytophagy on phylogenetically isolated trees: why hosts should escape their relatives. Ecology Letters 14:1117-1124.

4 Relevance of sex, gender and/or diversity

See Coordination Project

Project Description – Project Proposals

Christian Ammer, Prof. Dr.
University of Göttingen, Burckhardt Institute, Department of Silviculture and Forest Ecology of the Temperate Zones

Dominik Seidel, Dr.
University of Göttingen, Burckhardt Institute, Department of Silviculture and Forest Ecology of the Temperate Zones

Bernhard Schuldt, Prof. Dr.
University of Würzburg, Julius-von-Sachs-Institute of Biological Sciences, Chair of Ecophysiology and Vegetation Ecology

SP1: Forest structure and microclimate

Project Description

1 Starting Point

1.1 State of the art and preliminary work

State of the art

Theory and empirical findings suggest that increasing environmental heterogeneity positively affects biodiversity in both marine and terrestrial ecosystems (e.g. MacArthur and MacArthur 1961, Morse et al. 1985, Hixon and Beets 1993, Chabanet et al. 1997). However, in marine (e.g. Strain et al. 2021) as well as terrestrial ecosystems (e.g. Gazol et al. 2003, Heidrich et al. 2020) relationships were found to be not universally positive. The existence of a generalized environmental-heterogeneity–biodiversity (EH–BD) relationship, with the traditional MacArthurian niche-based hypothesis, is therefore still under debate (Seiferling et al. 2014) and seems to be scale dependent (Schall et al. 2018b). However, for an advancement of our ecological understanding of the relationship between ecosystem structure and its effect on biodiversity, it is fundamental to move from a two-dimensional to a three-dimensional perspective of ecosystem structure (Davies and Asner 2014), since new methods exist that allow to describe the aboveground structure of terrestrial ecosystems quantitatively (Seidel 2018). Considering the three-dimensional structure for example of forests will also increase our understanding of the importance of structural complexity on alpha (within plot) and beta (between plot) biodiversity, since species with different ranges may be differently affected by between-plot structural diversity (e.g. Katayama et al. 2014). For forests, increased β-biodiversity is expected to result from increased structural complexity in the forest landscape (Stein et al. 2014). However, it is not well-known which landscape composition and which gradient of forests with distinctly different structures drive biodiversity most in temperate forest ecosystems. For α-diversity, canopy openness, percentage of certain tree species and tree size (Kebrle et al. 2021) and the amount, diversity and exposition of deadwood (Müller et al. 2015, Seibold et al. 2016) have been identified as main positive drivers of biodiversity across taxa (Penone et al. 2019). It is likely that similar stand structural properties and related microclimatic conditions are important for β-diversity as well, but here their gradients (and not their mean level) drive differences in species assemblages between forest stands (and thus β-diversity).

The unclear role of forest structure for biodiversity has been related to the difficulty in describing the three-dimensional (3D) structure of a forest stand quantitatively. Only recently 3D laser scanning has opened the door for the derivation of quantitative data on forest structures at high resolution and in 3D (Seidel et al. 2011, Newnham et al. 2015, Disney et al. 2019, Calders et al. 2020), including measures of actual structural complexity (Ehbrecht et al. 2017, Seidel 2018, Seidel et al. 2019a, Atkins et al. 2020). As a holistic descriptor of stand structure, the 'structural complexity' is particularly promising to yield new insights since all animals live in a 3D physical habitat (Davies and Asner 2014) and physical determinants of the microclimate are also directly bound to the 3D structure of the vegetation (Parker et al. 2004, Kovacs et al. 2017, Ehbrecht et al. 2017, 2019). Structural complexity may be defined as 'all dimensional, architectural, and distributional patterns of plant individuals and their organs in a given forest space at a given point in time' (Seidel et al. 2021). Two recent measures, the stand structural complexity index (Ehbrecht et al. 2017) and the widely applicable box-dimension (Seidel 2018, 2020) are available from 3D point cloud approaches to quantify the complexity of forests holistically, that is considering all elements in a scanned scene at once, rather than selected plant elements. These new measures offer new possibilities to investigate the structural complexity-microclimate and the structural complexity-biodiversity relationship on stand level. In combination with inventory-based structural metrics this project aims at disentangling the importance of different structural properties of forests for the microclimate which has proven to substantially influence biodiversity (Seibold et al. 2016). However, it is not known whether, and if so, which treatments aimed at increasing structural heterogeneity at the landscape level actually lead to changes in microclimate and subsequent responses in biodiversity. The experimental setup established in this RU offers unique possibilities to address this open question.

Enhancement of Structural Beta Complexity (ESBC) treatments are expected to increase β-diversity since previous studies showed that increasing the horizontal heterogeneity of forests leads to increased species richness of plants, fungi and animals (Hilmers et al. 2018, Heidrich et al. 2020). However, there is limited knowledge to what extent the resulting structural changes alter the microclimate although knowledge of this relationship is crucial for a mechanistic understanding of the effects of forest management measures on biodiversity. Earlier studies detected a strong relationship between the 3D structural heterogeneity and the resulting microclimate (e.g. Ehbrecht et al. 2019), indicating that gaps increase microclimate variability on the landscape scale but reduce microclimatic stability at the patch level. However, not much is known on the effects of ESBC treatments other than gaps or combinations of different degrees of canopy openings and deadwood enrichment on microclimate. Similarly, it is not well known to what degree different ESBC treatments, even if they address different stand compartments, differ in microclimate. Thus, it may be that the net effect on microclimate variability and hence structural heterogeneity is smaller than assumed. For example, reductions in stand density do not lead proportionally to increases in light availability at the forest floor (Hale 2003). In any case, changes in canopy cover and composition are expected to influence forest organisms from the understory via the modulation of maximum temperatures (Zellweger et al. 2019). However, it is controversially discussed whether microclimatic change is the main driver of thermophilization in forest understories (Schall and Heinrichs 2020, Zellweger et al. 2020). Therefore, it is important to study the effects of different forest management practices on local microclimates and its impact on biodiversity (Zellweger et al. 2020).

From an ecological point of view, it is important to quantify which component of microclimate is most strongly influenced by ESBC interventions since different microclimatic variables are influential for both species richness and the composition of given organism groups, highlighting the importance of heterogeneous microclimatic conditions within stands (Tinya et al. 2021). It is thus important to record not only specific microclimatic properties. For example, Thom et al.

(2020) found that deadwood presence and type did not affect forest microclimate significantly. However, in this study light availability, temperature and air humidity were assessed only, but not changes in soil moisture. Lying deadwood, however, should impact the water content of the surrounding soil because of its water retention capacity (Blonska et al. 2018; Klamerus-Iwan et al. 2020), and soil moisture is known to positively affect the number of individual invertebrates (Ferguson & Berube 2004) and its interaction with light is crucial for tree regeneration growth and composition (Ammer et al. 2008, Wagner et al. 2009).

Here we want (i) to quantity the structural changes caused by ESBC interventions, to study (ii) which microclimate properties are influenced by these changes, (iii) how structural complexity after ESBC interventions change over time and (iv) if recently developed indices for structural complexity can be used as proxies for changes in microclimate conditions after ESBC interventions. We thus focus on the structural complexity - microclimate relationship as a stepping-stone for a mechanistic understanding of the relationship between forest structure and its heterogeneity, and biodiversity at the landscape level.

Preliminary work

The three PIs have extensive experience in assessing forest structure quantitatively, in measuring microclimate conditions and in contributing to synthesis work in the relationship of forest structure to biodiversity and ecosystem functioning. Christian Ammer has been working for more than 20 years on the relationship between forest management-induced interventions and resource availability such as increased light and/or soil moisture resulting from microclimate changes (Ammer 1996, Ammer et al. 2008) and their importance for tree regeneration, an important component of stand structure dynamics (Winter et al. 2015, Annighöfer et al. 2015, Stiers et al. 2019, Feldmann et al. 2020). More recently he has contributed to studies investigating the effect of mature tree species composition and forest management on stand structure (Schall et al. 2018a, Juchheim et al. 2020), microclimate (Ehbrecht et al. 2019) and their relationship to biodiversity and ecosystem functions and services (Felipe-Lucia 2018, Penone et al. 2019, Simons et al. 2021). Other recent studies have examined the effect of stand structure to light availability and tree growth (Seidel et al. 2019).

Dominik Seidel has been working on the quantification of tree and forest structure based on three-dimensional laser scanning for over ten years. His key research focus is on the drivers and passengers of structural complexity. He did research targeted towards the development of new indices to measure forest structural complexity (Ehbrecht et al. 2017, Seidel 2018, Willim et al. 2019, Seidel et al. 2020), the relationship between such measures and microclimate (Ehbrecht et al. 2019), the response of trees to environmental conditions (e.g. Dorji et al. 2019, Bebre et al. 2020) and management effects on forest structures (Stiers et al. 2018, Willim et al. 2020). Also, he investigated the effects of tree species diversity on forest structure (Juchheim et al. 2020, Zemp et al. 2019). His recent focus is on the application of fractal analysis on tree and forest structure assessment (Seidel et al. 2019a,b, 2021, Dorji et al. 2021).

Bernhard Schuldt has wide research experience in forest ecology and ecophysiology in temperate and tropical ecosystems. Since his studies, his focus has been on the carbon and water balance of trees driven by biotic and abiotic factors. He has profound knowledge of the installation and maintenance of field-based installations for monitoring microclimatic conditions and tree water use (Horna et al. 2011; Schuldt et al. 2011; Moser et al. 2014; Fuchs et al. 2017; Waite et al. 2019; Link et al. 2020). More recently, he is trying to relate local climatic and edaphic factors at various sites in Northern and Central Germany to tree physiological attributes with close relatedness to patterns of drought-induced tree mortality (Schuldt et al. 2016; Fuchs et al. 2021a,b; Weithmann et al., unpublished). So far, however, intra-specific trait variability in these physiological measurements does not seem suited to explain patterns of small-scale heterogeneity in tree vitality after the 2018/19 drought. Instead, local heterogeneity in soil properties and tree neighbourhood composition most likely predispose given individuals to drought damages, which is being investigated in his most recent DFG-funded joint project.

Preliminary work directly related to this RU involves a series of measurements that were already conducted on some of the study sites. In order to record the initial state of the stands before the ESBC treatments had started, we used terrestrial laser-scanning to quantify the stand structure of 60 patches of the University Forest (Region 1) in winter 2017/18 (no-leaves) and summer 2018 (leaves-on). We also conducted post-treatment scans on these 60 patches in region 1 as well as on the 30 control patches (total of 90 patches) in winter 2018/19, winter 2019/20, summer 2020 and summer 2021. In spring 2019, all 90 patches in region 1 were inventoried by registering the coordinates, size and species of all trees larger than 7 cm at breast height. During the vegetation period in 2019 a fence each (6 m x 6 m) was established in the centre of each of the 90 patches to protect the regeneration from predation. On 75 patches tree regeneration was recorded inside and outside fences on subplots 4 m^2 in size. Tree seedlings (> 1 year) and saplings of all tree species were recorded in height classes of 0 cm to 20 cm, 21 cm to 50 cm, 51 cm to 130 cm and >130 cm. Browsing damage was registered if the leader shoot was affected.

We found that the conducted ESBC treatments resulted in significant changes in the structure of the sites and can hence be considered successful. Treated patches (in this preliminary analysis not grouped based on the treatment layout (aggregated & distributed) showed an increase in canopy openness from 2018 to 2020 in all treatments (on average: 20% ± 14% SD), while in the control patches canopy openness dropped by 7%. Understory complexity remained steady in the control (+0.02 units) but increased in the treatments (0.5 to 1.4 units, depending on treatment). Overall stand structural complexity (considering all vertical layers) could also be increased with the initial treatments, most notably with the treatment that left standing and lying deadwood on site. This treatment resulted in an increase of structural complexity that exceeded the natural increment (control) between 2018 and 2020 by 97%.

Moreover, we found no differences neither in tree regeneration density nor in diversity of tree regeneration between distributed and aggregated ESBC treatments (for treatments please see Coordination Project) and between the situation inside and outside the fences (Fig. 1). All changes of tree species composition in the regeneration layer to be observed in the up-comings years can thus be traced back to the ESBC treatments and fencing.

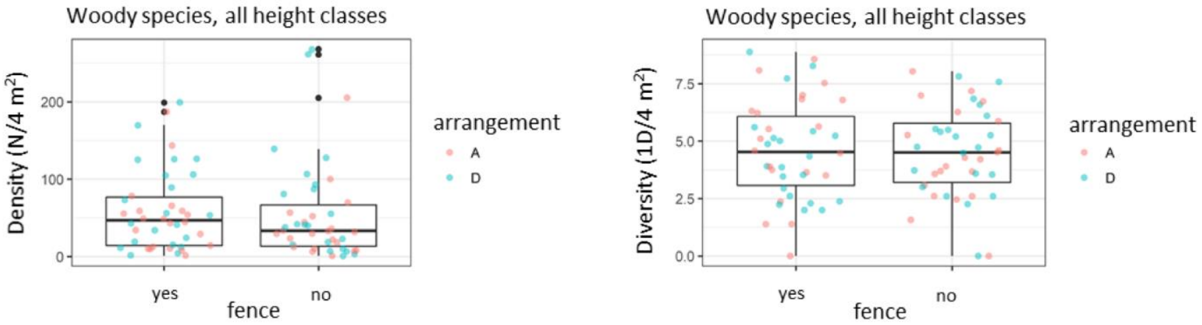


Fig. 1: Tree regeneration density (left) and diversity (right) on 75 patches at the University forest. Blue dots correspond to ESBC interventions resulting in distributed resources and more homogenous canopy openings while red dots correspond to aggregated attributes and resources (Honecker 2021, unpublished).

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. **Ammer C**, Stimm B, Mosandl R (2008) Ontogenetic variation in the relative influence of light and belowground resources on European beech seedling growth. Tree physiology 28: 721-728
2. Dorji Y, **Schuldt B**, Neudam L, Dorji R, Middleby K, Isasa E, Körber K, **Ammer C**, Annighöfer, P, **Seidel D** (2021) New insights into tree architecture from mobile laser scanning and geometry analysis. Trees - Structure and Function 35: 1385-1398.
3. Ehbrecht M, Schall P, **Ammer C**, **Seidel D** (2017) Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agricultural and Forest Meteorology 242: 1-9.
4. Glatthorn J, Annighöfer P, Balkenhol N, Leuschner C, Polle A, Scheu S, Schuldt A, **Schuldt B**, **Ammer C** (2021) An interdisciplinary framework to describe and evaluate the functioning of forest ecosystems. Basic and Applied Ecology 52: 1–14.
5. Schall P, Schulze E-D, Fischer M, Ayasse M, **Ammer C** (2018) Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology 32: 39-52.
6. Link RM, Fuchs S, Arias Aguilar D, Leuschner C, Castillo Ugalde M, Valverde Otarola JC, **Schuldt B** (2020) Tree height predicts the shape of radial sap flow profiles of Costa-Rican tropical dry forest tree species. Agricultural and Forest Meteorology 287: 107913.
7. **Schuldt B**, Leuschner C, Horna V, Moser G, Köhler M, van Straaten O, Barus H (2011) Change in hydraulic properties and leaf traits in a tall rainforest tree species subjected to long-term throughfall exclusion in the perhumid tropics. Biogeosciences 8: 2179–2194.
8. **Seidel D** (2018) A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis. Ecology and Evolution 8: 128–134.
9. **Seidel D**, Ehbrecht M, Annighöfer P, **Ammer C** (2019a) From tree to stand-level structural complexity- a case study from a temperate broad-leaved forest. Agricultural and Forest Meteorology 278: 107699.
10. **Seidel D**, Annighöfer P, Stiers M, Zemp CD, Burkardt K, Ehbrecht M, Willim K, Kreft H, Hölscher D, **Ammer C** (2019b) How a measure of structural complexity relates to architectural benefit-to-cost ratio, light availability and growth of trees. Ecology and Evolution 9: 7134-7142.

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.1.1 Patents

Not applicable

1.1.1.1 Pending

Not applicable

1.1.1.2 Issued

Not applicable

2 Objectives and work program

2.1 Anticipated total duration of the project

48 months.

2.2 Objectives

Overall, this subproject aims at quantifying (i) the change of stand structure and structural properties over time that have been induced by the ESBC treatments, including the establishment, growth and composition of natural regeneration. The forest structural measures serve as important co-factors for explaining the biodiversity patterns explored in the other subprojects of the RU. In dissimilarity modelling of β-diversity, distance matrices of forest structural measures replace the 15-factorial setup of the ESBC experiment. In this SP, we will further (ii) examine to what extent the diversity of stand structures on the landscape level can explain variation in complex spatial microclimate and (iii) whether measures of structural complexity could serve as proxies for microclimate attributes when it comes to explain β-diversity. In phase 2, the repeated inventory of all trees on all patches will (iv) provide above ground biomass productivity data for the quantification of multi-functionality in SP 9 (see **Data exchange and collaboration** below).

Besides providing essential data for the mechanistic understanding of β-diversity on the landscape level, we aim at testing the following three hypotheses within SP 1:

Hypothesis 1: *ESBC treatments significantly change forest structure and microclimate conditions leading to an increase of structural and microclimate heterogeneity on the landscape level but the differences between control plots and treated patches decline over time resulting in a constant decline of structural and microclimate heterogeneity.*

Our preliminary data show that ESBC treatments have clearly the potential to alter forest structure which should also affect microclimate. However, due to canopy closure by edge trees clearly structural heterogeneity of the mature stand may decline and so probably does microclimate variation.

Hypothesis 2: *Structural complexity and microclimate conditions are more strongly altered by aggregated spatial arrangements of canopy openings and deadwood when compared to distributed arrangement.*

We assume that patches with canopy gaps and aggregated deadwood differ more from the control (untreated stands) than those of the distributed arrangements, a result which we assume is due to the extinction coefficient in the formula of Beer-Lambert, describing the attenuation of light as it passes through the crown. We expect similar effects for soil moisture due to differences in interception.

Hypothesis 3: *Tree regeneration development increasingly buffers microclimate variation. This effect is delayed outside fences.*

Growth of seedlings and saplings increasingly absorb light and take up water which may lead to buffered microclimatic conditions at the forest floor. As a result, we expect a trend towards reduced microclimate variation with developing regeneration even though the regeneration layer may contribute to increased heterogeneity of structural complexity (Fig. 2). Heavy browsing may delay or even prevent this process.

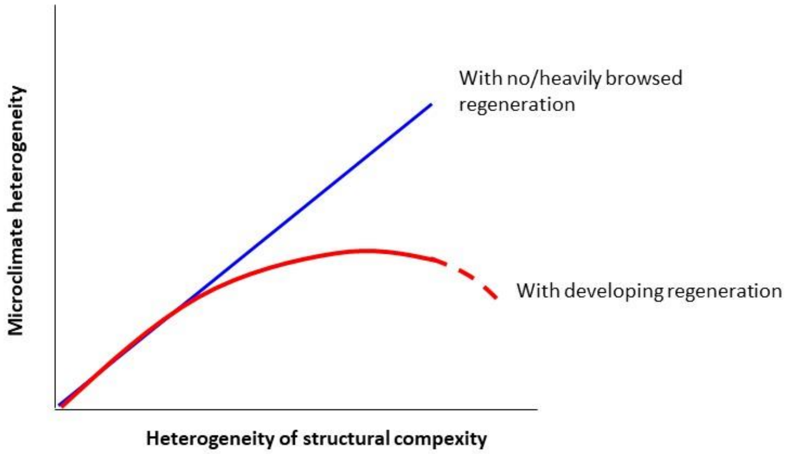


Fig. 2: Assumed relationship between heterogeneity of structural complexity and microclimate heterogeneity with (red line) and without (blue line) developing tree regeneration.

Data exchange and collaboration within the consortium

All subprojects of the RU will be provided with data on forest structure and its effect on the microclimate. All subprojects recording biodiversity data such as SP 2 (diversities of saproxylic beetles, their microbial symbionts and volatile organic compounds), SP 4 (soil biodiversity), SP 5 (macrofauna detrivores), SP 6 (plant-animal interactions), SP 7 (deadwood related microbial diversity), SP 8 (diversity of ground vegetation) and SP 9 (aboveground animal diversity) may use these data for explaining β-diversity of the respective taxonomic groups. With SP 8, we will join forces to investigate forest structure-herby layer diversity relationship as well as overstory - herb layer relations. A close cooperation is also planned with SP 3 with regard to conventional remote sensing measures that describe structure and vitality of the patches. This includes both, passive sensor data (imagery, hyperspectral data with standard products) as well as active sensor data like airborne LiDAR. Aboveground biomass productivity data for the quantification of multi-functionality will be provided for SP 9 in the second phase.

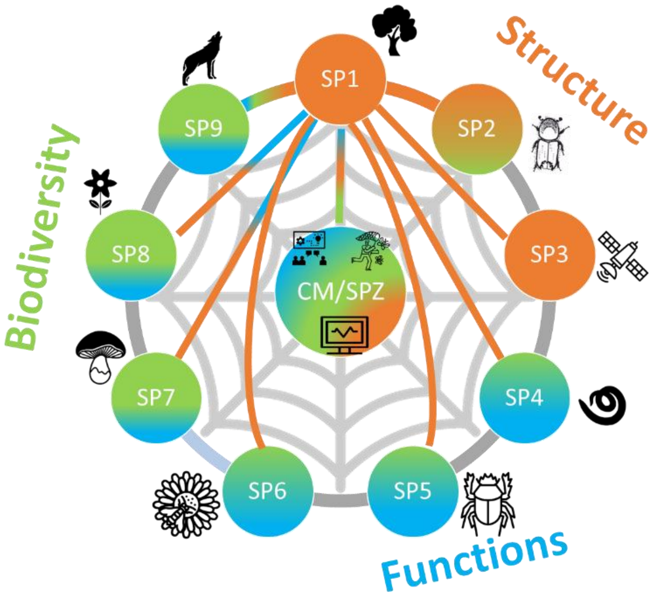


Fig. 2: Cooperation of SP1 with all other subprojects.

2.3 Work program including proposed research methods

The postdoc to be hired for SP 1 (‘*forestry postdoc*’, 50%) is also responsible for several tasks in SP Z (50%). These tasks include the regular exchange with the landowners and focus on analyses of the effects of forest management on structure, biodiversity and ecosystem functions and complement perfectly the SP 1 work program, which provides the structural data.

2.3.1 Work package 1: Assessment of tree regeneration

Tree regeneration will be recorded on all intensive sites (90 patches). This includes an inventory (repeated on 75 patches) of seedlings (< 1 year) and saplings inside (6 x 6 m) and outside the fences on subplots of 4 m^2 in size. For each individual tree species and tree height (in classes of 0 cm to 20 cm, 21 cm to 50 cm, 51 cm to 130 cm and >130 cm) will be determined. Browsing damage will be registered if the leader shoot is affected. For the 75 patches with repeated measurements changes of tree species composition and biomass productivity by using species specific allometric equations according to Annighöfer et al. (2016) will be calculated.

2.3.2 Work package 2: 3D laser scanning

First, we plan to continue the intensive measurements of structural dynamics in response to the ESBC treatments on all 60 patches in region 1 as well as on the 30 control patches in the same region (= 90 patches). We will therefore scan each patch every year (leaf-on in 2022, 2023, 2024, 2025) using terrestrial laser scanning in single scan mode as during the preliminary work. From this data we will derive canopy openness (Zheng et al. 2013), the structural complexity index (SSCI; Ehbrecht et al. 2021) and the understory complexity index (UCI; Willim et al. 2019, Seidel et al. 2021) to complete the monitoring of the structural dynamics. By doing so, we are able to characterize changes in the overstory (openness), understory (UCI) and overall forest structural complexity (SSCI) with high temporal resolution and for a total of seven years (three years finished, four years planned in this phase). We will investigate, which ESBC treatment altered the above mentioned (and additional) structural aspects of the patches the most (before vs. after), which treatment results in the longest time to recover from the artificial disturbance (recovery to before treatment complexity (negative recovery), to before treatment canopy openness and to before treatment understory complexity, and we will measure the effects of each treatment on the microclimate in the patches.

The same scans will be conducted on all 98 patches in the other climatic regions (region 2 to 6; Bohemian Forest, Saarland, Hunsrück (2), Lübeck) during summer condition to derive the same measures as for region 1 (canopy openness, understory complexity and overall complexity). All these 3D scans will be single-scan terrestrial (tripod-based) measurements that can be acquired efficiently (<3 m per patch) and provide a sound basis for comparison of the structures on all study patches of the RU, an important information for all SPs. The measurements will be conducted once on these sites.

However, in order to provide spatially explicit and detailed structural data for establishing the link between structure and microclimate, we will additionally scan each patch entirely using a mobile hand-held laser scanner (GeoSlam ZEB Horizon, GeoSlam, UK). The resulting 3D point clouds (see Fig. 3) provide a full 3D representation of the scanned scene, without occlusion effects that naturally occur in the single-scan approach. Therefore, they are more suitable to relate observed microclimatic conditions and their spatially pattern (see next WP) to the 3D structural pattern of the forest patches.

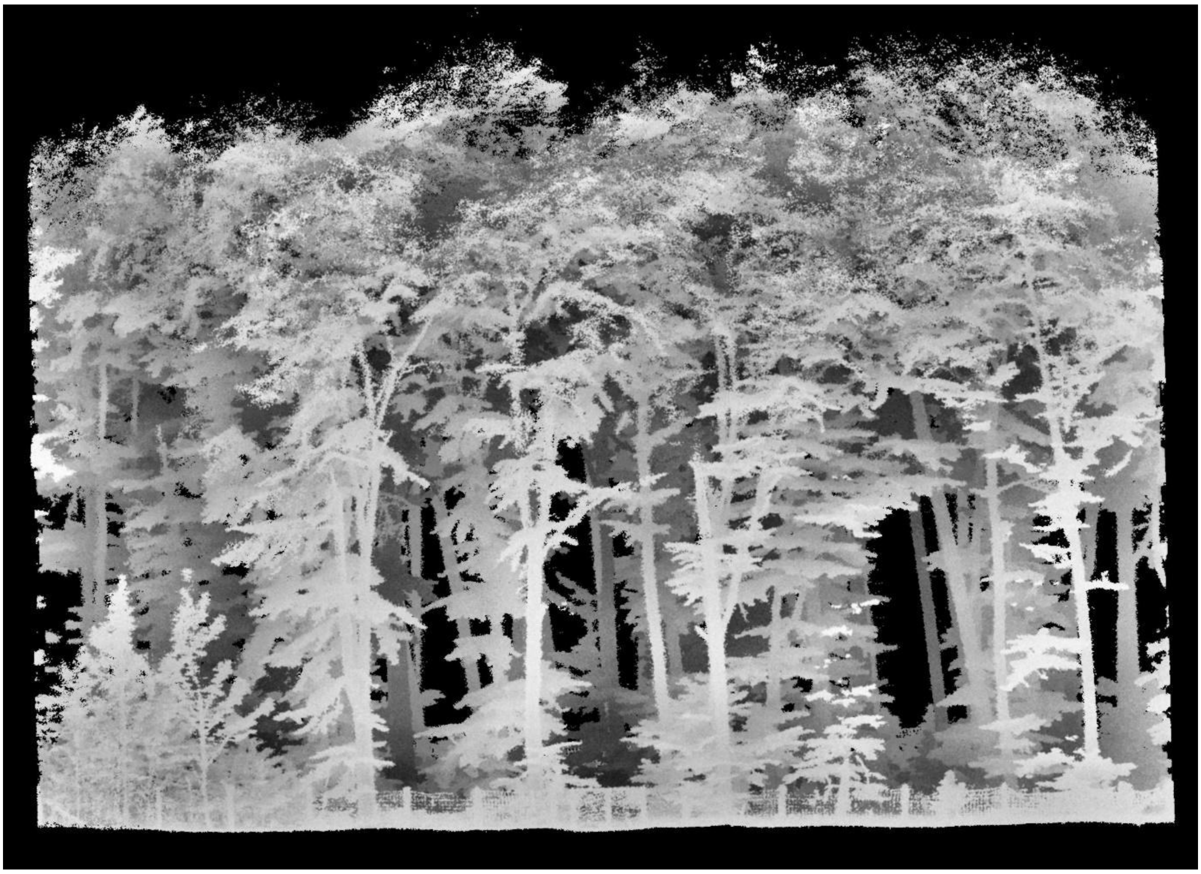


Fig. 3: Exemplary point cloud of a forest stand obtained from mobile laser scanning through a 10 min walk-through with the hand-held ZEB Horizon scanner.

All scan data will be post-process using either Faro Scene (Faro Technologies Inc., Lake Marry, USA) for the tripod-based scans or GeoSlam Hub (GeoSlam Ltd., UK) in order to remove erroneous data points (filtering) and for spatial coregistration (mobile scans) using the simultaneous localization and mapping (SLAM) algorithm provided in the GeoSlam software. Afterwards the scans are transformed into ASCII-files (.xyz) that represent the scanned scenes as 3D point clouds for further calculation of the structural measures mentioned above.

2.3.3 Work package 3: Structural heterogeneity and microclimate

For characterizing the effect of structural heterogeneity on spatial microclimatic conditions and its relatedness to biodiversity patterns, high-resolution soil moisture measurements will be supported by vertical profiles of air temperature (T) and air humidity (RH), annually in a subset of 15 patches. In 2022, a subset of five treatments (AW, DW, AS, DS, CC; for abbreviations see Fig. 12 of the Coordination Project) will be instrumented at each study site in the University Forest (site 1, 2 and 3; for details, please refer to SPZ Fig. 1). In 2023, three sites in the Bohemian Forest (site 4, 6, 8) will be monitored, and in 2024, the sites in Saarland (site 9), Hunsrück (site 10) and Lübeck (site 11) will be equipped. With this design, we are able to compare each two aggregated and two distributed treatments with the control patch across all regions at the landscape level. Per year, six weeks of field work are estimated for installation, maintenance and removal of the sensors.

Within each patch of 50 x 50 m, we will restrict our micro-climatic measurements to an inner circle with 30 m in diameter. In order to cover its entire ground area in equal distance to each other, 19 virtual circles of 6 m diameter will be integrated. In the centre of each of these virtual circles, one combined soil moisture and soil and air temperature sensor (TMS-4, Tomst, Czech Republic) will be installed, yielding 15 × 19 = 285 sensors in total. In case the identified centre of a circle is occupied by trees or stems, the sensor will be installed nearby, but leaving at least 1 m distance to the tree/stem. The TMS-4 sensors are based on the time transmission method (Wild et al. 2019). A recent sensor comparison study, however, has revealed a given discrepancy between the TMS-4 sensor and well-established and highly reliable time domain reflectometry sensors (Jackisch et al. 2020). Therefore, undisturbed soil samples will be collected in the field, and a laboratory comparison performed between the TMS-4 sensor (Tomst, Czech Republic) and a Trime Pico32 soil moisture sensor (Imko, Germany). The undisturbed soil samples will be watered until field capacity, and afterwards dried out in a climate chamber while logging the weight of the samples with a high-precision scale (PFB 6000-2, Kern, Germany). Scale and sensors will be connected to a CR1000X data logger (Campbell Scientific, Utah, US), and nine soil blocks will be measured in parallel. Sample collection in the field and laboratory measurements will be performed by a student assistant at JMU, supervised by the Postdoc.

In order to quantify the potential increase in physiological stress due to high evaporative demand, vertical profiles of air temperature (T) and air humidity (RH) will be measured at three height levels at the southern edge (low stress), centre and northern edge (high stress) of the 15 patches, yielding 15 × 3 × 3 = 135 T/RH-Sensors (Hobo MX2301A, BMC Solutions, Germany). Professional tree climbers will support the installation of robes spanning across the patch, for which one week of field work is estimated per year. These high-resolution measurements on a subset of patches will support the basic measurements provided by SP Z.

Based on our detailed description of the spatial pattern of microclimatic variables and their known position in the 3D scan data, we are able to investigate the relationship between structure and the microclimate. Since the microclimate is a result of the present structures but structures, e.g. increased understory complexity, may also be a result of microclimatic conditions (for example due to canopy openings), we will carefully examine the relationships and use theory to propose certain directionalities (dependent vs. independent variable). Subsequently, our data on spatial complexity and high-resolution microclimatic measurements, which are characterized on a subset of patches in all regions (n = 45), will be related to the basic measurements provided by SP Z in order to provide more complex information on microclimatic conditions for each single patch. To do so, we will make use of the fact that all patches in all regions are scanned.

2.3.4 Work package 4: Analyses and drafting manuscripts

The analysis comprises the statistical evaluation of all data within SP 1 along the three main hypotheses listed above, data preparation and contribution to the synthesis in SP Z together with the other postdoctoral researcher in SP Z (Fig. 4). Another important task within this work package is the preparation of scientific manuscripts to be published in well-recognized journals.

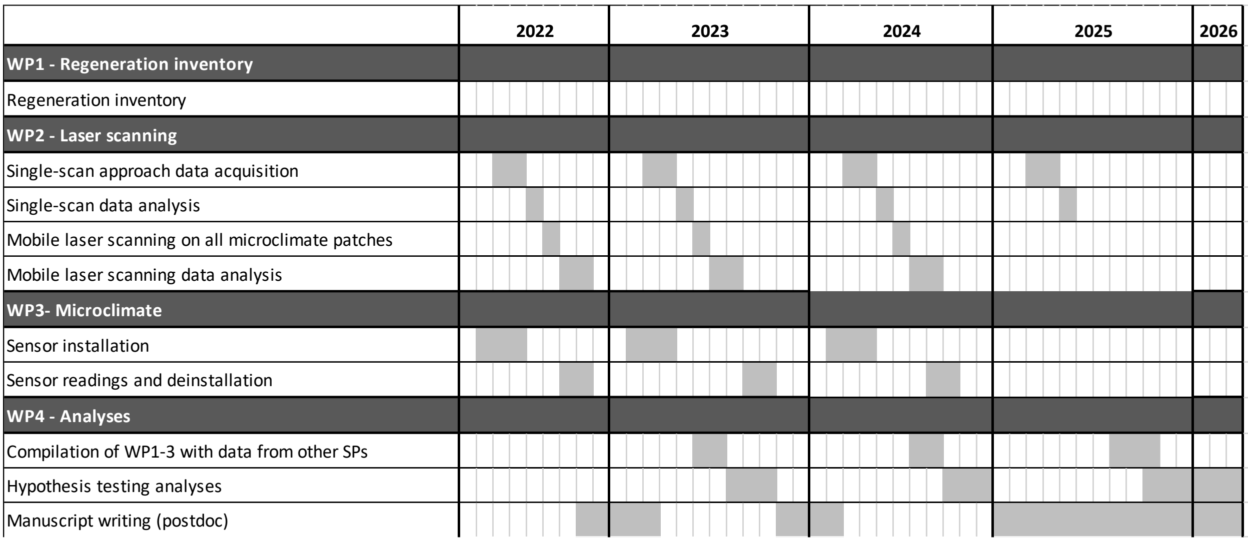


Fig. 4: Gantt chart of the timeline of the proposed project.

3 Bibliography concerning the state of the art, the research objectives, and the work program

Ammer C (1996) Konkurrenz um Licht. Zur Entwicklung der Naturverjüngung im Bergmischwald. Forstliche Forschungsberichte München Nr. 158. 198 pp

Ammer C, Stimm B, Mosandl R (2008) Ontogenetic variation in the relative influence of light and belowground resources on European beech seedling growth. Tree physiology 28: 721-728.

Annighöfer P, Ameztegui A, Ammer C, Balandier P, Bartsch N, Bolte N, Coll L, Collet C, Ewald J, Frischbier N, Gebereyesus F, Haase J, Hamm T, Hirschfelder B, Huth F, Kändler G, Kahl A, Kawaletz H, Kuehne C, Lacointe A, Lin N, Löf M, Malagoli P, Marquier A, Müller S, Promberger S, Provendier D, Röhle H, Sathornkich J, Schall P, Scherer-Lorenzen M, Schröder J, Seele C, Weidig J, Wirth C, Wolf H, Wollerstädt J, Mund M (2016) Species-specific and generic biomass equations for seedlings and saplings of European tree species. European Journal of Forest Research 135: 313-329.

Annighöfer P, Beckschäfer P, Vor T, Ammer C (2015) Regeneration patterns of European oak species (*Quercus petraea* (Matt.) Liebl., *Quercus robur* L.) in dependence of environment and neighborhood. PLoS ONE 10: e0134935.

Atkins JW, Bohrer G, Fahey RT, Hardiman BS, Morin TH, Stovall AEL, Zimmerman N, Gough CM (2018) Quantifying vegetation and canopy structural complexity from terrestrial LIDAR data using the forestr r package. Methods in Ecology and Evolution 9: 2057–2066.

Bebre I, Annighöfer P, Ammer C, Seidel D (2020) Growth, morphology, and biomass allocation of recently planted seedlings of seven European tree species along a light gradient. iForest - Biogeosciences and Forestry 13: 261–269.

Błońska E, Klamerus-Iwan A, Łagan S, Lasota J (2018) Changes to the water repellency and storage of different species of deadwood based on decomposition rate in a temperate climate. Ecohydrology 11: e2023.

Calders K, Adams J, Armston J, Bartholomeus H, Bauwens S, Bentley LP, Chave J, Danson FM, Demol M, Disney M, et al. (2020) Terrestrial laser scanning in forest ecology: Expanding the horizon. Remote Sensing of Environment 251: 112102.

Chabanet P, Ralambondrainy H, Amanieu M, Faure G, Galzin R (1997) Relationships between coral reef substrata and fish. Coral Reefs 16: 93–102.

Davies AB, Asner GP (2014) Advances in animal ecology from 3D-LiDAR ecosystem mapping. Trends in Ecology & Evolution 29: 681-691.

Disney M (2019) Terrestrial Li DAR: a three-dimensional revolution in how we look at trees. New Phytologist 222: 1736-1741.

Dorji Y, Annighöfer P, Ammer C, Seidel D (2019) Response of Beech (Fagus sylvatica L.) Trees to Competition—New Insights from Using Fractal Analysis. Remote Sensing 11: 2656.

Dorji Y, Schuldt B, Neudam L, Dorji R, Middleby K, Isasa E, Körber K, Ammer C, Annighöfer P, Seidel D (2021) Three-dimensional quantification of tree architecture from mobile laser scanning and geometry analysis. Trees 35: 1385–1398.

Ehbrecht M, Schall P Ammer C, Seidel D (2017) Quantifying stand structural complexity and its relationship with forest management, tree species diversity and microclimate. Agricultural and Forest Meteorology 242: 1-9.

Ehbrecht M, Schall P, Ammer C, Seidel D (2019) Effects of structural heterogeneity on the diurnal temperature range in temperate forest ecosystems. Forest Ecology and Management 432: 860-867.

Ehbrecht M, Seidel D, Annighöfer P, Kreft H, Köhler M, Zemp DC, Puettmann K, Nilus R, Babweteera F, Willim K, Stiers M, Soto D, Boehmer HJ, Fisichelli N, Burnett M, Juday G, Stephens S, Ammer C (2021) Global patterns and climatic controls of forest structural complexity. Nature Communications 12: 519.

Feldmann E, Glatthorn J, Ammer C, Leuschner C (2020) Regeneration dynamics following the formation of understory gaps in a Slovakian beech virgin forest. Forests 11: 585.

Felipe-Lucia MR, Soliveres S, Penone C, Manning P, van der Plas F, Boch S, Prati D, Ammer C, Schall P, Gossner MM, et al. (2018) Multiple forest attributes underpin the supply of multiple ecosystem services. Nature Communications 9: 4839.

Ferguson SH, Berube DKA (2004) Invertebrate Diversity under Artificial Cover in Relation to Boreal Forest Habitat Characteristics. The Canadian Field-Naturalist 118:386.

Fuchs S, Leuschner C, Link R, Coners H, Schuldt B (2017) Calibration and comparison of thermal dissipation, heat ratio and heat field deformation sap flow probes for diffuse-porous trees. Agricultural and Forest Meteorology 244–245: 151–161.

Fuchs S, Leuschner C, Link RM, Schuldt B (2021a) Hydraulic variability of three temperate broadleaf tree species along a water availability gradient in central Europe. New Phytologist 231: 1387–1400.

Fuchs S, Schuldt B, Leuschner C (2021b) Identification of drought-tolerant tree species through climate sensitivity analysis of radial growth in Central European mixed broadleaf forests. Forest Ecology and Management 494: 119287.

Gazol A, Tamme R, Price JN, Hiiesalu I, Laanisto L, Pärtel M (2013) A negative heterogeneity–diversity relationship found in experimental grassland communities. Oecologia, 173: 545-555.

Hale SE (2003) The effect of thinning intensity on the below-canopy light environment in a Sitka spruce plantation. Forest Ecology and Management, 179: 341-349.

Heidrich L, Bae S, Levick S, Seibold S, Weisser W, Krzystek P, Magdon P, Nauss T, Schall P, Serebryanyk A, et al. (2020) Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. Nature Ecology & Evolution 4: 1204–1212.

Hilmers T, Friess N, Bässler C, Heurich M, Brandl R, Pretzsch H, Seidl R, Müller J (2018) Biodiversity along temperate forest succession. Journal of Applied Ecology 55: 2756–2766.

Hixon MA, Beets JP (1993) Predation, prey refuges, and the structure of coral-reef fish assemblages. Ecological Monographs 63: 77-101.

Horna V, Schuldt B, Brix S, Leuschner C (2011) Environment and tree size controlling stem sap flux in a perhumid tropical forest of Central Sulawesi, Indonesia. Annals of Forest Science 68: 1027–1038.

Jackisch C, Germer K, Graeff T, Andrä I, Schulz K, Schiedung M, Haller-Jans J, Schneider J, Jaquemotte J, Helmer P, et al. (2020) Soil moisture and matric potential – an open field comparison of sensor systems. Earth System Science Data 12: 683–697.

Juchheim J, Ehbrecht M, Schall P, Ammer C, Seidel D (2019) Effect of tree species mixing on stand structural complexity. Forestry: An International Journal of Forest Research 93: 75–83.

Katayama N, Amano T, Naoe S, Yamakita T, Komatsu I, Takagawa S, Sato N, Ueta M, Miyashita T (2014) Landscape Heterogeneity–Biodiversity Relationship: Effect of Range Size. PLoS ONE 9: e93359.

Kebrle D, Zasadil P, Hošek J, Barták V, Šťastný K (2021) Large trees as a key factor for bird diversity in spruce-dominated production forests: Implications for conservation management. Forest Ecology and Management 496: 119460.

Klamerus-Iwan A, Lasota J, Błońska E (2020) Interspecific Variability of Water Storage Capacity and Absorbability of Deadwood. Forests 11:575.

Kovács B, Tinya F, Ódor P (2017) Stand structural drivers of microclimate in mature temperate mixed forests. Agricultural and Forest Meteorology 234: 11-21.

Link RM, Fuchs S, Arias Aguilar D, Leuschner C, Castillo Ugalde M, Valverde Otarola JC, Schuldt B (2020) Tree height predicts the shape of radial sap flow profiles of Costa-Rican tropical dry forest tree species. Agricultural and Forest Meteorology 287: 107913.

MacArthur RH, MacArthur JW (1961) On bird species diversity. Ecology: 42: 594-598.

Morse DR, Lawton JH, Dodson MM, Williamson MH (1985) Fractal dimension of vegetation and the distribution of arthropod body lengths. Nature 314: 731-733.

Moser G, Schuldt B, Hertel D, Horna V, Coners H, Barus H, Leuschner C (2014) Replicated throughfall exclusion experiment in an Indonesian perhumid rainforest: wood production, litter fall and fine root growth under simulated drought. Global Change Biology 20: 1481–1497.

Müller J, Brustel H, Brin A, Bussler H, Bouget C, Obermaier E, Heidinger IMM, Lachat T, Förster B, Horak J, et al. (2015) Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. Ecography 38: 499–509.

Newnham GJ, Armston JD, Calders K, Disney MI, Lovell JL, Schaaf CB, Strahler AH, Danson FM. (2015) Terrestrial Laser Scanning for Plot-Scale Forest Measurement. Current Forestry Reports 1: 239–251.

Parker GG, Harmon ME, Lefsky MA, Chen J, Pelt R V, Weis SB, Thomas SC, Winner WE, Shaw DC, Frankling JF. (2004) Three-dimensional Structure of an Old-growth Pseudotsuga-Tsuga Canopy and Its Implications for Radiation Balance, Microclimate, and Gas Exchange. Ecosystems 7: 440–453.

Penone C, Allan E, Soliveres S, Felipe-Lucia MR, Gossner MM, Seibold S, Simons NK, Schall P, Plas F, Manning P, et al. (2019) Specialisation and diversity of multiple trophic groups are promoted by different forest features. Ecology Letters 22: 170–180.

Schall P, Gossner MM, Heinrichs S, Fischer M, Boch S, Prati D, Jung K, Baumgartner V, Blaser S, Böhm S, et al. (2018a) The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. Journal of Applied Ecology 55: 267–278.

Schall P, Schulze E-D, Fischer M, Ayasse M, Ammer C (2018b) Relations between forest management, stand structure and productivity across different types of Central European forests. Basic and Applied Ecology 32: 39–52.

Schall P, Heinrichs S (2020) Comment on “Forest microclimate dynamics drive plant responses to warming”. Science 370: 6522.

Schuldt B, Leuschner C, Horna V, Moser G, Köhler M, van Straaten O, Barus H (2011) Change in hydraulic properties and leaf traits in a tall rainforest tree species subjected to long-term throughfall exclusion in the perhumid tropics. Biogeosciences 8: 2179–2194.

Schuldt B, Knutzen F, Delzon S, Jansen S, Müller-Haubold H, Burlett R, Clough Y, Leuschner C (2016) How adaptable is the hydraulic system of European beech in the face of climate change-related precipitation reduction? New Phytologist 210: 443–458.

Seibold S, Bässler C, Brandl R, Büche B, Szallies A, Thorn S, Ulyshen MD, Müller J. (2016) Microclimate and habitat heterogeneity as the major drivers of beetle diversity in dead wood. Journal of Applied Ecology 53: 934–943.

Seidel D, Fleck S, Leuschner C, Hammett T (2011) Review of ground-based methods to measure the distribution of biomass in forest canopies. Annals of Forest Science 68: 225-244.

Seidel D (2018) A holistic approach to determine tree structural complexity based on laser scanning data and fractal analysis. Ecology and Evolution 8: 128–134.

Seidel D, Ehbrecht M, Annighöfer P, Ammer C (2019a) From tree to stand-level structural complexity- a case study from a temperate broad-leaved forest. Agricultural and Forest Meteorology 278: 107699.

Seidel D, Annighöfer P, Stiers M, Zemp CD, Burkardt K, Ehbrecht M, Willim K, Kreft H, Hölscher D, Ammer C (2019) How a measure of structural complexity relates to architectural benefit-to-cost ratio, light availability and growth of trees. Ecology and Evolution 9 (12): 7134-7142.

Seidel D, Annighöfer P, Ehbrecht M, Magdon P, Wöllauer S, Ammer C (2020) Deriving stand structural complexity from airborne laser scanning data- what does it tell us about a forest? Remote Sensing 12: 1854.

Seidel D, Soto DP, Annighöfer PJ, Ehbrecht M, Willim K, Ammer C (2021) Drivers of shrublayer complexity in absence of management. Remote Sensing 13: 1513.

Seiferling I, Proulx R, Wirth C (2014) Disentangling the environmental-heterogeneity–species-diversity relationship along a gradient of human footprint. Ecology 95: 2084-2095.

Simons NK, Felipe-Lucia MR, Schall P, Ammer C, Bauhus J, Blüthgen N, Boch S, Buscot F, Fischer M, Goldmann K, Gossner MM, Hänsel H, Jung K, Manning P, Nauss T, Oelmann Y, Pena R, Polle A, Renner SC, Schloter M, Schöning I, Schulze E-D, Solly EF, Sorkau E, Stempfhuber B, Wubet T, Müller J, Seibold S, Weisser WW (2021) National Forest Inventories capture the multifunctionality of managed forests in Germany. Forest Ecosystems 8: 5.

Stein A, Gerstner K, Kreft H (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology letters 17: 866-880.

Stiers M, Willim K, Seidel D, Ehbrecht M, Kabal M, Ammer C, Annighöfer P (2018) A quantitative comparison of the structural complexity of managed, lately unmanaged and primary European beech (Fagus sylvatica L.) forests. Forest Ecology and Management 430: 357–365.

Stiers M, Willim K, Seidel D, Ammer C, Kabal M, Stillhard J, Annighöfer P (2019) Analyzing spatial distribution patterns of European beech (Fagus sylvatica L.) regeneration in dependence of canopy openings. Forests 10: 637.

Strain EMA, Steinberg PD, Vozzo M, Johnston EL, Abbiati M, Aguilera MA, Airoldi L, Aguirre JD, Ashton G, Bernardi M, et al. (2021) A global analysis of complexity–biodiversity relationships on marine artificial structures. Global Ecology and Biogeography 30: 140–153.

Thom D, Sommerfeld A, Sebald J, Hagge J, Müller J, Seidl R. (2020) Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agricultural and Forest Meteorology 291: 108066.

Tinya F, Kovács B, Bidló A, Dima B, Király I, Kutszegi G, Lakatos F, Mag Z, Márialigeti S, Nascimbene J, et al. (2021) Environmental drivers of forest biodiversity in temperate mixed forests – A multi-taxon approach. Science of The Total Environment 795: 148720.

Wagner S, Madsen P, Ammer C (2009) Evaluation of different approaches for modelling individual tree seedling height growth. Trees 23: 701–715.

Waite P-A, Schuldt B, Mathias Link R, Breidenbach N, Triadiati T, Hennings N, Saad A, Leuschner C (2019) Soil moisture regime and palm height influence embolism resistance in oil palm (F Meinzer, Ed.). Tree Physiology 39: 1696–1712.

Wild J, Kopecký M, Macek M, Šanda M, Jankovec J, Haase T (2019) Climate at ecologically relevant scales: A new temperature and soil moisture logger for long-term microclimate measurement. Agricultural and Forest Meteorology 268: 40–47.

Willim K, Stiers M, Annighöfer P, Ammer C, Ehbrecht M, Kabal M, Stillhard J, Seidel D (2019) Assessing Understory Complexity in Beech-dominated Forests (Fagus sylvatica L.) in Central Europe—From Managed to Primary Forests. Sensors 19: 1684.

Willim K, Stiers M, Annighöfer P, Ehbrecht M, Ammer C, Seidel D (2020) Spatial Patterns of Structural Complexity in Differently Managed and Unmanaged Beech-Dominated Forests in Central Europe. Remote Sensing 12: 1907.

Winter MB, Baier R, Ammer C (2015) Regeneration dynamics and resilience of unmanaged mountain forests in the Northern Limestone Alps following bark beetle induced spruce dieback. European Journal of Forest Research 134: 949-968

Zellweger F, Coomes D, Lenoir J, Depauw L, Maes SL, Wulf M, Kirby KJ, Brunet J, Kopecký M, Máliš F, et al. (2019) Seasonal drivers of understorey temperature buffering in temperate deciduous forests across Europe. Global Ecology and Biogeography 28: 1774–1786.

Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, Baeten L, Hédl R, Berki I, Brunet J, et al. (2020) Response to Comment on "Forest microclimate dynamics drive plant responses to warming". Science 370: eabf2939.

Zemp DC, Ehbrecht M, Seidel D, Ammer C, Craven D, Erkelenz J, Irawan B, Sundawati L, Hölscher D, Kreft H (2019) Mixed-species tree plantings enhance structural complexity in oil palm plantations. Agriculture, Ecosystems & Environment 283: 106564.

Zheng G, Moskal LM, Kim S-H (2013) Retrieval of Effective Leaf Area Index in Heterogeneous Forests With Terrestrial Laser Scanning. IEEE Transactions on Geoscience and Remote Sensing 51: 777–786.

4 Relevance of sex, gender and/or diversity

We fully support the gender equality police of the RU presented in the Coordination Project. Our subproject does not involve specific issues of sex, gender or diversity. We encourage the application of female or diverse post-docs through active recruiting.

Project Description – Project Proposals

Prof. Dr. Peter Biedermann, Freiburg (PI)
Prof. Dr. Thomas Schmitt, Würzburg (PI)

SP2: Volatilome and Symbiosis

Project Description

1 Starting Point

1.1 State of the art and preliminary work

1.1.1 State of the art

All living organisms emit volatile organic compounds (VOCs) into the headspace around them (Baldwin et al. 2006; Mansurova et al. 2018; Pichersky and Dudareva 2020). These VOCs can be either simple by-products of the metabolism or might be compounds which are biosynthesized to interact with their biotic environment (communication, defense etc.) (Davis et al. 2013; Raffa 2001). Thus, the composition of all VOCs in a specific environment (volatilome) is expected to match the diversity of local communities, from microbes to insects, to trees up to large mammals (Mansurova et al. 2018). Since many organisms rely on olfactory cues and signals, these compounds might attract or repel key species in these communities and lead to a turn-over of the species composition.

In forests, volatiles are emitted or actively produced e.g. by all kind of organisms and organic material such as living plants, microorganisms and insects, dying plants as well as necromass like dung, carrion and degrading plants (Allison et al. 2004; Baldwin et al. 2006; Byers 1989; Davis et al. 2013; Francke et al. 1995; Frank et al. 2018; Frank et al. 2017; Haberer et al. 2017; Kandasamy et al. 2016; Kimmerer and Kozlowski 1982; Koban et al. 2016; Ranger et al. 2018; von Hoermann et al. 2016; Weissbecker et al. 2004; Weithmann et al. 2020; Wurmitzer et al. 2017). It is also expected that the volatilomes are affected by abiotic factors (temperature, humidity, season or microclimate) (Mansurova et al. 2018). Hence, many animals, in particular insects orient and communicate primarily through chemicals transferring information between a sender and a receiver (semiochemicals) (e.g. Byers 1989; Louis et al. 2005). But despite their great importance for ecological interactions (and probably due to their invisibility) it is hardly known what determines the volatilome in complex 3D forests. It is likely that volatiles filter local insect assemblages and may be as important as forest structures or the composition of plant communities (Heidrich et al. 2020) for determining local assemblies and thus for diversity at local α- and between patch β-scale.

Only a few studies have been conducted to understand the significance of the volatilomes as representatives for local communities (or environmental conditions) and their function to attract and repel key species (Davis et al. 2013; Pascual et al. 2017). Nevertheless, the variation in volatilome composition in space and time might form a critical, but invisible 4th dimension, beyond the 3D structure of trees, which might help to understand unexplained variance in observed community compositions and diversities of forest insects (Heidrich et al. 2020). Saproxylic beetles as species depend at least part of their life on deadwood, represent a variety of ecological guilds, trophic levels and morphological adaptions to different deadwood niches (Hagge et al. 2021; Kirkendall et al. 2015; Seibold et al. 2015; Ulyshen et al. 2018). Bark and ambrosia beetles (BABs) among them comprise more than 100 species in Germany (Bussler et al. 2011a) and are well known as forest pests and invasive because a small minority of BAB species can compete successfully with humans and flourish within anthropogenically homogenized forests (Biedermann et al. 2019; Hulcr and Dunn 2011; Kirkendall et al. 2015). The vast majority of BABs and saproxylic beetles end up on the losing side in these human-managed forests, however (Grove 2002), and so many saproxylic beetles are currently threatened.

The few BAB species that are regarded pests are intensively studied and models in chemical ecology, known to use VOCs to communicate intraspecifically as well as for location of their host trees (Byers 1989; Kandasamy et al. 2016; Raffa 2001). BABs respond to volatiles of stressed or dying trees (e.g. ethanol), conspecific aggregation and anti-aggregation pheromones as well as VOCs of their fungal mutualists when colonizing new host trees (i.e., kairomones like terpenoides and phenolics) (Birkemoe et al. 2018; Davis et al. 2013; Kimmerer and Kozlowski 1982; Netherer et al. 2021; Pichersky and Dudareva 2020; Ranger et al. 2018). The latter remain poorly studied so far, but are responsible for the characteristic smell of BAB colonized wood (Kandasamy et al. 2019; Netherer et al. 2021; Weissbecker et al. 2004). Hence, BABs form a perfect model group of species to disentangle the effect of the variation of the volatilome in a forest in space and time. For this it is required not only to disentangle the determinants of space, plant diversity, deadwood type and microclimate for the diversity of volatiles (Müller et al. 2020), but also the specific volatiles associated with saproxylic beetles (Byers 1989).

Among BABs, phloem-colonizing bark beetles are typically specialized on specific host-tree species, while xylem-boring ambrosia beetles are largely tree-host generalists (Kirkendall et al. 2015). The reason is that the latter engage in obligate mutualisms with beetle-species specific and host-tree generalist fungal symbionts for nutrition, which they selectively transmit in extra-cuticular glandular pouches (i.e., mycetangia) (Biedermann and Vega 2020; Francke-Grosmann 1956; Lehenberger et al. 2021). More recent research shows that beneficial fungal mutualists are also important for many phloem-colonizing bark beetles, but for other purposes: (i) for nutrition by translocating nutrients from inside the xylem to the phloem (Six and Elser 2019; Six and Elser 2020), (ii) for detoxification of plant-defensive compounds and (iii) probably in a few species also for accelerating the killing of tree-hosts (Birkemoe et al. 2018; Hofstetter et al. 2015; Hulcr et al. 2020; Wadke et al. 2016; Zhao et al. 2019). These beneficial fungal mutualists are part of a fungal symbiont community with neutral or negative effects on the beetles, because many of these other fungi are beetle or fungal pathogens or at least competitors for nutrients (Birkemoe et al. 2018; Hofstetter et al. 2015; Six and Elser 2019; Six and Klepzig 2021). The factors determining the diversity and abundance of these antagonistic fungal symbionts in beetle nests are not studied, but it is clear that they are acquired from the environment and a few correlative studies already suggest that more heterogenous (forest) environments facilitate their diversity (Kirschner 1998; Kolařík and Jankowiak 2013; Rassati et al. 2019). The beneficial effect of the symbiosis (fungal mutualism) on individual beetle fitness may thus be determined also by the heterogeneity of the environment and may be an example for enemy release (of antagonistic symbionts) in more homogenous forests. Such effects of more homogenous forests are well known for non-microbe natural enemies like parasitoides, predatory beetles or larger predators of BABs (Wegensteiner et al. 2015).

The ESC/ESBC interventions of the Coordination Project created various types of deadwood, differentially exposed to sunlight and infested by different fungal species (analyzed by SP7). Exposure to sunlight has a major influence on saproxylic beetles including BABs and wood-colonizing microbes (Thorn et al. 2018b). Therefore, we expect strong responses on α-, β- and γ-diversity in BABs, their associated symbionts and the volatilomes we sample on each of the experimental forest patches and districts. Volatilomes will not only reflect the volatiles of dying trees, BABs and their symbionts, but will very likely correlate with the diversity and abundance of many of the other organisms and functions sampled by the other subprojects. To our knowledge ours is the first approach to correlate the volatilome of an area with its organismal complexity. Understanding the impact of the volatilome on local and landscape-wide variation in saproxylic beetles in general and BABs in particular will strongly improve our understanding how forests assemble their local communities. Because a number of techniques have been tested to estimate the volatilome or part of it via Remote sensing techniques (Hong et al. 2021; Lin et al. 2021; Mäki et al. 2019), this would open the avenue to transfer the mechanisms on large landscapes if both are combined.

1.1.2 Preliminary work

Volatilome. The volatilome was recorded at each patch on the intensive study district in the University forest in Sailershausen before (in 2018) and since the ESBC treatments (2019-2021). In 2018, we used tenax/carboxen traps with subsequent solvent (hexane) extraction before gas chromatography/mass spectrometry analysis. Main compounds of the volatilome could already be identified. From 2020 onwards, we used the recently installed gas chromatograhy/mass spectrometry unit coupled with a thermo desorption unit, which improved the sensitivity of the analysis to also cover compounds with very low amounts. In 2021, a master student is collecting the volatilome at three different times from spring to autumn. Preliminary results reveal that season has the largest effect on the volatilome composition. Thus, we will collect the volatilome three times during the season for the next years (2022-25). Furthermore, we studied the effect of bark treatment of dead wood in attracting BABs. We found significant effects in the volatilome immediately after the treatment, which disappeared over time. These results correlated with the abundance of BABs on these differently treated deadwood pieces.

BABs and natural enemies. In 2018 we started to collect BABs with ethanol-baited traps and flight-interception traps (see SP9) on the intensive study district (University forest in Sailershausen). It turned out that ethanol-baited traps are not suitable for measuring α-diversity of BABs on these patches, as only very few BABs could be caught relative to flight-interception traps. So, the ethanol-trapping method was skipped after 2018 and for the proposed project we will focus solely on the catches of BABs with flight-interception traps. This latter method worked very well, however, and allows us to also link BAB communities with some of their natural enemies (e.g., parasitoid flies and wasps, some predatory beetles).

BABs and their natural enemies were present in the catches of the first four years (2018-2021) and a preliminary analysis of BABs on all patches before and after the ESBC treatment (2018 vs. 2019) showed a striking increase in diversity and abundance (Fig.1). This is very likely due to the sudden increase of fresh deadwood on the patches caused by the treatments. The collecting data of BABs and their natural enemies over four years from the intensive study district is already available and ready for more detailed analyses on α-, β- and γ-diversity, which will be done in the course of the proposed project. By adding another two (or more) collection years to the dataset, we will be able to also observe the (potentially) consecutive succession of BAB and natural enemy communities.

Symbiosis. In addition to measuring BABs by flight interception traps, J. Müller and his group developed a technique for assessing the colonization of saproxylic beetles and their natural enemies using freshly-cut branches that are hung up within the forest (Vogel et al. 2021a; Vogel et al. 2021b). This technique turns out to be excellent for attracting and colonization of branches by specific BABs. Given positive evaluation of this proposal, we will specifically attract common pest BABs like the Sixtoothed spruces bark beetle (*Pityogenes chalcographus*), the Small beech bark beetle (*Taphorychus bicolor*) and the invasive Asian ambrosia beetle (*Xylosandrus germanus*) using branches of beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*) to determine their fungal symbionts in relation to the ESBC treatments (see below). Classical fungal metabarcoding using ITS primers is not suitable for characterizing BAB fungal symbionts, because these primers do not work for the typical fungal mutualists in the Ophiostomatales (Ascomycetes) (Ibarra-Juarez et al. 2020; Kostovcik et al. 2014). We therefore developed specific LSU primers for identification of BAB fungal symbionts using metabarcoding (Nuotclà et al. 2021).

Furthermore, we have ongoing characterizations of volatiles from dozens of BAB fungal symbionts, which will be helpful for relating specific compounds in the volatilome to specific BABs/symbionts on the patches.

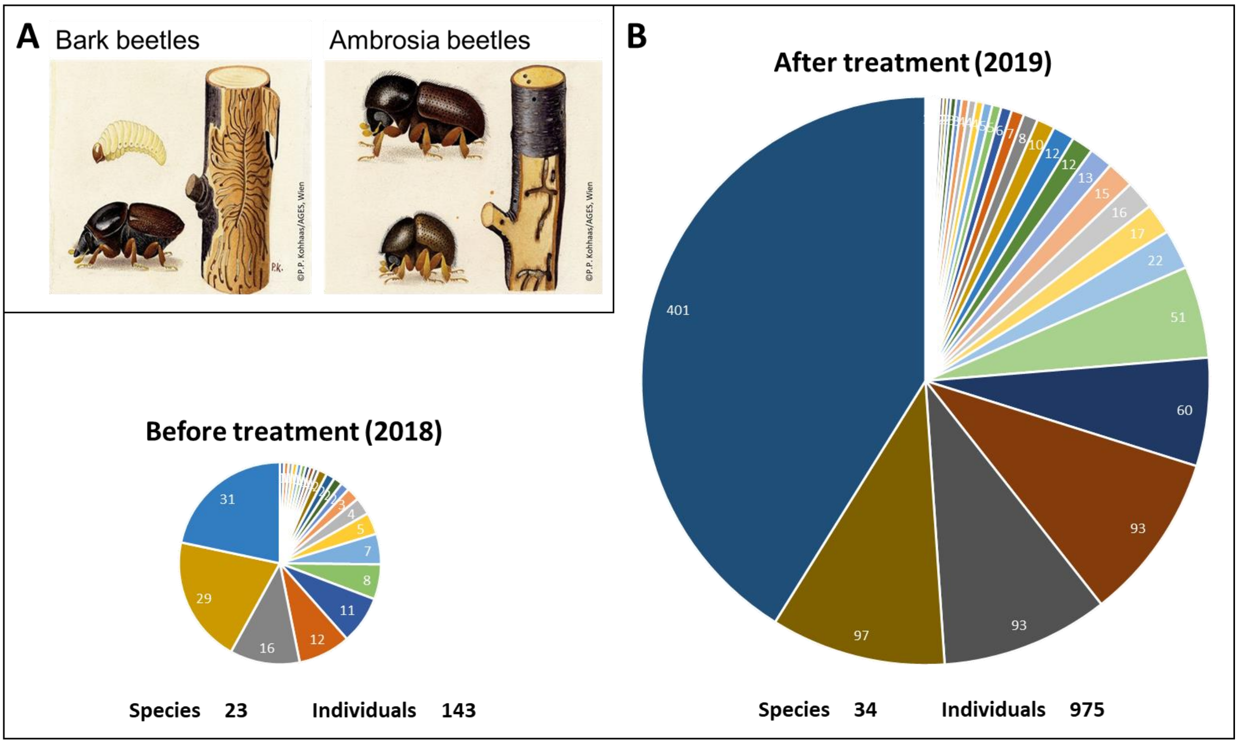


Fig. 1. Bark and ambrosia beetle catches before and after the ESC/ESBC treatment. (A) Illustration of the typical bark and ambrosia beetle biology, breeding either under the bark or inside the wood; (B) BAB communities on all patches before and after the treatment (year 2018 vs. 2019); different colors indicate different species, with numbers indicating numbers of individuals; pie-sizes reflect the total number of BABs.

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. Walther C, Baumann P, Luck K, Rothe B, **Biedermann PHW**, Gershenzon J, Köllner TG, Unsicker SB (2021). Volatile emission and biosynthesis in endophytic fungi colonizing black poplar leaves. Beilstein Journal of Organic Chemistry 17, 1698-711.
2. Lehenberger M, Foh N, Göttlein A, Six D, **Biedermann PHW** (2021) Nutrient-poor breeding substrates of ambrosia beetles are enriched with biologically important elements. Frontiers in Microbiology 12, 927.
3. Weithmann S, von Hoermann C, **Schmitt T**, Steiger S, Ayasse M (2020) The attraction of the dung beetle *Anoplotrupes stercorosus* (Coleoptera: Geotrupidae) to volatiles from vertebrate cadavers. Insects 11, 476.
4. **Biedermann PHW**, Müller J, Gregoire, J-C, Gruppe A, Hagge J, Hammerbacher A, Hofstetter R, Kandasamy D, Kolar M, Kostovcik M, Krokene P,…, Bässler C (2019) Bark Beetle Population Dynamics in the Anthropocene: Challenges and Solutions. Trends in Ecology and Evolution 34, 914-24.
5. Ranger CM, **Biedermann PH**, Phuntumart V, Beligala GU, Ghosh S, Palmquist DE, Mueller R, Barnett J, Schultz PB, Reding ME, Benz JP. Symbiont selection via alcohol benefits fungus farming by ambrosia beetles (2018). Proceedings of the National Academy of Sciences 115, 4447-52.
6. Birkemoe T, Jacobsen R.M, Sverdrup-Thygeson A, **Biedermann PHW** (2018) Insect-Fungus Interactions in Dead Wood Systems. In: Ulyshen M. (eds) Saproxylic Insects. Zoological Monographs. Springer, Cham.
7. Frank K, Brückner A, Blüthgen N, **Schmitt T** (2018) In search of cues: dung beetle attraction and the significance of volatile composition of dung. Chemoecology 28, 145-152.
8. Haberer W, **Schmitt T**, Schreier P, Eggert A-K, Müller JK (2017) Volatiles emitted by calling males of burying beetles and Ptomascopus morio (Coleoptera: Silphidae: Nicrophorinae) are biogenetically related. Journal of Chemical Ecology 43, 971-977.
9. Frank ET, **Schmitt T**, Hovestadt T, Mitesser O, Stiegler J & Linsenmair K E (2017) Saving the injured: Rescue behavior in the termite-hunting ant Megaponera analis. Science Advances 3, e1602187.
10. Wurmitzer C, Blüthgen N, Krell F-T, Maldonado B, Ocampo F, Müller JK, **Schmitt T** (2017) Attraction of dung beetles to herbivore dung and synthetic compounds in comparative field study. Chemoecology 27, 75-84.

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.2.3 Patents

Not applicable

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

April 2022 to March 2025

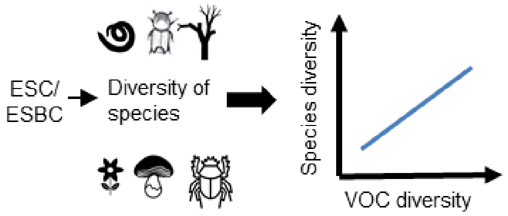
2.2 Objectives

The overall focus of our subproject is to measure the effects of the ESC/ESBC treatments on the diversity and abundance of (i) volatile organic compounds, (ii) saproxylic beetles, with a focus on bark and ambrosia beetles (BABs), as well as (iii) natural enemies and fungal symbionts of BABs. The latter will deliver effects of the treatments on the function *symbiosis*, which is a measure for fitness of the target BAB species.

We will do surveys at specific times and combine them with expert efforts to identify cryptic species and with results from fungal-symbiont metabarcoding, as recommended for multitrophic studies (Seibold et al. 2018). We will support the fieldwork and sample sorting of the PhD-student by technical and student assistants. Parts of our data, like saproxylic beetles (including BABs) and fungal symbionts, are collected in collaboration with SP9 and SP7 and all our data is shared with SPZ and other interested SPs (see Fig. 2 below). Specifically, we aim to test the following five major hypotheses:

All organisms emit VOCs into the environment. A part of these VOCs are highly species specific and will contribute to the specificity and the diversity of the volatilome in a particular environment. Thus, the diversity of the volatilome in ESC/ESBC treatments should increase with the diversity of the species in these treatments relative to control sites.

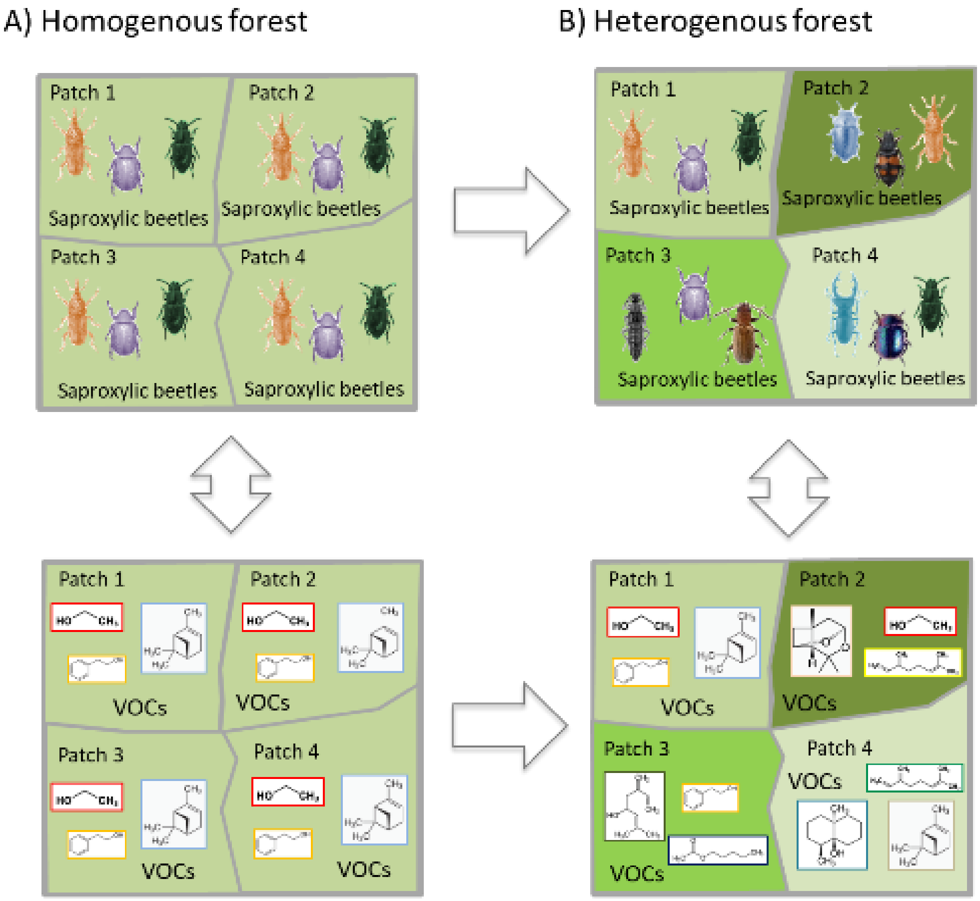
Hypothesis 1: The diversity of the volatilomes in a patch mirrors the diversity of the organisms in the patch.



<u>Method 1:</u> Diversity of volatilomes are analysed with gas chromatography/mass spectrometry coupled with a thermodesorption unit. The volatiles are trapped at each ESC/ESBC treatment three times a year with Tenax/Carboxen traps from the air in each patch and analysed using already existing pipelines (Metaboanalyst). The diversity indices of the volatilomes will be compared with the diversity indices of all investigated groups of organisms (BABs, their symbionts and other subprojects).

Saproxylic beetles are primarily using VOCs for picking suitable breeding substrates in living, dying or dead wood (Ulyshen et al. 2018). These may be emitted/produced by the host plants (Kimmerer and Kozlowski 1982; Pichersky and Dudareva 2020), microorganisms inside the plants (Davis et al. 2013) or the insects themselves (i.e., pheromones (Byers 1989; Stökl and Steiger 2017; Symonds and Elgar 2004)). Therefore, we expect that the diversity of saproxylic beetle communities is determined by the diversity of the plant volatilome per patch, which may affect specific saproxylic beetle taxa differently (i.e., host generalists vs. specialists; see also H3). The presence of specific BABs may be also recognized by the presence of their pheromones.

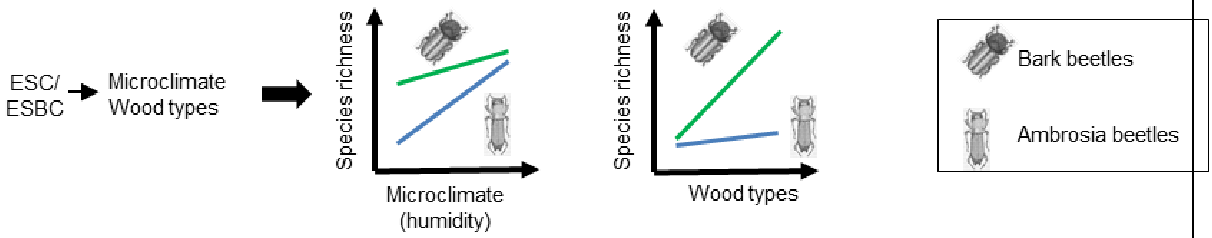
Hypothesis 2: The diversity of volatiles within a forest landscape explains the composition and diversity of saproxylic beetle communities. This effect is independent of space, physiognomy of the forest and tree species composition.



Method 2: Diversity of saproxylic beetle communities are determined by flight-interception traps and rearing out of experimentally set-up deadwood at each patch. Volatilomes are determined by three VOC collections per year with volatile traps at each patch and subsequent analysis via gas chromatography/mass spectrometry coupled with thermodesorption. Forest characteristics are recorded by SPZ, SP1 and SP3. For details see WP1 and WP2.

Among saproxylic beetles most biological knowledge is available for the weevil subfamily Scolytinae, the bark and ambrosia beetles (BABs), because of its common pest status. Bark beetles breed inside the phloem and are closely adapted to specific parts (e.g., stem, stump, branches) of specific host-tree species (Vega and Hofstetter 2015). Ambrosia beetles are typically tree-host generalists as they obligately depend on tree-host generalist fungal mutualists that they cultivate in tunnels inside the xylem of dying or dead trees with a certain humidity (Beaver 1989; Kirkendall et al. 2015). Therefore, we would expect that bark and ambrosia beetles respond differently to the ESBC treatment (i.e., deadwood diversity, microclimate).

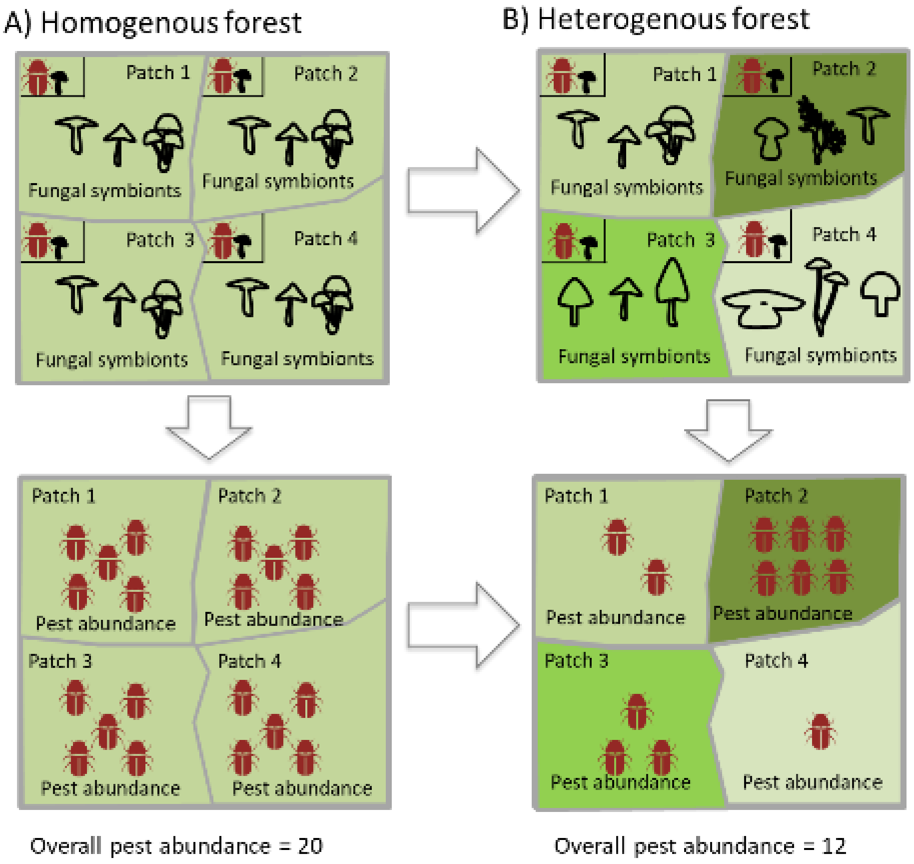
Hypothesis 3: Within BAB communities the less host-specific ambrosia beetles are determined more strongly by microclimate, whereas phloem-colonizing bark beetles are determined more strongly by the availability of specific tree types.



Method 3: Diversity of BABs are determined by flight-interception traps and rearing out of experimentally set-up deadwood at each patch. Data on microclimate and tree-species diversity are collected by SP1 and SPZ. For details see WP2.

BABs are ubiquitously associated with a community of ectosymbiotic fungal symbionts, among which one or two species are typically species-specific and have beneficial effects on beetle fitness (i.e., fungal mutualists; Harrington 2005; Kirisits 2004). The rest of the ectosymbiotic fungal symbionts is comprised by an unspecific community of more or less generalist species, which typically use the beetles as vectors for dispersal and dissemination (Birkemoe et al. 2018; Kirschner 2001). These species typically negatively affect their host beetle species, because they compete with their fungal mutualists for nutrients (Beaver 1989; Six 2003). Experimental studies in the lab have shown that the presence of these fungal antagonists within BAB galleries lead to reduced growth of fungal mutualists and thus reduced reproductive output (i.e., fitness) of individual beetles (Cardoza et al. 2012; Klepzig et al. 2001; Nuotclá et al. 2019; Six and Paine 1998). Moreover, there is already some evidence that a more heterogenous environment increases the diversity and abundance of these antagonistic symbionts within BAB galleries (Kirschner 1998; Kirschner 2001; Rassati et al. 2019).

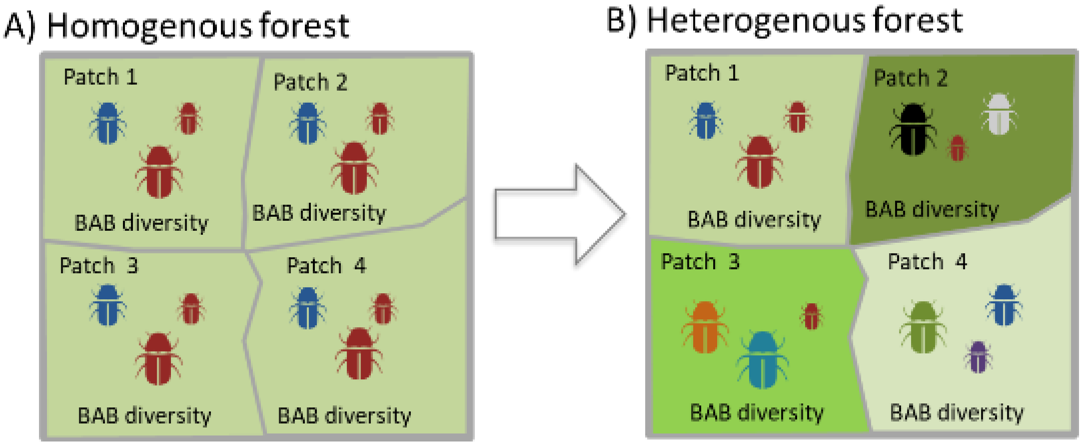
Hypothesis 4: A more heterogenous patch or landscape leads to a higher diversity of fungal symbionts in BAB species. This in turn reduces the fertility of these species.



Method 4: Diversity of ectosymbiotic fungal symbionts is determined by taking samples from galleries of a few target BAB species from the experimentally set-up deadwood at each patch. The reproductive output of the beetles (relative to the symbiont community) will be determined by collecting all emerging individuals from the same BAB galleries. Data on microclimate and tree-species diversity are collected by SP1 and SPZ and will be included in the models explaining the symbiont diversity. For details see WP3 and WP4.

Among more than 100 BAB species in Germany less than a third can have detrimental economic impact on forestry (Bussler et al. 2011b; Lieutier 2004). Ambrosia beetles are among the most invasive insect groups worldwide due to adaptations to inbreeding by many of their species (Faccoli et al. 2020; Hulcr and Dunn 2011). A few invasive ambrosia beetle species like the Asian ambrosia beetle (*X. germanus*) already dominate German forests (Bussler et al. 2011a; Bussler and Immler 2007) Like in agricultural monocultures it is likely that also homogenous forest stands (that are typical for German forestry) facilitate certain "anthropophilus species" (if we want to expand this concept to forests that are strongly influenced by human activities). Simulations of empirical data from the Bavarian Forest National Park suggest that the more heterogenous a forest gets the less problematic BABs are for forestry (i.e. abundance of pest species decreases; Sommerfeld et al. 2021). Here we first aim to show that effect empirically and secondly, we will try to discern whether this effect is more bottom-up (availability of suitable hosts) or top-down driven (natural enemies, antagonistic symbionts).

Hypothesis 5: The more heterogenous districts with ESBC show higher γ-diversity of BABs and antagonistic symbionts, but reduced abundance and diversity of pest and invasive BAB species.



Note that the red „pest“ species disappear in heterogenous forests.

Method 5: For each district we compare the diversity and abundance of pest and non-pest BABs on homogenous patches and heterogenous patches. β-diversity analyses between patches will allow us to determine if bottom-up or top-down factors drive BAB abundance and diversity more strongly. For details see WP1.

Data exchange and collaboration within the consortium

For the Coordination Project and syntheses in SPZ we provide structural data about the volatile organic compounds and biodiversity data on the response of saproxylic beetles (including BABs), BAB natural enemies and fungal symbionts of selected target BAB species to the ESC/ESBC treatment for all 234 patches for at least one year. Additionally, to contribute to multifunctionality we will measure the response of *symbiosis* to the treatment by linking symbiont diversity with fitness of selected bark beetle pest species.

We will closely collaborate with SP1 and SP9 to receive forest structure and microclimatic data as well as saproxylic insect data from their flight-interception traps for each patch (Fig. 2). Both will be used to link it with our volatile measurements. Together with SP7 we will expose the same pieces of standardized wood to link our saproxylic beetle and symbiont data with their microbial succession and decomposition processes. Variables related to the environmental conditions at each patch (e.g., humidity) and structural measures at different scales, sampled on a landscape level via remote sensing in SP3 and the basic meteorological background data from SPZ will be used as potential predictors in our models. For analyses of multifunctionality and statistical analyses, we will closely collaborate with SPZ. Finally, to reduce sampling effort we will harmonize sampling across SPs mentioned here and particularly use sampling support from SPZ.

A close collaboration with Diana Six (Mercator Fellow), who is an expert on bark beetle-fungus symbioses, will be of great help in project design, analyses and interpretation of results.

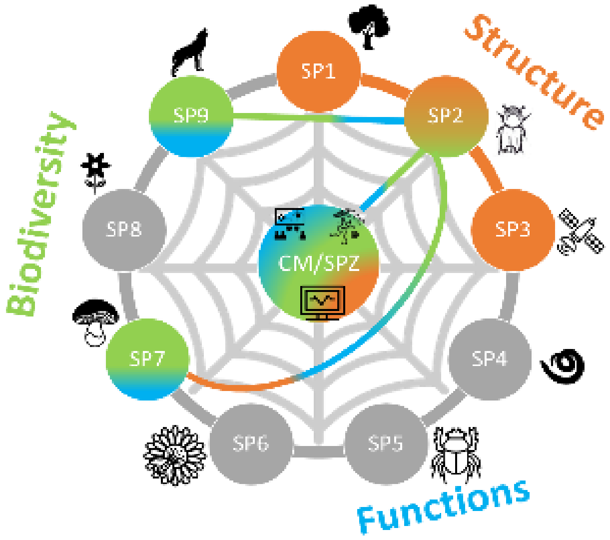


Fig. 2: Cooperation of SP2 with other subprojects. The colour of arrows indicates the type of data exchanged; green: species data, blue: functions, orange: structure.

2.3 Work program including proposed research methods

The following data will be collected by our subproject:

(WP1) Volatilomes from patches: We aim to trap volatiles in all experimental patches over the whole project period (4 years) using self-produced Tenax/Carboxen traps (see Table 1). Since we expect large seasonal differences we will collect the VOCs at three time windows between spring and autumn. The volatiles will be trapped for 10 minutes directly from the environment in the middle of all patches using a portable vacuum pump. The samples will be stored in a freezer and analyzed in the lab of T. Schmitt using a high sensitive gas chromatograph/mass selective detector coupled to a thermodesorption unit (GC/MS/TD) from Agilent and Markes. We will use the software MassHunter and ChemStation in combination with commercially available spectra library to identify compounds and qualitatively and quantitatively analyze the VOCs from each patch. Tentatively identified compounds will be verified using commercially available standards if possible. We will use a metabolomics approach to statistically assess the α-diversity of the volatilomes of each patch and compare ß-diversities of the volatilomes between patches.

(WP2) Saproxylic beetles including BABs and their natural enemies: Saproxylic beetles including BABs and their natural enemies (parasitoids, predatory beetles) are collected by two different methods (Vogel et al. 2021a; Vogel et al. 2021b). First, we will receive the abundance and diversity of already identified species collected with two flight interception traps per patch by SP9 (in their WP3). This data is already available since 2018 (before the treatment) from the intensive study district (University forest Sailershausen) and will be collected every year. Second, starting in April 2022 we will expose standardized, freshly cut pieces of wood (diameter ~10cm, length 50 cm) of two tree species (*Fagus sylvatica, Picea abies*) for two months for colonization by saproxylic beetles at each patch (Vogel et al. 2021a; Vogel et al. 2021b). The *F. sylvatica* piece is the same used also by SP7 (in their WP1) and will be split in half after two months, with only the piece for SP7 remaining in the forest for measuring microbial colonization and degradation. This will allow to correlate saproxylic beetle presence (that we measure) with the succession of microbial colonization and degradation afterwards (as measured by SP7).

By exposing these two pieces of wood per patch for only two months we particular target three ubiquitous forest pest BABs, the Sixtoothed spruce bark beetle, *P. chalcographus*, with the piece from Norway spruce (*P. abies*), the Small beech bark beetle, *T. bicolor,* and the invasive Asian ambrosia beetles, *X. germanus*, with the piece from beech (*F. sylvatica*). Preliminary analyses have shown that these species are present on >80% of patches in the intensive study district in Sailershausen. After these two months for colonization by beetles, three gallery entrances per beetle will be marked per wood piece for detailed investigations of beetle associated fungal symbionts, beetle reproductive output and VOCs (see WP1, WP3 and WP4). Between June 2022 and June 2023 all pieces from the 180 patches are put in a rearing station out of plastic tubes with trapping bottles attached that will collect all emerging saproxylic beetles and their natural enemies (see rearing station on Fig. 1f in Coordination Project) (for details on this method see (Vogel et al. 2021a)). This rearing station will be built in the months before at the Forest Entomology chair at the University of Freiburg and will allow consecutive rearing of saproxylic beetles from up to 400 pieces of wood. Saproxylic beetle samples will be sorted with support of a technician and of student helpers under the supervision of the PhD student. Identification of saproxylic beetles, BABs and their natural enemies will be conducted by external experts.in a joint effort with SP9 (see their WP3).

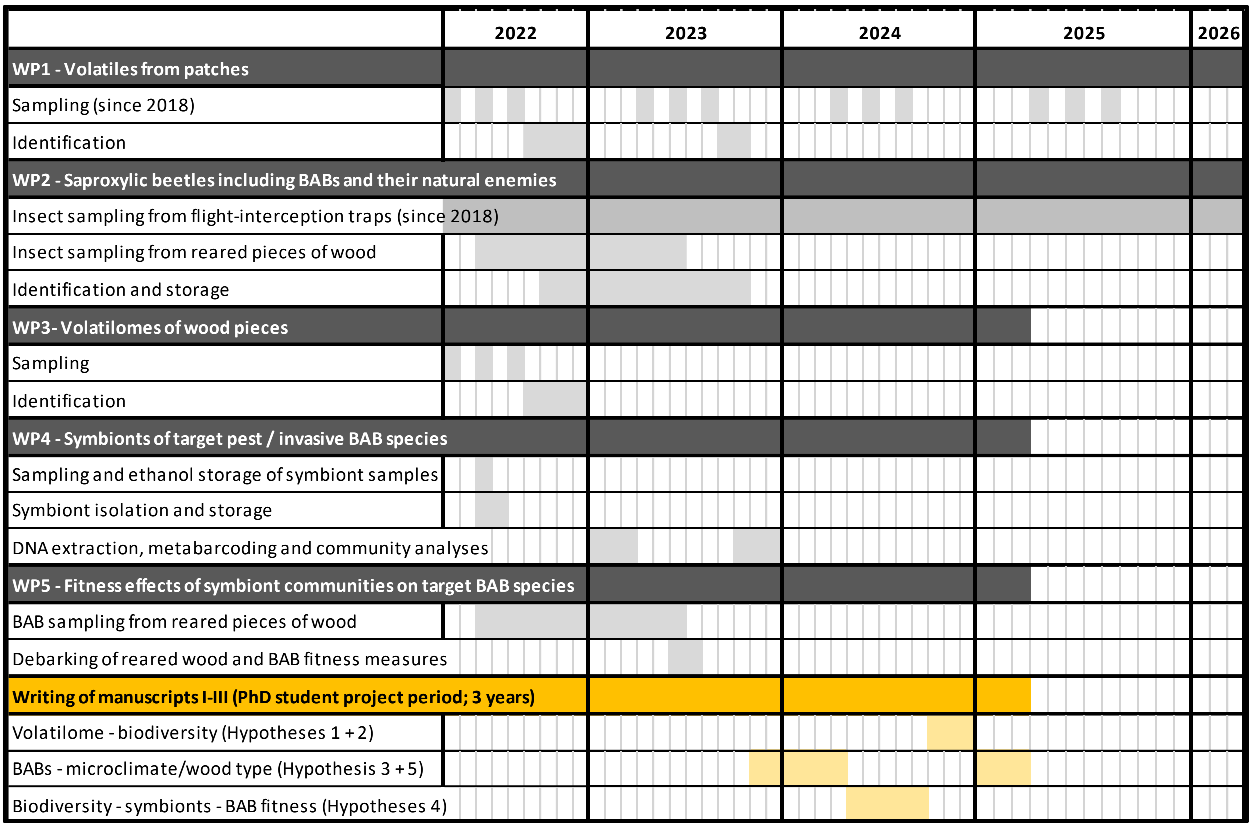
(WP3) Volatilomes of wood pieces: In addition to the rearing of saproxylic beetles, we will also use pieces of wood to follow the succession of volatiles emitted by the wood, saproxylic insects or colonizing microorganisms. We will collect the VOCs from the standardized wood objects exposed by SP7 three times between spring and autumn (Table 1). The VOC concentration in the headspace around the dead wood will be enriched by enclosing the dead wood in an oven bag. Oven bags are frequently used for volatile collection because they do not emit contaminants as other plastic material does. After 30 min of VOC accumulation in the oven bag, the volatiles will be collected using the same method as described in WP1. We will qualitatively and quantitatively analyze the volatilome. In addition, we will use Random Forest analysis to extract key components potentially responsible for the occurrence of specific beetle species.

(WP4) Symbionts of target pest / invasive BAB species: Two pieces of wood containing galleries of the three target BAB species are collected in June 2022 from every of the 180 patches and brought to the rearing station in Freiburg (Table 1). Galleries of these three species can be easily identified by the size of the entrance hole and the typical boring dust (brown for the two bark beetles, white for the ambrosia beetle). All entrance holes on each of the wood pieces are marked and three entrance holes per species located somewhere in the center (to avoid contaminations with environmental fungi) are randomly picked for detailed investigations of fungal symbiont communities. From each of these entrances we take a sample of phloem (bark beetles) or xylem (ambrosia beetles) containing a beetle tunnel with a 5 mm coredrill (“Dendrobohrer”), collect the phloem/xylem sample of interest and seal the bored hole with the piece of removed bark. Afterwards samples are grinded under sterile conditions, the three samples per beetle species are pooled and afterwards used to extract DNA using commercial kits. DNA is purified and then used for metabarcoding with specific LSU primers developed in the Biedermann lab for barcoding ophiostomatoid and all other bark beetle-associated fungi (for details see Nuotclà et al. 2021). Additionally, we will use a few pieces of wood out of the whole collection to isolate the main fungal mutualists from every bark beetle species for comparing the LSU sequences and the volatiles.

(WP5) Fitness effects of symbiont communities on target BAB species: The three target BAB species are reared on the experimental wood pieces inside the rearing tubes (10x50 cm) and all offspring emerging per target species over the following year is counted. These wood pieces are relatively small, but have been successfully used in the same forest area before to determine saproxylic beetle communities and their natural enemies (Vogel et al. 2021a; Vogel et al. 2021b). They have been chosen in this size to not affect the general processes on the patches. As they dry out quite quickly, they allow only a single BAB generation to develop, which is exactly what we are interested in. After one year wood pieces are removed from the rearing tubes and debarked for counting the number of total galleries per target species (galleries are visible in the bark after beetles left). Average offspring numbers per target BAB on each wood piece are calculated. This fitness measure will be correlated with the symbiont diversity (see WP3) to calculate the function *symbiosis* benefit under different ESC/ESBC treatments.

Statistical analyses: In our models, we will use diversity measures of volatiles, beetles and symbionts as well as beetle fitness (as a measure for symbiosis) at α- and β-level as response variables for each patch. As predictors we will use variables gathered within the consortium for each patch like forest structure and tree-species composition, amount and type of dead wood and microclimate conditions.

Table 2: Overview of work programme and schedule. The sampling schedule will be in accordance with the schedule of the coordination module. Our PhD project ends after three years, but we will continue sampling of volatiles and saproxylic insects in 2024 and 2025 (other group members and MSc students).



	2022	2023	2024	2025	2026
WP1 - Volatiles from patches	▨	▨	▨	▨	▨
Sampling (since 2018)	▨	▨	▨	▨	
Identification	▨	▨			
WP2 - Saproxylic beetles including BABs and their natural enemies		▨	▨	▨	▨
Insect sampling from flight-interception traps (since 2018)	▨	▨	▨	▨	▨
Insect sampling from reared pieces of wood	▨	▨			
Identification and storage	▨	▨			
WP3- Volatilomes of wood pieces	▨	▨	▨	▨	
Sampling	▨				
Identification	▨				
WP4 - Symbionts of target pest / invasive BAB species		▨	▨	▨	
Sampling and ethanol storage of symbiont samples	▨				
Symbiont isolation and storage	▨				
DNA extraction, metabarcoding and community analyses		▨			
WP5 - Fitness effects of symbiont communities on target BAB species		▨	▨	▨	
BAB sampling from reared pieces of wood	▨	▨			
Debarking of reared wood and BAB fitness measures		▨			
Writing of manuscripts I-III (PhD student project period; 3 years)		▨	▨	▨	
Volatilome - biodiversity (Hypotheses 1 + 2)			▨		
BABs - microclimate/wood type (Hypothesis 3 + 5)		▨	▨	▨	
Biodiversity - symbionts - BAB fitness (Hypotheses 4)			▨		

3 Bibliography concerning the state of the art, the research objectives, and the work programme

Allison JD, Borden JH, Seybold SJ (2004) A review of the chemical ecology of the Cerambycidae (Coleoptera). Chemoecology 14:123-150

Baldwin IT, Halitschke R, Paschold A, von Dahl CC, Preston CA (2006) Volatile signaling in plant-plant interactions: "talking trees" in the genomics era. Science 311:812-815. doi: 10.1126/science.1118446

Beaver RA (1989) Insect-fungus relationships in the bark and ambrosia beetles. In: Wilding N, Collins NM, Hammond PM, Webber JF (eds) Insect-fungus interactions. Academic Press, London, pp 121-143

Biedermann PHW, Müller J, Grégoire J-C, Gruppe A, Hagge J, Hammerbacher A, Hofstetter RW, Kandasamy D, Kolarik M, Kostovcik M, Krokene P, Sallé A, Six DL, Turrini T, Vanderpool D, Wingfield MJ, Bässler C (2019) Bark beetle population dynamics in the Anthropocene: challenges and solutions. Trends in Ecology & Evolution 34:914-924. doi: https://doi.org/10.1016/j.tree.2019.06.002

Biedermann PHW, Vega FE (2020) Ecology and Evolution of Insect–Fungus Mutualisms. Annual Review of Entomology 65:431-455. doi: 10.1146/annurev-ento-011019-024910

Birkemoe T, Jacobsen RM, Sverdrup-Thygeson A, Biedermann PHW (2018) Insect-fungus interactions in dead wood systems. In: Ulyshen MD (ed) Saproxylic Insects. Springer, pp 377-427

Bussler H, Bouget C, Brustel H, Brandle M, Riedinger V, Brandl R, Muller J (2011a) Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. Forest Ecology and Management 262:1887-1894

Bussler H, Bouget C, Brustel H, Brändle M, Riedinger V, Brandl R, Müller J (2011b) Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. Forest Ecology and Management 262:1887-1894

Bussler H, Immler T (2007) Neue Borkenkäferarten in Bayern. Forstschutz Aktuell 38:5-8

Byers JA (1989) Chemical ecology of bark beetles. Experientia 45:271-283

Cardoza Y, Hofstetter R, Vega F (2012) Insect-Associated Microorganisms and Their Possible Role in Outbreaks. pp 155-174

Davis TS, Crippen TL, Hofstetter RW, Tomberlin JK (2013) Microbial volatile emissions as insect semiochemicals. Journal of Chemical Ecology 39:840-859. doi: 10.1007/s10886-013-0306-z

Faccoli M, Gallego D, Branco M, Brockerhoff EG, Corley J, Coyle DR, Hurley BP, Jactel H, Lakatos F, Lantschner V, Lawson S, Martínez G, Gómez DF, Avtzis D (2020) A first worldwide multispecies survey of invasive Mediterranean pine bark beetles (Coleoptera: Curculionidae, Scolytinae). Biol Invasions. doi: 10.1007/s10530-020-02219-3

Francke-Grosmann H (1956) Hautdrüsen als Träger der Pilzsymbiose bei Ambrosiakäfern. Zeitschrift für Ökologie und Morphologie der Tiere 45:275-308

Francke W, Bartels J, Meyer H, Schroder F, Kohnle U, Baader E, Vite JP (1995) Semiochemicals from Bark Beetles - New Results, Remarks, and Reflections. Journal of Chemical Ecology 21:1043-1063

Grove SJ (2002) Saproxylic Insect Ecology and the Sustainable Management of Forests. Annual Review of Ecology and Systematics 33:1-23. doi: 10.1146/annurev.ecolsys.33.010802.150507

Hagge J, Müller J, Birkemoe T, Buse J, Christensen RHB, Gossner MM, Gruppe A, Heibl C, Jarzabek-Müller A, Seibold S (2021) What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. Journal of Animal Ecology

Harrington TC (2005) Ecology and evolution of mycophagous bark beetles and their fungal partners. In: Vega FE, Blackwell M (eds) Ecological and evolutionary advances in insect-fungal associations. Oxford University Press, New York, pp 257-291

Heidrich L, Bae S, Levick S, Seibold S, Weisser W, Krzystek P, Magdon P, Nauss T, Schall P, Serebryanyk A (2020) Heterogeneity–diversity relationships differ between and within trophic levels in temperate forests. Nature ecology & evolution 4:1204-1212

Hofstetter RW, Dinkins-Bookwalter J, Davis TS, Klepzig KD (2015) Symbiotic associations of bark beetles. In: Vega FE, Hofstetter RW (eds) Bark Beetles: Biology and Ecology of Native and Invasive Species. Academic Press, pp 209-245

Hong Q, Liu C, Hu Q, Zhang Y, Xing C, Su W, Ji X, Xiao S (2021) Evaluating the feasibility of formaldehyde derived from hyperspectral remote sensing as a proxy for volatile organic compounds. Atmospheric Research 264:105777. doi: https://doi.org/10.1016/j.atmosres.2021.105777

Hulcr J, Barnes I, De Beer ZW, Duong TA, Gazis R, Johnson AJ, Jusino MA, Kasson MT, Li Y, Lynch S, Mayers C, Musvuugwa T, Roets F, Seltmann KC, Six D, Vanderpool D, Villari C (2020) Bark beetle mycobiome: collaboratively defined research priorities on a widespread insect-fungus symbiosis. Symbiosis. doi: 10.1007/s13199-020-00686-9

Hulcr J, Dunn RR (2011) The sudden emergence of pathogenicity in insect–fungus symbioses threatens naive forest ecosystems. Proceedings of the Royal Society B: Biological Sciences 278:2866-2873. doi: 10.1098/rspb.2011.1130

Ibarra-Juarez LA, Burton MAJ, Biedermann PHW, Cruz L, Desgarennes D, Ibarra-Laclette E, Latorre A, Alonso-Sánchez A, Villafan E, Hanako-Rosas G, López L, Vázquez-Rosas-Landa M, Carrion G, Carrillo D, Moya A, Lamelas A (2020) Evidence for Succession and Putative Metabolic Roles of Fungi and Bacteria in the Farming Mutualism of the Ambrosia Beetle Xyleborus affinis. mSystems 5:e00541-00520. doi: 10.1128/mSystems.00541-20

Kandasamy D, Gershenzon J, Andersson M, Hammerbacher A (2019) Volatile organic compounds influence the interaction of the Eurasian spruce bark beetle (Ips typographus) with its fungal symbionts. The ISME journal doi.org/10.1038/s41396-019-0390-3:1. doi: 10.1038/s41396-019-0390-3

Kandasamy D, Gershenzon J, Hammerbacher A (2016) Volatile organic compounds emitted by fungal associates of conifer bark beetles and their potential in bark beetle control. Journal of Chemical Ecology 42:952-969. doi: 10.1007/s10886-016-0768-x

Kimmerer TW, Kozlowski TT (1982) Ethylene, Ethane, Acetaldehyde, and Ethanol Production By Plants under Stress. Plant Physiol 69:840-847

Kirisits T (2004) Fungal associates of European bark beetles with special emphasis on the ophiostomatoid fungi. In: Lieutier F, Keith RD, Battisti A, Gregoire J-C, Evans HF (eds) Bark and Wood Boring Insects in Living Trees in Europe, a synthesis. Springer, Dordrecht, pp 181-237

Kirkendall LR, Biedermann PHW, Jordal BH (2015) Evolution and diversity of bark and ambrosia beetles. In: Vega FE, Hofstetter RW (eds) Bark Beetles: Biology and Ecology of Native and Invasive Species. Academic Press, pp 85-156

Kirschner R (1998) Diversität mit Borkenkäfern assoziierter filamentöser Mikropilze, Eberhard-Karls-Universität Tübingen, Tübingen

Kirschner R (2001) Diversity of Filamentous Fungi in Bark Beetle Galleries in Central Europe. In: Misra JK, Horn BW (eds) Trichomycetes and Other Fungal Groups: Professor

Robert W. Lichtwardt Commemoration Volume. Science Publishers Inc., Enfield (NH), USA, pp 175-196

Klepzig KD, Moser JC, Lombardero FJ, Hofstetter RW, Ayres MP (2001) Symbiosis and competition: Complex interactions among beetles, fungi and mites. Symbiosis 30:83-96

Koban MB, Gossner MM, Müller J, Steidle JL, Bässler C, Hothorn T, Unsicker SB, Seibold S (2016) Short-distance attraction of saproxylic Heteroptera to olfactory cues. Insect Conservation and Diversity 9:254-257

Kolařík M, Jankowiak R (2013) Vector Affinity and Diversity of Geosmithia Fungi Living on Subcortical Insects Inhabiting Pinaceae Species in Central and Northeastern Europe. Microbial Ecology:1-19. doi: 10.1007/s00248-013-0228-x

Kostovcik M, Bateman CC, Kolarik M, Stelinski LL, Jordal BH, Hulcr J (2014) The ambrosia symbiosis is specific in some species and promiscuous in others: evidence from community pyrosequencing. ISME J. doi: 10.1038/ismej.2014.115

Lehenberger M, Foh N, Göttlein A, Six D, Biedermann PH (2021) Nutrient-poor breeding substrates of ambrosia beetles are enriched with biologically important elements. Frontiers in Microbiology 12:927

Lieutier F (2004) Bark and Wood Boring Insects in Living Trees in Europe, A Synthesis. Springer

Lin Y, Lun X, Tang W, Zhang Z, Jing X, Fan C, Wang Q (2021) Characteristics and chemical reactivity of biogenic volatile organic compounds from dominant forest species in the Jing-Jin-Ji area, China. Forest Ecosystems 8:52. doi: 10.1186/s40663-021-00322-y

Louis MS, Joop JAvL, Marcel D (2005) Insect-Plant Biology. OUP Oxford, Oxford

Mäki M, Krasnov D, Hellén H, Noe SM, Bäck J (2019) Stand type affects fluxes of volatile organic compounds from the forest floor in hemiboreal and boreal climates. Plant and Soil 441:363-381. doi: 10.1007/s11104-019-04129-3

Mansurova M, Ebert BE, Blank LM, Ibáñez AJ (2018) A breath of information: the volatilome. Curr Genet 64:959-964

Müller J, Ulyshen M, Seibold S, Cadotte M, Chao A, Bässler C, Vogel S, Hagge J, Weiß I, Baldrian P (2020) Primary determinants of communities in deadwood vary among taxa but are regionally consistent. Oikos 129:1579-1588

Netherer S, Kandasamy D, Jirosová A, Kalinová B, Schebeck M, Schlyter F (2021) Interactions among Norway spruce, the bark beetle Ips typographus and its fungal symbionts in times of drought. Journal of Pest Science. doi: 10.1007/s10340-021-01341-y

Niehuis O, Buellesbach J, Gibson JD, Pothmann D, Hanner C, Mutti NS, Judson AK, Gadau J, Ruther J, Schmitt T (2013) Behavioural and genetic analyses of Nasonia shed light on the evolution of sex pheromones. Nature 494:345. doi: 10.1038/nature11838

https://www.nature.com/articles/nature11838#supplementary-information

Nuotclà J, Diehl J, Taborsky M (2021) Habitat Quality Determines Dispersal Decisions and Fitness in a Beetle – Fungus Mutualism. Frontiers in Ecology and Evolution 9. doi: 10.3389/fevo.2021.602672

Nuotclá JA, Biedermann PHW, Taborsky M (2019) Pathogen defence is a potential driver of social evolution in ambrosia beetles. Proceedings of the Royal Society B: Biological Sciences. doi: http://dx.doi.org/10.1098/rspb.2019.2332

Pascual J, von Hoermann C, Rottler-Hoermann AM, Nevo O, Geppert A, Sikorski J, Huber KJ, Steiger S, Ayasse M, Overmann J (2017) Function of bacterial community dynamics in the formation of cadaveric semiochemicals during in situ carcass decomposition. Environ Microbiol 19:3310-3322. doi: 10.1111/1462-2920.13828

Pichersky E, Dudareva N (2020) Biology of Plant Volatiles. CRC/Taylor & Francis.

Raffa KF (2001) Mixed messages across multiple trophic levels: the ecology of bark beetle chemical communication systems. Chemoecology 11:49-65

Ranger CM, Biedermann PHW, Phuntumart V, Beligala GU, Ghosh S, Palmquist DE, Mueller R, Barnett J, Schultz PB, Reding ME, Benz JP (2018) Symbiont selection via alcohol benefits fungus farming by ambrosia beetles. Proceedings of the National Academy of Sciences 115:4447-4452. doi: 10.1073/pnas.1716852115

Rassati D, Marini L, Malacrinò A (2019) Acquisition of fungi from the environment modifies ambrosia beetle mycobiome during invasion. PeerJ. doi: 10.7717/peerj.8103

Seibold S, Brandl R, Buse J, Hothorn T, Schmidl J, Thorn S, Müller J (2015) Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. Conservation Biology 29:382-390

Seibold S, Cadotte MW, MacIvor JS, Thorn S, Müller J (2018) The necessity of multi-tropic approaches in community ecology Trends in Ecology and Evolution 33:754-764

Six DL (2003) Bark beetle-fungus symbioses. In: Bourtzis K, Miller TA (eds) Insect Symbiosis. CRC Press, Boca Raton, pp 97-114

Six DL, Elser JJ (2019) Extreme ecological stoichiometry of a bark beetle-fungus mutualism. Ecological Entomology *in press*

Six DL, Elser JJ (2020) Mutualism is not restricted to tree-killing bark beetles and fungi: the ecological stoichiometry of secondary bark beetles, fungi, and a scavenger. Ecological Entomology 45:1134-1145. doi: 10.1111/een.12897

Six DL, Klepzig K (2021) Context dependency in bark beetle-fungus mutualisms revisited: Assessing potential shifts in interaction outcomes against varied genetic, ecological, and evolutionary backgrounds. Frontiers in Microbiology 12:1161

Six DL, Paine TD (1998) Effects of mycangial fungi and host tree species on progeny survival and emergence of *Dendroctonus ponderosae* (Coleoptera : Scolytidae). Environmental Entomology 27:1393-1401

Sommerfeld A, Rammer W, Heurich M, Hilmers T, Müller J, Seidl R (2021) Do bark beetle outbreaks amplify or dampen future bark beetle disturbances in Central Europe? Journal of Ecology 109:737-749. doi: https://doi.org/10.1111/1365-2745.13502

Stökl J, Steiger S (2017) Evolutionary origin of insect pheromones. Current Opinion in Insect Science 24:36-42. doi: https://doi.org/10.1016/j.cois.2017.09.004

Symonds MRE, Elgar MA (2004) The mode of pheromone evolution: evidence from bark beetles. Proceedings of the Royal Society of London Series B-Biological Sciences 271:839-846

Ulyshen MD, Ulyshen MD, Koerner (2018) Saproxylic insects. Springer

Vega FE, Hofstetter RW (2015) Bark Beetles: Biology and Ecology of Native and Invasive Species. Elsevier Science

Vogel S, Bussler H, Finnberg S, Müller J, Stengel E, Thorn S (2021a) Diversity and conservation of saproxylic beetles in 42 European tree species: an experimental approach using early successional stages of branches. Insect Conservation and Diversity 14:132-143. doi: https://doi.org/10.1111/icad.12442

Vogel S, Prinzing A, Bußler H, Müller J, Schmidt S, Thorn S (2021b) Abundance, not diversity, of host beetle communities determines abundance and diversity of parasitoids in deadwood. Ecology and Evolution 11. doi: 10.1002/ece3.7535

von Hoermann C, Ruther J, Ayasse M (2016) Volatile organic compounds of decaying piglet cadavers perceived by Nicrophorus vespilloides. Journal of chemical ecology 42:756-767

Wadke N, Kandasamy D, Vogel H, Lah L, Wingfield BD, Paetz C, Wright LP, Gershenzon J, Hammerbacher A (2016) The bark-beetle-associated fungus, *Endoconidiophora polonica*, utilizes the phenolic defense compounds of its host as a carbon source. Plant Physiology 171:914-931

Wegensteiner R, Wermelinger B, Herrmann M (2015) Natural enemies of bark beetles: predators, parasitoids, pathogens, and nematodes. In: Vega FE, Hofstetter RW (eds) Bark Beetles: Biology and Ecology of Native and Invasive Species. Academic Press, San Diego, pp 247-304

Weissbecker B, Holighaus G, Schütz S (2004) Gas chromatography with mass spectrometric and electroantennographic detection: analysis of wood odorants by direct coupling of insect olfaction and mass spectrometry. Journal of Chromatography A 1056:209-216. doi: http://dx.doi.org/10.1016/j.chroma.2004.06.120

Zhao T, Kandasamy D, Krokene P, Chen J, Gershenzon J, Hammerbacher A (2019) Fungal associates of the tree-killing bark beetle, *Ips typographus*, vary in virulence, ability to degrade conifer phenolics and influence bark beetle tunneling behavior. Fungal Ecology doi.org/10.1016/j.funeco.2018.06.003

4 Relevance of sex, gender and/or diversity

Project Description – Project Proposals

Prof. Dr. Claudia Kuenzer, Würzburg (PI)
Dr. Martin Wegmann, Würzburg (Co-PI)

SP3: Novel Earth Observation techniques for forest structure analyses and multi-scale characterization of forests

---

Project Description

1 Starting Point

1.1 State of the art and preliminary work

Earth Observation (EO) based forest research takes place at different spatial scales (very local to global), at differing spatial and temporal resolution, with a large variety of sensors, and a multitude of thematic foci. Global forest information at lower spatial resolution (500 m) was already made available in the early 2000s via a Vegetation Continuous Fields (VCF) product containing percent tree cover by the MODIS (Moderate Resolution Imaging Spectrometer) Science Team on an annual basis (Hansen et al. 2002). The German Aerospace Center, DLR, released a 50 m resampled mono-temporal global forest map based on radar data of the TanDEM-X mission (Martone et al. 2018). The Copernicus Land Monitoring Service of the European Union, EU, provides EO derived forest information for Europe (2013, 2015, 2018 so far), namely tree cover density (0-100%), tree dominant leaf type (deciduous or broadleaf majority), and forest type according to criteria of the Food and Agricultural Organization (FAO). Annual global forest maps (forest/non-forest and forest cover change) based on 30 m Landsat satellite data were first presented by Townshend et al. (2012) and Hansen et al. (2013), followed by a large record of publications on forest change and forest loss in individual countries based on annual (and locally intra-annual) updates of this geoinformation product (Potapov et al. 2015). In these studies, emphasis was on deforestation due to the enormous expansion of monoculture crops, such as soybean, oil palms, banana, citrus, and rubber (Song et al. 2021).

However, despite the enormous value of global or continental products and analyses, many of them do not satisfy specific local needs and lack of thematic detail and precision. Therefore, spectral unmixing-based approaches were developed to overcome limits of spatial resolution and retrieve forest cover fractions (Senf et al. 2020) or forest degradation (Chen et al. 2021). Beyond the discrimination of forest and non-forest, recent research is focused on forest type mapping (Dostálová et al. 2021), and individual tree species mapping (Axelsson et al. 2021; Immitzer et al. 2016; Maschler et al. 2018). The monitoring of forest disturbance and recovery is an essential application of EO (Frazier et al. 2015; Griffiths et al. 2014; Kennedy et al. 2010; White et al. 2017). Recent work has a focus on near-real time detection of forest disturbance (Pasquarella et al. 2017; Ye et al. 2021), particularly in the context of tropical forests (Hoekman et al. 2020; Reiche et al. 2021), also targeting discrimination and attribution of disturbances (Sebald et al. 2021). EO-based forest research for Europe and Germany is focusing more and more on a few selected topics. Firstly, excess of large-scale forest mortality, which is clearly linked to recent year droughts and impacts especially monoculture fir and spruce stands (Senf et al. 2020a; Senf et al. 2018). Secondly, assessments of smaller-scale forest mortality due to disturbances such as fire, storms, and bark beetle outbreaks (Latifi et al. 2018; Latifi et al. 2014a; Latifi et al. 2014b; Senf and Seidl 2021; Senf et al. 2017).

LIDAR data is currently indispensable for the assessment of forest structure (particularly the vertical dimension) (Coops et al. 2021; Jarron et al. 2020). Potapov et al. (2021) derived global forest canopy height at 30 m spatial resolution based on Landsat and Global Ecosystem Dynamics Investigation (GEDI) data; a light detection and ranging (LIDAR) instrument observing forests from the International Space Station (ISS). The product shows a R^2 0,61 correlation with airborne LIDAR data at a high level of significance. Airborne (also UAV based) laser scanning systems (ALS) mainly aiming at the estimation of single tree or stem counts, basal area, diameter breast height (DBH), stem volume, and crown coverage (Heurich 2008; Heurich and Thoma 2008). UAV based high spatial resolution orthomosaics can compete with LIDAR-based point clouds in the quantification of wood debris (Thiel et al. 2020a) and can be used to detect selective logging with very high accuracy. Thiel et al. (2020b) report precision >95% and recall >90% for the detection of selective logging in pine stands in Eastern Germany. The combination of LIDAR or field data with time series of operational systems such as Landsat and Sentinel-2 is powerful for the large-area estimation of biomass and forest structure (Bolton et al. 2020; Fang et al. 2019; Matasci et al. 2018a; Matasci et al. 2018b; Puliti et al. 2021).

In terms of methodological progress, deep learning has opened the floor for new applications at unprecedented levels of accuracy, e.g. single tree identification from high resolution images (Brandt et al. 2020; Onishi and Ise 2021), or the prediction of bark beetle outbreaks (Rammer and Seidl 2019). Forest condition monitoring over time based on indices such as the Normalized Differenced (or the Enhanced) Vegetation Index (NDVI, EVI) (Hermosilla et al. 2019; Philipp et al. 2021) or Leaf Area Index (LAI) allows for very local and highly accurate assessments of disturbances due to storms, forest fire, and pests (e.g. bark beetle outbreaks) (Einzmann et al. 2017; Huo et al. 2021), as well as 3D forest structure characterization, including information on tree and stem height, stem diameter, crown shape, and others.

With regard to biodiversity, the spectral species concept (Feret and Asner 2014) was an important step towards spatially explicit mapping of α- and β-diversity. The authors of this study used the Shannon index of spectral features derived from airborne hyperspectral data and found high correlation with field α-diversity estimates. They estimated variations in species composition (β-diversity) based on Bray-Curtis dissimilarity and achieved fairly good results (r = 0.61-0.76). (Rocchini et al. 2021) demonstrated applicability of the spectral species concept on larger areas. They used MODIS data to map biodiversity across Europe. Due to the low spatial resolution of 500 m, the spectral species in their approach represent species assemblages, habitats, or ecosystems rather than single (plant) species. Rocchini et al. (2018) proposed a set of innovative approaches to map β-diversity from aerial or satellite images. These comprise (1) multivariate statistical analysis (e.g. ordination techniques (Feilhauer et al. 2011; Feilhauer and Schmidtlein 2009; Hernández-Stefanoni et al. 2012)), (2) the spectral species concept (Feret and Asner 2014; Lausch et al. 2016), (3) self-organizing feature maps (Kohonen 1982), (4) multidimensional distance matrices (Legendre et al. 2005), and the (5) Rao's Q diversity (Rocchini et al. 2015).

During the last five years, EO has experienced a paradigm shift and entered a new era. The temporally highly resolved low and medium spatial resolution (per pixel resolution between 250 m and 1 km) multispectral sensors such as the Advanced Very High Resolution Radiometer (AVHRR, covering the last 4 decades (Dech et al. 2021)) and MODIS (covering the last two decades) and the Landsat system (16 day repeat cycle at 30 m spatial resolution) were supplemented by the Sentinel satellites. Given a relatively high degree of cloud cover in Germany, Landsat data availability was often limited to only a few cloud-free observations of an area per year. However, the European Space Agency (ESA) has launched the Sentinel satellite fleet, with the C-band synthetic aperture radar (SAR) sensor Sentinel 1a (launched 2014) and 1b (launched 2016), offering a SAR monitoring capacity at roughly 10 m spatial resolution with a repetition rate of six days with two satellites. Additionally, the multispectral sensors of Sentinel-2 (also a and b) were launched into orbit in 2015 and 2017, respectively, allowing for a 5-daily monitoring capacity with 12 spectral bands at 10 m spatial resolution. Combining this data with Landsat allows for even denser temporal observations. Additional EO sensors, such as the hyperspectral Italian sensor PRISMA (Hyperspectral Precursor of the Application Mission), the DLR Earth Sensing Imaging Spectrometer (DESIS) on board of ISS, the German TerraSAR-X and TanDEM-X X-band SAR sensors, or highest resolution optical sensors such as Worldview or Planet, offering a better than 1 m pixel resolution as well as airborne data (LIDAR, hyperspectral) and data acquired by unmanned aerial vehicles (UAVs, equipped with e.g. LIDAR, multispectral, thermal cameras) can complement the above-mentioned sensor “working horses” (Fig. 1). Furthermore, it is nowadays state of the art, that not only the spectral reflectance or backscatter of a pixel is of relevance for data analyses, but a much higher value usually comes with the temporal signature (reflectance-, backscatter- or index-behaviour of a pixel) over the course of time – e.g., a complete year or several years. Time series analyses of reflectance, temperature, backscatter, vegetation indices, or other geophysical parameters allow for the assessment of mean behaviour, minima, maxima, variability, and the derivation of trends and anomalies (Kuenzer et al. 2019; Kuenzer 2015).

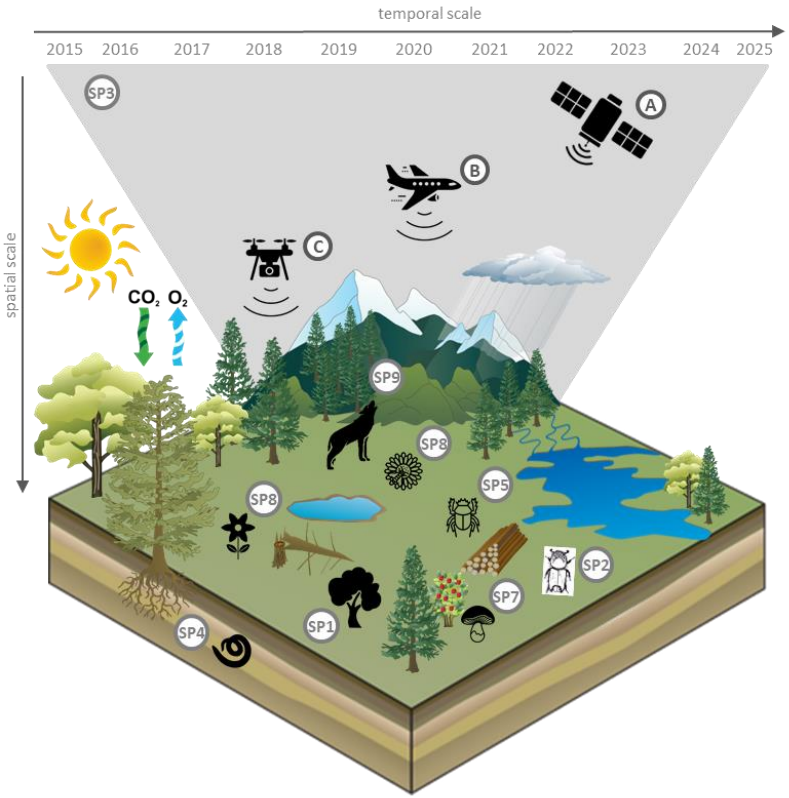


Figure adapted from Holzwarth et. al 2020
Courtesy of the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/symbols/), and the Noun project (https://thenounproject.com)

Fig. 1: The different sources and scales (A – satellite, B – airborne, C – UAV) of remote sensing data used for forest-related research in this project (SP1-9, see Fig. 2)

Due to eased data access to Sentinel fleet type satellite sensor data and free and open processing tools, also non-EO scientists started to analyse the data, yielding excellent cross-fertilization, such as e.g. Bae et al. (2019). They showed that Sentinel-1 SAR data to map the biodiversity of twelve taxa across five temperate forest regions performed similar to ALS data, and additionally found a good predictive ability of radar data on the species composition of selected birds and beetles.

State of the art EO-based research on forests in Germany was summarized by Holzwarth et al. (2020). From the 166 SCI papers and additional 101 literature and report sources published in the last two decades and reviewed in this article, it becomes obvious that EO assessments of forests in Germany still lack the exploitation of the full potential of EO as well as the trans-disciplinary cooperation. Only few of the reviewed papers take advantage of dense time series. There is a direct correlation for all studies between the EO platform used, the spatial resolution of the data, the size of the study area, and the object scale investigated (tree, stand, forest, landscape) (Holzwarth et al. 2020). This review also revealed that there is hardly any study that uses the full range of sensor types and characteristics (spatial, spectral, temporal resolution).

This research unit (RU) offers the possibility of trans-disciplinary approaches between biologists, conservationists, forest scientists, and EO-focused geoscientists, which are needed to exploit the full methodical potential of all tools available to characterize forests at tree, stand, regional, and landscape level based on remote sensing. To our knowledge there is no study exploring systematically the predictive power of remote sensing-based variables from various sensor systems with different sensor characteristics to model biodiversity and ecosystem function. Referring to this, we will support answering the question of the RU, whether the Enhancement of Structural Beta Complexity (ESBC) in forests by silviculture or natural disturbances will increase biodiversity and multifunctionality in formerly homogeneously structured production forests (see Coordination Project).

Preliminary work

Both, the PI and Co-PI from the University of Würzburg supervise and support the work of the PhD student. Additional scientists listed from the Earth Observation Center (EOC) of DLR assist this project “in kind”. They have over 20 year working experience in multi-sensor EO data analyses based on optical, multispectral, hyperspectral, SAR, and thermal data (Kuenzer 2013), including the in-depth analyses of dense multi-year time series (Kuenzer 2015), documented in over 300 SCI journal paper contributions.

We are strong in deriving phenological parameters, variability, trends, and anomalies, amongst others from time series of vegetation indices or biophysical parameters (NDVI, EVI, LAI, PAR etc.) or temperature and backscatter time series (Frey et al. 2017; Nguyen et al. 2015; Reinermann et al. 2019), as well as specific forest change information (Thonfeld et al. 2016; Thonfeld et al. 2015). This can be achieved by working with multi-sensor data from global (Dietz et al. 2015; Klein et al. 2017; Kuenzer et al. 2014a) down to very local scale (AVHRR, MODIS, Landsat, ASAR, PALSAR, Sentinel-1, Sentinel-2, DESIS, TerraSAR-X, TanDEM-X, Quickbird, Worldview, airborne AVIRIS, HySpex, UAV etc.), including EO data analyses and in-depth in-situ work, bridging the gap between the landscape and the field scale (Shi et al. 2018). C. Kuenzer and her team have successfully completed numerous forest ecosystem service-related studies combining remote sensing and in situ work to quantify ecosystem service functions and values in selected protected mangrove areas and biosphere reserves of Vietnam. This work included EO based individual tree species mapping, forest structure analyses, and forest disturbance assessments leading to quantitative assessments of different ecosystem service values for conservationists and decision makers (Kuenzer et al. 2011;

Kuenzer and Tuan 2013; Vo et al. 2012; Vo et al. 2013; Vo et al. 2015). C. Kuenzer has supervised a PhD thesis developing a novel approach for biomass modelling (net primary productivity, NPP) in semi-arid environments with accuracies exceeding 90% when compared to destructive biomass field sampling for validation (Eisfelder et al. 2017; Eisfelder et al. 2014; Eisfelder et al. 2011; Eisfelder et al. 2013), and supervised studies on reforestation and afforestation in primary and secondary forests of Latin America and Southeast Asia based on multi-decadal time series (Da Ponte et al. 2015; Da Ponte et al. 2017a; Da Ponte et al. 2017b; Da Ponte et al. 2017c), for the first time quantifying country-wide forest loss for all of Paraguay and the transboundary Mekong Basin (Leinenkugel et al. 2015). The team of C. Kuenzer supports the Data Pool Initiative for the Bohemian Forest Ecosystem (Latifi et al. 2021) including EO data analyses e.g. very localized plant functional trait mapping linking equivalent water thickness, leaf mass per area and leaf chlorophyll retrieved from hyperspectral airborne data to airborne lidar derived metrics with an accuracy exceeding 83% (Shi et al. 2018). Not only these activities foster a strong link with biology. Furthermore, we have cooperated with biologists on frameworks of trans-disciplinary cooperation and data analyses connecting EO with bioscience and biodiversity research (Kuenzer et al. 2014b; Skidmore et al. 2021), and contributed to EO projects with colleagues from insect research in projects on locust spread in Kazakhstan and Africa proving remote sensing to be a powerful tool for the early detection of locust colonies aiming at the suppression of swarming (Klein et al. 2021; Klein in preparation). Our recent forest-related activities in Germany resulted in a comprehensive review based on over 160 SCI journal papers analysed towards the potential of EO for forest mapping and analyses supporting forest management in Germany (Holzwarth et al. 2020), with C. Kuenzer as initiator and actively writing senior author. Furthermore, we are mapping the impacts of recent drought years (2018, 2019) on forests in Germany at national scale, completing a country-wide inventory of forest loss over the past three years at monthly resolution (under preparation for publication by Frank Thonfeld., submission still in 2021). Preliminary results suggest massive losses of forest, especially within spruce monoculture stands but also in selected broadleaf and mixed forest stands, summing up to between 3 and 25% of forest loss in the individual administrative regions (Landkreise).

This goes in line with the activities of Co-PI Martin Wegmann, focusing on remote sensing for ecology and biodiversity research, heavily contributing to the work of GEO BON (the Group on Earth Observations Biodiversity Observation Network) (Pereira et al. 2013; Pettorelli et al. 2018; Rocchini et al. 2015; Rocchini et al. 2018; Rocchini et al. 2021; Skidmore et al. 2021; Skidmore et al. 2015). In this context, he has published on forest fragmentation and spatial indices, finding out that commonly used simple fragmentation measures are not adequate to derive fragmentation information in forests (Wegmann et al. 2014) and developed novel methods for improved fragmentation mapping (Wegmann et al. 2017). Just this year, he co-published a study underlining that remote sensing-based harmonic analyses of MODIS-based NDVI time series do provide adequate information on forest drought conditions covering complete Germany (Philipp et al. 2021).

Method-wise we are currently largely involved in the development of innovative deep learning algorithms for high-volume, multi-source data analyses based on convolutional neural networks and transferable generic algorithm training approaches (Hoeser et al. 2020; Hoeser and Kuenzer 2020).

Overall, our group has a very sound understanding of the potentials as well as the limitations of remote sensing based EO and all currently existing individual sensor systems. We have developed a large pool of methods for EO data pre-processing such as sensor calibration, systematic distortion correction, geometric- and topographic correction, atmospheric correction (de Los Reyes et al. 2020; Dech et al. 2021; Dietz et al. 2017), have sound tools for data analyses such as transformation, classification, sub-pixel approaches, and index derivation (Huth et al. 2012; Lu et al. 2015; Mack et al. 2016; Wegmann 2016; Wegmann 2020), and are especially strong in dense time series analyses of high-volume complex optical, multispectral, thermal, and SAR data (Dech et al. 2021; Hu et al. 2019; Klein et al. 2017; Knauer et al. 2017; Reinermann et al. 2019; Uereyen submitted), which will be of high relevance and benefit for our contribution to this RU.

In terms of remote sensing data acquisition, we have access to all relevant operational satellite data from the Landsat and Copernicus (Sentinels) programs free of charge, including also all archived data of the past years. We also have access to data from various flight campaigns over the Bavarian Forest National Park and the Sailershausen test site acquired in the past. These data include airborne hyperspectral and LIDAR data. Two airborne campaigns were conducted in the intensive sites before the treatment with two different imaging spectrometer systems (AVIRIS-NG at a spatial resolution of 1.9 m and 3.8 m, HySpex at a spatial resolution of 1.5 m (VNIR) and 3.0 m (SWIR)). We carried out another flight campaign with the imaging spectrometer system HySpex in summer 2020, hence after the treatment. Airborne LIDAR Scanning (ALS) data was collected before and after. Furthermore, an extensive data cube of spaceborne data form the above-mentioned variety of sensors is currently being generated. DLR runs state-of-the-art facilities and infrastructure for consistent processing of large data volumes.

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. Da Ponte E., Fleckenstein M., Leinenkugel P., Parker A., Oppelt N., **Kuenzer C.** (2015). Tropical forest cover dynamics for Latin America using Earth observation data: a review covering the continental, regional, and local scale. International Journal of Remote Sensing 36:3196-3242.
2. Da Ponte E., Mack B., Wohlfart C., Rodas O., Fleckenstein M., Oppelt N., Dech S., & **Kuenzer C.** (2017). Assessing Forest Cover Dynamics and Forest Perception in the Atlantic Forest of Paraguay, Combining Remote Sensing and Household Level Data. Forests, 8
3. Da Ponte E., **Kuenzer C.**, Parker A., Rodas O., Oppelt N., Fleckenstein M. (2017a) Forest cover loss in Paraguay and perception of ecosystem services: A case study of the Upper Parana Forest. Ecosystem Services 24:200-212.
4. Da Ponte E., Roch M., Leinenkugel P., Dech S., **Kuenzer C.** (2017c) Paraguay's Atlantic Forest cover loss – Satellite-based change detection and fragmentation analysis between 2003 and 2013. Applied Geography 79:37-49.
5. Hoeser T. & **Kuenzer C.** (2020). Object Detection and Image Segmentation with Deep Learning on Earth Observation Data: A Review-Part I: Evolution and Recent Trends. Remote Sensing, 12
6. Holzwarth S., Thonfeld F., Abdullahi S., Asam S., Canova E.P., Gessner U., Huth J., Kraus T., Leutner B., & **Kuenzer C.** (2020). Earth Observation Based Monitoring of Forests in Germany: A Review. Remote Sensing, 12
7. Klein I., Oppelt N. & **Kuenzer C.** (2021). Application of Remote Sensing Data for Locust Research and Management-A Review. Insects, 12
8. **Kuenzer C.** & Tuan V.Q. (2013). Assessing the ecosystem services value of Can Gio Mangrove Biosphere Reserve: Combining earth-observation- and household-survey-based analyses. Applied Geography, 45, 167-184
9. **Kuenzer C.**, Ottinger, M., Wegmann, M., Guo, H., Wang, C., Zhang, J., Dech, S., Wikelski, M. (2014b) Earth observation satellite sensors for biodiversity monitoring: potentials and bottlenecks. International Journal of Remote Sensing 35:6599-6647
10. Leinenkugel P., Wolters M.L., Oppelt N. & **Kuenzer C.** (2015). Tree cover and forest cover dynamics in the Mekong Basin from 2001 to 2011. Remote Sensing of Environment, 158, 376-392

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.2.3 Patents

Not applicable

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

Four years

2.2 Objectives

Our main objective is to bridge the scales of in-situ measurements of forest structure, biodiversity and functionality, fine-scale near-distance remote sensing (UAV type, airborne), and space-borne satellite remote sensing. We aim at an improved understanding if and how the joint analyses of multi-sensor data at different spectral, spatial and temporal resolutions with a focus on biodiversity and ecosystem functions can contribute to assessments at in-situ level, including the patch level, as well as the forest district (Fig. 1). Therefore, we follow a strategy to consider as many different remote sensing technologies and data types as currently available, including data from multi-sensor UAV (multispectral, thermal, Lidar), airborne hyperspectral and spaceborne multispectral, hyperspectral, thermal, and SAR at various spectral, spatial, radiometric, and temporal resolutions. As we consider time and multitemporal information crucial for the assessment of biodiversity and ecosystem function and their variation, all data will be available as multi-seasonal time series.

We aim on testing three major hypotheses for our subproject with a focus on forest structure retrieval at various scales:

Hypothesis 1: *The variety of experimental forest disturbances taking place on multiple vertical and horizontal dimensions can be observed by remote sensing data to a sensor-specific extent.*

Due to the ecosystem's disturbance-specific post-disturbance recovery dynamics and its vertical and horizontal spatial characteristics and due to the remote sensing system's characteristics (sensor type, spatial, spectral, temporal resolution), the possibility to observe the different disturbances is time- and sensor-dependent. To test hypothesis 1, we will take advantage of state-of-the-art data processing methodologies to quantify which information (e.g. spectral index) of which sensor is capable to detect which disturbance to what extent. Consequently, we will categorize the temporality of the disturbances, i.e. if and how long they can be detected with the various sensors.

Hypothesis 2: *Multi-sensor data explains the relationship of Earth Observation and biodiversity field data (forest β- and γ-diversity at patch, district and larger landscape scale) better than single sensor data.*

While most recent scientific studies make use of single sensors to map biodiversity and ecosystem function over larger areas, we will assess a comprehensive suite of sensors to identify the best variables (and hence required sensor characteristics) to model β-diversity derived from in-situ measurements at patch level and scale out towards γ-diversity at larger landscape level, also in areas where in-situ data is not available.

Hypothesis 3: *Space-borne remote sensing time series data are suitable to capture the variation of β-diversity and ecosystem function at larger landscape scale over time.*

The approaches allowing for the modelling of biodiversity and ecosystem function in space (H2) will be extended to monitor biodiversity and ecosystem function changes over space and time. To test this hypothesis, we explore if temporal high-resolution space-borne data are suitable to capture the variation of essential biodiversity and ecosystem function variables for the forest districts over time, with a special focus on extreme events such as droughts.

Data exchange and collaboration within the consortium

For the whole RU and syntheses in SPZ, we generate time series of parameters and indices derived from remote sensing data that link to forest structure and ecosystem function primary productivity, with strongest links to SP1, SP7, and SP9 (Fig. 2). Our data will be supplemented by forest structure data derived from terrestrial laser scanning (TLS) from SP1, which will help us to bridge the scale of in-situ measurements and large-coverage spaceborne EO data and regionalize the estimation of β-diversity. Reversely, SPZ will provide us with the field data at patch level regarding species occurrence, and inventory data in general. The data and parameters we processed are shared with partners as needed, e.g. with SP7 for integration into their models, and with SP9 and SP1 as comparative information from satellite data, among others. Furthermore, data on forest structure will be exchanged with SP2, SP4, and SP6.

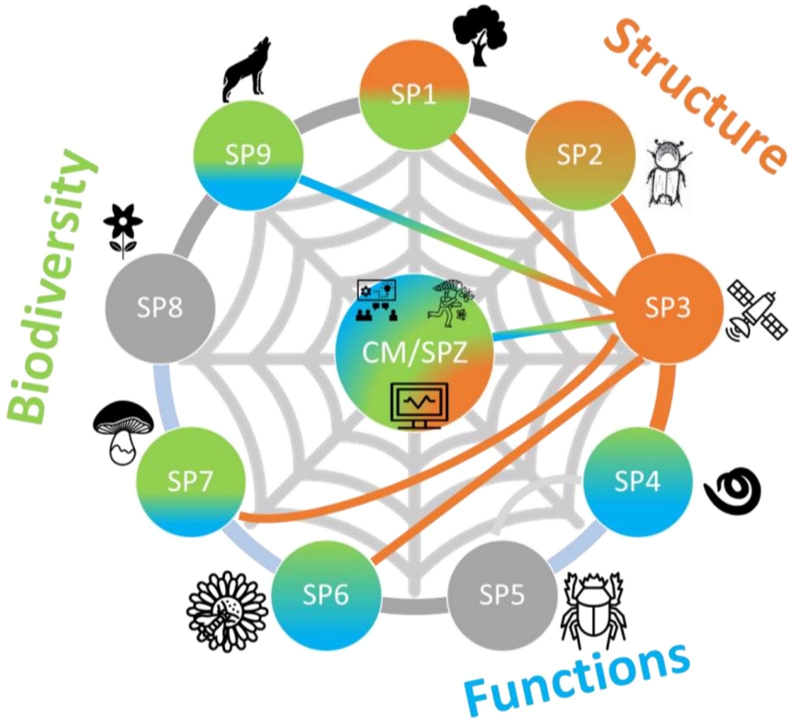


Fig 2: Close cooperation of SP3 with other subprojects, the colour of arrows indicates the type of data exchanged.

2.3 Work programme including proposed research methods

All tasks are within the responsibility of the PhD student and will be supervised by C. Kuenzer. Support is given by S. Holzwarth, J. Huth and F. Thonfeld, all with expertise in remote sensing of forests, data acquisition and processing. M. Wegmann and a team of students will conduct the UAV flights. He will also support the PhD student in data processing. Due to the diversity and size of the data and the organizational challenges particularly related to the UAV campaigns, we focus on three major test sites (Sailershausen, Bavarian Forest National Park, Lübeck) where drone flights will be conducted. However, all districts will be considered for method validation.

WP1: Data pre-processing and harmonization

This work package includes the consistent pre-processing of the various data. DLR facilities and processing routines will be used to continuously supplement the data record with new acquisitions. Given the huge variety of sensor types and data characteristics, harmonization of the data is mandatory, aiming at consistent data cubes with geometrically and atmospherically corrected (if applicable cross-calibrated) data using state-of-the-art methods and reproducible code. This work package will be supported by student assistants. Organization and planning of UAV flight campaigns are part of this work package and will happen in close collaboration with M. Wegmann.

WP2: Multisensor categorization of the temporal domain of different disturbances at various spatial scales

This work package is related to Hypothesis 1 and aims at categorizing the temporality of the experimental treatments with regard to the different sensors. Therefore, a set of meaningful parameters and indices will be derived from the remote sensing data, including e.g. structural parameters from LIDAR (such as canopy surface height or standard deviation of canopy height), spectral indices, and SAR backscatter indices. Taking advantage of data taken before the treatments and afterwards, the PhD student will quantify if, when (under which conditions, e.g. leaf-on vs. leaf-off) and how long the different disturbances can be detected by the different remote sensing-derived parameters by comparing the treatments with the control plots and accounting for the different data properties (Bae et al. 2019).

WP3: Benchmarking spatial, spectral, and temporal resolution and sensor type for the assessment of forest β- and γ-diversity

This work package is linked to Hypothesis 2. The PhD student will use machine learning regression approaches and models to link the spatial variation of essential biodiversity variables enabled with remote sensing , so-called RS-EBV (Skidmore et al. 2021), and ecosystem functions (β-diversity) at the forest district level to species diversity and functions recorded in-situ within the different patches (field data including taxa data from SPZ and other SPs). The work includes the identification of the best-suited parameters (and combinations) and models. In the next step, the patch level information will be transferred to the complete forest ecosystem by suitable models (Deneu et al. 2021). Methods will consider the latest scientific findings and recommendations as summarized in (Rocchini et al. 2018) and demonstrated in (Frye et al. 2021; Rocchini et al. 2021), e.g. multivariate statistical analysis (ordination techniques, (Feilhauer and Schmidtlein 2009)), spectral species concept (Feret and Asner 2014), self-organizing feature maps, multidimensional distance matrices, and Rao's Q diversity. Ordination techniques, for example, are suitable to quantitatively describe multivariate gradual transitions in the species composition of sampled sites. Each pixel of the image data is assigned to a specific position in the ordination space that indicates its species composition. The resulting gradient maps allow for analyses of β diversity across different spatial scales. The spectral species concept will be used to map α- and β-diversity over large areas with coarser spatial resolution remote sensing data (Rocchini et al. 2021). We will focus on Sentinel-2 like data.

With respect to scale, the PhD student will investigate the impact of decreased spatial and spectral resolution (space-borne sensors vs. airborne and UAV) on the ability to properly differentiate ecologically meaningful spectral species across landscapes and over regions.

WP4: Track variation of essential biodiversity and ecosystem function variables

While WP3 has a focus on the spatial dimension, this WP4 is more related to the temporal domain and linked to Hypothesis 3. Consequently, the PhD will analyse the variation of biodiversity and ecosystem function related parameters (and hence β- and γ-diversity) over time. Data available before and after the treatments will be used to characterise discernible effects of the interventions at patch scale (WP2). The PhD student will build upon findings of WP2 and WP3 to extract most powerful variables from Satellite data and apply them to the extensive sites and over time. For all sites, large coverage satellite data (e.g. Sentinel-1/2) are publicly available for all before and after treatment years.

Table 2: Time table of the work program by month.

	2022									2023												2024												2025												2026		
WP 1 - Data pre-processing and harmonization																																																
data collection	▨	▨	▨	▨	▨	▨	▨			▨	▨											▨	▨											▨	▨													
data pre-processing	▨	▨	▨	▨	▨	▨	▨			▨	▨											▨	▨											▨	▨													
data harmonization					▨	▨	▨	▨	▨																																							
WP 2 - Multisensor categorization of the temporal domain																																																
indices and parameter derivation										▨	▨	▨	▨	▨	▨	▨	▨																															
multisensor data analyses												▨	▨	▨	▨	▨	▨	▨	▨																													
temporal domain analyses														▨	▨	▨	▨	▨	▨	▨	▨																											
WP 3 - Benchmarking spatial, spectral and temporal resolution and sensor type																																																
adaptation of taxa data																						▨	▨	▨	▨	▨	▨																					
regression analyses combined with taxa																										▨	▨	▨	▨	▨																		
method selection																												▨	▨	▨																		
up-scaling and assessment of results																														▨	▨	▨	▨															
WP 4 - Track variation of essential biodiversity and ecosystem function variable																																																
satellite time series analyses																																		▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨			
estimation of ecosystem diversity																																						▨	▨	▨	▨	▨	▨	▨	▨	▨		
spatial transfer to extensive sites																																										▨	▨	▨	▨	▨	▨	▨

3 Bibliography concerning the state of the art, the research objectives, and the work programme

Axelsson A, Lindberg E, Reese H, Olsson H (2021) Tree species classification using Sentinel-2 imagery and Bayesian inference. International Journal of Applied Earth Observation and Geoinformation 100. doi: 10.1016/j.jag.2021.102318

Bae S et al. (2019) Radar vision in the mapping of forest biodiversity from space. Nat. Commun. 10:10. doi: 10.1038/s41467-019-12737-x

Bolton DK et al. (2020) Optimizing Landsat time series length for regional mapping of lidar-derived forest structure. Remote Sens Environ 239. doi: 10.1016/j.rse.2020.111645

Brandt M et al. (2020) An unexpectedly large count of trees in the West African Sahara and Sahel. Nature 587:78-82. doi: 10.1038/s41586-020-2824-5

Chen S et al. (2021) Monitoring temperate forest degradation on Google Earth Engine using Landsat time series analysis. Remote Sens Environ 265. doi: 10.1016/j.rse.2021.112648

Coops NC et al. (2021) Modelling lidar-derived estimates of forest attributes over space and time: A review of approaches and future trends. Remote Sens Environ 260. doi: 10.1016/j.rse.2021.112477

Da Ponte E, Fleckenstein M, Leinenkugel P, Parker A, Oppelt N, Kuenzer C (2015) Tropical forest cover dynamics for Latin America using Earth observation data: a review covering the continental, regional, and local scale. International Journal of Remote Sensing 36:3196-3242. doi: 10.1080/01431161.2015.1058539

Da Ponte E, Kuenzer C, Parker A, Rodas O, Oppelt N, Fleckenstein M (2017a) Forest cover loss in Paraguay and perception of ecosystem services: A case study of the Upper Parana Forest. Ecosystem Services 24:200-212. doi: 10.1016/j.ecoser.2017.03.009

Da Ponte E et al. (2017b) Assessing Forest Cover Dynamics and Forest Perception in the Atlantic Forest of Paraguay, Combining Remote Sensing and Household Level Data. Forests 8. doi: 10.3390/f8100389

Da Ponte E, Roch M, Leinenkugel P, Dech S, Kuenzer C (2017c) Paraguay's Atlantic Forest cover loss – Satellite-based change detection and fragmentation analysis between 2003 and 2013. Applied Geography 79:37-49. doi: 10.1016/j.apgeog.2016.12.005

de Los Reyes R et al. (2020) PACO: Python-Based Atmospheric COrrection. Sensors (Basel) 20. doi: 10.3390/s20051428

Dech S et al. (2021) Potential and Challenges of Harmonizing 40 Years of AVHRR Data: The TIMELINE Experience. Remote Sensing 13. doi: 10.3390/rs13183618

Deneu B, Servajean M, Bonnet P, Botella C, Munoz F, Joly A (2021) Convolutional neural networks improve species distribution modelling by capturing the spatial structure of the environment. PLoS Comput Biol 17:e1008856. doi: 10.1371/journal.pcbi.1008856

Dietz A, Frey C, Ruppert T, Bachmann M, Kuenzer C, Dech S (2017) Automated Improvement of Geolocation Accuracy in AVHRR Data Using a Two-Step Chip Matching Approach—A Part of the TIMELINE Preprocessor. Remote Sensing 9. doi: 10.3390/rs9040303

Dietz AJ, Kuenzer C, Dech S (2015) Global SnowPack: a new set of snow cover parameters for studying status and dynamics of the planetary snow cover extent. Remote Sensing Letters 6:844-853. doi: 10.1080/2150704x.2015.1084551

Dostálová A, Lang M, Ivanovs J, Waser LT, Wagner W (2021) European Wide Forest Classification Based on Sentinel-1 Data. Remote Sensing 13. doi: 10.3390/rs13030337

Einzmann K, Immitzer M, Bock S, Bauer O, Schmitt A, Atzberger C (2017) Windthrow Detection in European Forests with Very High-Resolution Optical Data. Forests 8:26. doi: 10.3390/f8010021

Eisfelder C, Klein I, Bekkuliyeva A, Kuenzer C, Buchroithner MF, Dech S (2017) Above-ground biomass estimation based on NPP time-series − A novel approach for biomass estimation in semi-arid Kazakhstan. Ecological Indicators 72:13-22. doi: 10.1016/j.ecolind.2016.07.042

Eisfelder C, Klein I, Niklaus M, Kuenzer C (2014) Net primary productivity in Kazakhstan, its spatio-temporal patterns and relation to meteorological variables. Journal of Arid Environments 103:17-30. doi: 10.1016/j.jaridenv.2013.12.005

Eisfelder C, Kuenzer C, Dech S (2011) Derivation of biomass information for semi-arid areas using remote-sensing data. International Journal of Remote Sensing 33:2937-2984. doi: 10.1080/01431161.2011.620034

Eisfelder C, Kuenzer C, Dech S, Buchroithner (2013) Comparison of Two Remote Sensing Based Models for Regional Net Primary Productivity Estimation—A Case Study in Semi-Arid Central Kazakhstan. IEEE Journal of Selected Topics in Applied Earth Observations and Remote Sensing 6:1843-1856. doi: 10.1109/jstars.2012.2226707

Fang L, Yang J, Zhang W, Zhang W, Yan Q (2019) Combining allometry and landsat-derived disturbance history to estimate tree biomass in subtropical planted forests. Remote Sens Environ 235. doi: 10.1016/j.rse.2019.111423

Feilhauer H, Faude U, Schmidtlein S (2011) Combining Isomap ordination and imaging spectroscopy to map continuous floristic gradients in a heterogeneous landscape. Remote Sens Environ 115:2513-2524. doi: 10.1016/j.rse.2011.05.011

Feilhauer H, Schmidtlein S (2009) Mapping continuous fields of forest alpha and beta diversity. Applied Vegetation Science 12:429-439. doi: 10.1111/j.1654-109X.2009.01037.x

Feret JB, Asner GP (2014) Mapping tropical forest canopy diversity using high-fidelity imaging spectroscopy. Ecol Appl 24:1289-1296. doi: 10.1890/13-1824.1

Frazier RJ, Coops NC, Wulder MA (2015) Boreal Shield forest disturbance and recovery trends using Landsat time series. Remote Sens Environ 170:317-327. doi: 10.1016/j.rse.2015.09.015

Frey C, Kuenzer C, Dech S (2017) Assessment of Mono- and Split-Window Approaches for Time Series Processing of LST from AVHRR—A TIMELINE Round Robin. Remote Sensing 9. doi: 10.3390/rs9010072

Frye HA et al. (2021) Plant spectral diversity as a surrogate for species, functional and phylogenetic diversity across a hyper-diverse biogeographic region. Global Ecology and Biogeography 30:1403-1417. doi: 10.1111/geb.13306

Griffiths P et al. (2014) Forest disturbances, forest recovery, and changes in forest types across the Carpathian ecoregion from 1985 to 2010 based on Landsat image composites. Remote Sens Environ 151:72-88. doi: 10.1016/j.rse.2013.04.022

Hansen MC, DeFries RS, Townshend JRG, Sohlberg R, Dimiceli C, Carroll M (2002) Towards an operational MODIS continuous field of percent tree cover algorithm: examples using AVHRR and MODIS data. Remote Sens Environ 83:303-319. doi: 10.1016/s0034-4257(02)00079-2

Hansen MC et al. (2013) High-resolution global maps of 21st-century forest cover change. Science 342:850-853. doi: 10.1126/science.1244693

Hermosilla T, Wulder MA, White JC, Coops NC, Pickell PD, Bolton DK (2019) Impact of time on interpretations of forest fragmentation: Three-decades of fragmentation dynamics over Canada. Remote Sens Environ 222:65-77. doi: 10.1016/j.rse.2018.12.027

Hernández-Stefanoni JL, Gallardo-Cruz JA, Meave JA, Rocchini D, Bello-Pineda J, López-Martínez JO (2012) Modeling α- and β-diversity in a tropical forest from remotely sensed and spatial data. International Journal of Applied Earth Observation and Geoinformation 19:359-368. doi: 10.1016/j.jag.2012.04.002

Heurich M (2008) Automatic recognition and measurement of single trees based on data from airborne laser scanning over the richly structured natural forests of the Bavarian Forest National Park. For. Ecol. Manage. 255:2416-2433. doi: 10.1016/j.foreco.2008.01.022

Heurich M, Thoma F (2008) Estimation of forestry stand parameters using laser scanning data in temperate, structurally rich natural European beech (Fagus sylvatica) and Norway spruce (Picea abies) forests. Forestry 81:645-661. doi: 10.1093/forestry/cpn038

Hoekman D et al. (2020) Wide-Area Near-Real-Time Monitoring of Tropical Forest Degradation and Deforestation Using Sentinel-1. Remote Sensing 12. doi: 10.3390/rs12193263

Hoeser T, Bachofer F, Kuenzer C (2020) Object Detection and Image Segmentation with Deep Learning on Earth Observation Data: A Review—Part II: Applications. Remote Sensing 12. doi: 10.3390/rs12183053

Hoeser T, Kuenzer C (2020) Object Detection and Image Segmentation with Deep Learning on Earth Observation Data: A Review-Part I: Evolution and Recent Trends. Remote Sensing 12. doi: 10.3390/rs12101667

Holzwarth S et al. (2020) Earth Observation Based Monitoring of Forests in Germany: A Review. Remote Sensing 12. doi: 10.3390/rs12213570

Hu Z, Dietz A, Kuenzer C (2019) The potential of retrieving snow line dynamics from Landsat during the end of the ablation seasons between 1982 and 2017 in European mountains. International Journal of Applied Earth Observation and Geoinformation 78:138-148. doi: 10.1016/j.jag.2019.01.010

Huo L, Persson HJ, Lindberg E (2021) Early detection of forest stress from European spruce bark beetle attack, and a new vegetation index: Normalized distance red & SWIR (NDRS). Remote Sens Environ 255. doi: 10.1016/j.rse.2020.112240

Huth J, Kuenzer C, Wehrmann T, Gebhardt S, Tuan VQ, Dech S (2012) Land Cover and Land Use Classification with TWOPAC: towards Automated Processing for Pixel- and Object-Based Image Classification. Remote Sensing 4:2530-2553. doi: 10.3390/rs4092530

Immitzer M, Vuolo F, Atzberger C (2016) First Experience with Sentinel-2 Data for Crop and Tree Species Classifications in Central Europe. Remote Sensing 8:27. doi: 10.3390/rs8030166

Jarron LR, Coops NC, MacKenzie WH, Tompalski P, Dykstra P (2020) Detection of sub-canopy forest structure using airborne LiDAR. Remote Sens Environ 244. doi: 10.1016/j.rse.2020.111770

Kennedy RE, Yang Z, Cohen WB (2010) Detecting trends in forest disturbance and recovery using yearly Landsat time series: 1. LandTrendr — Temporal segmentation algorithms. Remote Sens Environ 114:2897-2910. doi: 10.1016/j.rse.2010.07.008

Klein I, Gessner U, Dietz AJ, Kuenzer C (2017) Global WaterPack – A 250 m resolution dataset revealing the daily dynamics of global inland water bodies. Remote Sens Environ 198:345-362. doi: 10.1016/j.rse.2017.06.045

Klein I, Oppelt N, Kuenzer C (2021) Application of Remote Sensing Data for Locust Research and Management-A Review. Insects 12. doi: 10.3390/insects12030233

Klein I, van der Woude, S., Muratova, N., Malakhov, D., Oppelt, N., Kuenzer, C. (in preparation) Breeding Habitat Suitability for Locust Species – A combined approach to identify suitable breeding areas based on multiple datasets.

Knauer K, Gessner U, Fensholt R, Forkuor G, Kuenzer C (2017) Monitoring Agricultural Expansion in Burkina Faso over 14 Years with 30 m Resolution Time Series: The Role of Population Growth and Implications for the Environment. Remote Sensing 9. doi: 10.3390/rs9020132

Kohonen T (1982) Analysis of a simple self-organizing process. Biological Cybernetics 44:135-140. doi: 10.1007/bf00317973

Kuenzer, Heimhuber, Huth, Dech (2019) Remote Sensing for the Quantification of Land Surface Dynamics in Large River Delta Regions—A Review. Remote Sensing 11. doi: 10.3390/rs11171985

Kuenzer C, Bluemel A, Gebhardt S, Quoc TV, Dech S (2011) Remote Sensing of Mangrove Ecosystems: A Review. Remote Sensing 3:878-928. doi: 10.3390/rs3050878

Kuenzer C., Dech, S., and Wagner, W., (2015) Remote Sensing Time Series - Revealing Land Surface Dynamics. Remote Sensing and Digital Image Processing. Springer, Cham. doi: 10.1007/978-3-319-15967-6

Kuenzer C, Leinenkugel P, Vollmuth M, Dech S (2014a) Comparing global land-cover products – implications for geoscience applications: an investigation for the trans-boundary Mekong Basin. International Journal of Remote Sensing 35:2752-2779. doi: 10.1080/01431161.2014.890305

Kuenzer C et al. (2014b) Earth observation satellite sensors for biodiversity monitoring: potentials and bottlenecks. International Journal of Remote Sensing 35:6599-6647. doi: 10.1080/01431161.2014.964349

Kuenzer C, Tuan VQ (2013) Assessing the ecosystem services value of Can Gio Mangrove Biosphere Reserve: Combining earth-observation- and household-survey-based analyses. Applied Geography 45:167-184. doi: 10.1016/j.apgeog.2013.08.012

Kuenzer C., Dech, S. (2013) Thermal Infrared Remote Sensing. Sensors, Methods, Applications. Remote Sensing and Digital Image Processing, volume 17. Springer. doi: 10.1007/978-94-007-6639-6

Latifi H et al. (2021) A laboratory for conceiving Essential Biodiversity Variables (EBVs)—The 'Data pool initiative for the Bohemian Forest Ecosystem'. Methods in Ecology and Evolution. doi: 10.1111/2041-210x.13695

Lausch A et al. (2016) Linking Earth Observation and taxonomic, structural and functional biodiversity: Local to ecosystem perspectives. Ecological Indicators 70:317-339. doi: 10.1016/j.ecolind.2016.06.022

Legendre P, Borcard D, Peres-Neto PR (2005) Analyzing beta diversity: Partitioning the spatial variation of community composition data. Ecological Monographs 75:435-450. doi: Doi 10.1890/05-0549

Leinenkugel P, Wolters ML, Oppelt N, Kuenzer C (2015) Tree cover and forest cover dynamics in the Mekong Basin from 2001 to 2011. Remote Sens Environ 158:376-392. doi: 10.1016/j.rse.2014.10.021

Lu L, Kuenzer C, Wang C, Guo H, Li QJRS (2015) Evaluation of Three MODIS-Derived Vegetation Index Time Series for Dryland Vegetation Dynamics Monitoring. 7:7597-7614

Mack B, Leinenkugel P, Kuenzer C, Dech S (2016) A semi-automated approach for the generation of a new land use and land cover product for Germany based on Landsat time-series and Lucas in-situ data. Remote Sensing Letters 8:244-253. doi: 10.1080/2150704x.2016.1249299

Martone M et al. (2018) The global forest/non-forest map from TanDEM-X interferometric SAR data. Remote Sens Environ 205:352-373. doi: 10.1016/j.rse.2017.12.002

Maschler J, Atzberger C, Immitzer M (2018) Individual Tree Crown Segmentation and Classification of 13 Tree Species Using Airborne Hyperspectral Data. Remote Sensing 10. doi: 10.3390/rs10081218

Matasci G et al. (2018a) Three decades of forest structural dynamics over Canada's forested ecosystems using Landsat time-series and lidar plots. Remote Sens Environ 216:697-714. doi: 10.1016/j.rse.2018.07.024

Matasci G et al. (2018b) Large-area mapping of Canadian boreal forest cover, height, biomass and other structural attributes using Landsat composites and lidar plots. Remote Sens Environ 209:90-106. doi: 10.1016/j.rse.2017.12.020

Nguyen D, Clauss K, Cao S, Naeimi V, Kuenzer C, Wagner W (2015) Mapping Rice Seasonality in the Mekong Delta with Multi-Year Envisat ASAR WSM Data. Remote Sensing 7:15868-15893. doi: 10.3390/rs71215808

Onishi M, Ise T (2021) Explainable identification and mapping of trees using UAV RGB image and deep learning. Sci Rep 11:903. doi: 10.1038/s41598-020-79653-9

Pasquarella V, Bradley B, Woodcock C (2017) Near-Real-Time Monitoring of Insect Defoliation Using Landsat Time Series. Forests 8. doi: 10.3390/f8080275

Pereira HM et al. (2013) Ecology. Essential biodiversity variables. Science 339:277-278. doi: 10.1126/science.1229931

Pettorelli N et al. (2018) Satellite remote sensing of ecosystem functions: opportunities, challenges and way forward. Remote Sensing in Ecology and Conservation 4:71-93. doi: 10.1002/rse2.59

Philipp M, Wegmann M, Kübert-Flock C (2021) Quantifying the Response of German Forests to Drought Events via Satellite Imagery. Remote Sensing 13. doi: 10.3390/rs13091845

Potapov P et al. (2021) Mapping global forest canopy height through integration of GEDI and Landsat data. Remote Sens Environ 253. doi: 10.1016/j.rse.2020.112165

Potapov PV et al. (2015) Eastern Europe's forest cover dynamics from 1985 to 2012 quantified from the full Landsat archive. Remote Sens Environ 159:28-43. doi: 10.1016/j.rse.2014.11.027

Puliti S, Breidenbach J, Schumacher J, Hauglin M, Klingenberg TF, Astrup R (2021) Above-ground biomass change estimation using national forest inventory data with Sentinel-2 and Landsat. Remote Sens Environ 265. doi: 10.1016/j.rse.2021.112644

Rammer W, Seidl R (2019) Harnessing Deep Learning in Ecology: An Example Predicting Bark Beetle Outbreaks. Front Plant Sci 10:1327. doi: 10.3389/fpls.2019.01327

Reiche J et al. (2021) Forest disturbance alerts for the Congo Basin using Sentinel-1. Environmental Research Letters 16. doi: 10.1088/1748-9326/abd0a8

Reinermann S, Gessner U, Asam S, Kuenzer C, Dech S (2019) The Effect of Droughts on Vegetation Condition in Germany: An Analysis Based on Two Decades of Satellite Earth Observation Time Series and Crop Yield Statistics. Remote Sensing 11:21. doi: 10.3390/rs11151783

Rocchini D et al. (2015) Satellite remote sensing to monitor species diversity: potential and pitfalls. Remote Sensing in Ecology and Conservation 2:25-36. doi: 10.1002/rse2.9

Rocchini D et al. (2018) Measuring β-diversity by remote sensing: A challenge for biodiversity monitoring. Methods in Ecology and Evolution 9:1787-1798. doi: 10.1111/2041-210x.12941

Rocchini D et al. (2021) From local spectral species to global spectral communities: A benchmark for ecosystem diversity estimate by remote sensing. Ecological Informatics 61. doi: 10.1016/j.ecoinf.2020.101195

Sebald J, Senf C, Seidl R (2021) Human or natural? Landscape context improves the attribution of forest disturbances mapped from Landsat in Central Europe. Remote Sens Environ 262. doi: 10.1016/j.rse.2021.112502

Senf C, Laštovička J, Okujeni A, Heurich M, van der Linden S (2020) A generalized regression-based unmixing model for mapping forest cover fractions throughout three decades of Landsat data. Remote Sens Environ 240. doi: 10.1016/j.rse.2020.111691

Shi YF et al. (2018) Tree species classification using plant functional traits from LiDAR and hyperspectral data. International Journal of Applied Earth Observation and Geoinformation 73:207-219. doi: 10.1016/j.jag.2018.06.018

Skidmore AK et al. (2021) Priority list of biodiversity metrics to observe from space. Nat Ecol Evol 5:896-906. doi: 10.1038/s41559-021-01451-x

Skidmore AK et al. (2015) Environmental science: Agree on biodiversity metrics to track from space. Nature 523:403-405. doi: 10.1038/523403a

Song XP et al. (2021) Massive soybean expansion in South America since 2000 and implications for conservation. Nat Sustain 2021. doi: 10.1038/s41893-021-00729-z

Thiel C et al. (2020a) UAS Imagery-Based Mapping of Coarse Wood Debris in a Natural Deciduous Forest in Central Germany (Hainich National Park). Remote Sensing 12. doi: 10.3390/rs12203293

Thiel C et al. (2020b) Monitoring Selective Logging in a Pine-Dominated Forest in Central Germany with Repeated Drone Flights Utilizing A Low Cost RTK Quadcopter. Drones 4. doi: 10.3390/drones4020011

Thonfeld F, Feilhauer H, Braun M, Menz G (2016) Robust Change Vector Analysis (RCVA) for multi-sensor very high resolution optical satellite data. International Journal of

Applied Earth Observation and Geoinformation 50:131-140. doi: 10.1016/j.jag.2016.03.009

Thonfeld F, Hecheltjen A, Menz G (2015) Bi-temporal Change Detection, Change Trajectories and Time Series Analysis for Forest Monitoring. Photogrammetrie - Fernerkundung - Geoinformation 2015:129-141. doi: 10.1127/pfg/2015/0259

Townshend JR et al. (2012) Global characterization and monitoring of forest cover using Landsat data: opportunities and challenges. International Journal of Digital Earth 5:373-397. doi: 10.1080/17538947.2012.713190

Uereyen S, Bachofer, F., Kuenzer, C. (submitted) A framework for large scale analyses of land surface dynamics using multidecadal and multivariate time series. Remote Sensing of Environment.

Vo QT, Kuenzer C, Vo QM, Moder F, Oppelt N (2012) Review of valuation methods for mangrove ecosystem services. Ecological Indicators 23:431-446. doi: 10.1016/j.ecolind.2012.04.022

Vo QT, Oppelt N, Leinenkugel P, Kuenzer C (2013) Remote Sensing in Mapping Mangrove Ecosystems - An Object-Based Approach. Remote Sensing 5:183-201. doi: 10.3390/rs5010183

Vo TQ, Kuenzer C, Oppelt N (2015) How remote sensing supports mangrove ecosystem service valuation: A case study in Ca Mau province, Vietnam. Ecosystem Services 14:67-75. doi: 10.1016/j.ecoser.2015.04.007

Wegmann M et al. (2017) r.pi : A grass gis package for semi-automatic spatial pattern analysis of remotely sensed land cover data. Methods in Ecology and Evolution 9:191-199. doi: 10.1111/2041-210x.12827

Wegmann M et al. (2014) Role of African protected areas in maintaining connectivity for large mammals. Philos Trans R Soc Lond B Biol Sci 369:20130193. doi: 10.1098/rstb.2013.0193

Wegmann ML, B.; Dech, S. (2016) Remote Sensing and GIS for Ecologists: Using Open Source Software

Wegmann MS-W, J.; Dech, S. (2020) An Introduction to Spatial Data Analysis

White JC, Wulder MA, Hermosilla T, Coops NC, Hobart GW (2017) A nationwide annual characterization of 25 years of forest disturbance and recovery for Canada using Landsat time series. Remote Sens Environ 194:303-321. doi: 10.1016/j.rse.2017.03.035

Ye S, Rogan J, Zhu Z, Eastman JR (2021) A near-real-time approach for monitoring forest disturbance using Landsat time series: stochastic continuous change detection. Remote Sens Environ 252. doi: 10.1016/j.rse.2020.112167

4 Relevance of sex, gender and/or diversity

The participating institutions are committed to the goal of actively supporting career perspectives of female scientists; diversity and internationalization in academia (see *2.5 Measures to advance research careers* in the General Introduction). The applicants will make their graduate students aware of the support and workshops provided in their institutions and by this Research Unit (*3.2.4 Gender Equality Measures in Research Networks Module*). The DLR department led by the PI Prof. Claudia Kuenzer is a department of currently 56 scientists, of which half are female scientists and half are male. A gender paygap does not exist. Scientists in the department currently come from 9 different nationalities. Similar metrics exist at the Remote Sensing Chair at the University of Würzburg. Currently 32 scientists from 7 nationalities, among them 12 female scientists work at the department o

Project Description – Project Proposals

Dr. Simone Cesarz, Leipzig (PI)
Prof. Dr. Nico Eisenhauer, Leipzig (PI)

SP4: Soil biodiversity and functioning

Project Description

1 Starting Point

1.1 State of the art and preliminary work

Soil biodiversity indicators

Soil harbors an astonishing biodiversity that drives essential ecosystem functions, such as nutrient cycling and decomposition (Bardgett and van der Putten 2014; FAO et al. 2020). Consequently, the integrity of soils has attracted increasing scientific, public, and political attention (Wall et al. 2015; FAO et al. 2020). Homogenization of the landscape threatens biodiversity with potential consequences for soil ecosystem functioning (Eisenhauer 2016; FAO et al. 2020). Presumably, different mechanisms act above and belowground in driving species diversity and ecosystem functioning, as indicated by a mismatch of global above- and belowground diversity distribution (Cameron et al. 2019) and their spatial drivers at the regional scale (Le Provost et al. 2021).

Among the biodiversity in soil, soil microorganisms and nematodes are the most abundant and diverse taxa and are often used as bioindicators of soil health. Microorganisms are regarded as the "functional backbones" of ecosystems (van der Heijden et al., 2008). Bacteria and fungi form many trophic and non-trophic interactions with nematodes and many other organisms. Nematodes are the most abundant Metazoa on Earth (Hodda et al. 2009), and studies from the last two decades provide evidence that the distribution of nematodes is predictable over different spatial scales (Cesarz et al. 2017; van den Hoogen et al. 2019). Most nematodes are free-living, occupy all trophic levels of the soil food web, have a variety of trophic groups, with the main groups being bacterial-, fungal-, and plant-feeding nematodes as well as omnivorous and predatory nematodes. These diverse roles link nematodes to many other soil organisms and ecosystem functions. In addition to such critical taxonomic and trophic information, free-living soil nematodes reflect the disturbance/stability of a system based on their life-history traits (Ferris et al. 2001). Therefore, nematodes are used as a powerful indicator taxon reflecting soil food web conditions, functional diversity, system enrichment, and information about food web complexity (Eisenhauer et al. 2011a; Cesarz et al. 2015).

Soil biodiversity dispersal and assembly

At the microscale, the maximum active dispersal of nematodes is about 15 cm within 48 h (Moyle and Kaya 1981). Passive dispersal of nematodes occurs by wind, water, animals, and plants and can be higher than that of other soil fauna (Ptatscheck et al. 2018) and within very short timeframes (Ptatscheck and Traunspurger 2020). Dispersal by arthropods occurs via feces, trachea, or via attachment to the body (Türke et al. 2018). It can be assumed that a more diverse arthropod community can increase the spatial spreading due to a higher probability of more niches that are reached by the arthropod community. Since microorganisms are the main food resource for most nematodes, they influence each other in multiple facets. The community structure of microorganisms determines nematode community composition (Moll et al. 2021), whereby feeding on microorganisms can lead to changes in the microbial community structure, for instance, an increase in microbial diversity, likely by reducing dominant species (de Deyn et al., 2003).

Habitat complexity is known to increase species diversity (Dainese et al. 2019; Tscharntke et al. 2021) due to more niches and higher productivity, and a larger surface area (Kovalenko et al. 2012). In forest ecosystems, complexity can be increased spatially and temporally by forest gaps. This type of disturbance increases light availability, moisture, and strongly changes microclimatic conditions with significant effects on soil organisms (Mueller et al. 2016). Due to regeneration processes of the surrounding vegetation, gaps provide variable habitat niches over time (Mueller et al. 2016). Higher light availability at the forest floor induces changes in the plant community structure with changes in the amount and quality of resources (Muscolo et al. 2014) and substantial effects on soil biodiversity and community composition (Mueller et al. 2016). Gap size increases the functional diversity of nematodes (Shen et al. 2019). At the same time, also the nematode community composition changes as indicated by high proportions of plant-feeding nematodes, omnivores, and predators leading to a more even distribution of trophic groups (Shen et al. 2019).

Microclimatic conditions also change with forest gap size, as a more open canopy increases the variability of the temperature and moisture during the day, while a closed canopy has a strong buffering effect (Gray et al. 2002). Such microclimatic effects have been reported to cascade to the belowground food web (Mueller et al. 2016), including soil microbial communities and related functions (Gottschall et al. 2019), as well as nematode communities (Thakur et al., 2014; Mueller et al., 2016).

The addition of deadwood increases habitat complexity due to the supply of many different substrates (roots, trunks, heartwood, sapwood) and decay stages that generally boost diversity (Seibold et al. 2015). In addition, the identity of the deadwood tree species influences the microbial and nematode community composition, mainly due to changes in pH and water content (Moll et al. 2021). Moreover, decomposition is a long-term process, which is why substrate properties and their effects on biodiversity are assumed to change with time (Gołębiewski et al. 2019). For instance, the decomposition of deadwood can influence the soil's physical and chemical properties compared to bulk soil (Piaszczyk et al. 2020; Šamonil et al. 2020). Since the biomass, activity, and community composition of soil microorganisms are strongly affected by water and resource availability, as well as soil pH (Serna-Chavez et al. 2013) this will likely cascade to microorganisms and nematodes. In more detail, soil water-holding capacity and soil water content are often higher close to deadwood due to enhanced organic matter content (Piaszczyk et al. 2020). Higher carbon storage and nutrient availability result from the decomposition process, as well as a high abundance and diversity of organisms colonizing deadwood (Moll et al. 2021). Further, the stability of soil aggregates increases close to deadwood due to increased soil microbial activity (Piaszczyk et al. 2020). Aggregate size, in turn, can influence soil nematodes, as it filters nematodes based on their size and thereby indirectly by their trophic level (Briar et al. 2011). In a nutshell, changes at the large scale, i.e., forest gap size and deadwood strongly influence small scale drivers that affect microbial and nematode communities, i.e., soil water content, carbon content, and soil pH.

The habitat complexity-biodiversity-ecosystem functioning nexus

Recent research shows that habitat complexity is the basis for biodiverse and well-functioning ecosystems (Dainese et al. 2019), with multiple benefits for ecosystem services at the landscape scale (Dainese et al. 2019; Tscharntke et al. 2021). Similar principles are likely to apply to smaller spatial scales and microbial processes. For instance, increasing habitat and resource complexity in experimental microcosms were shown to enhance the functioning of algal (Cardinale 2011) and bacterial communities (Jousset et al. 2011), respectively, and to increase the strength of positive biodiversity effects, particularly complementarity effects. The positive effect of habitat complexity and, therefore, biodiversity on ecosystem functions becomes even more important when considering multiple functions simultaneously (Hector and Bagchi 2007; Meyer et al. 2018). There is strong empirical evidence that a loss in α-diversity will also cause a loss in multifunctionality (Zavaleta et al. 2010; Isbell et al. 2011; Gamfeldt et al. 2013). However, only a few studies have investigated the consequences of changes in β-diversity (e.g., Hautier et al., 2020; Wang et al., 2021), especially for belowground biodiversity and ecosystem functions. From a theoretical point of view, a reduction in β-diversity should have a strong impact on multifunctionality, since only different communities provide different sets of functions under varying environmental conditions (Isbell et al. 2011; Loreau et al. 2021). This suggests that an increase in spatial variation due to enhanced structural complexity (ESC) combined with dissimilar communities decreases the functional redundancy at larger spatial scales and therefore increases multifunctionality (Hillebrand and Matthiessen 2009; Mori et al. 2016). Despite some first evidence that these relationships are also critical for soil communities and functioning (e.g., Eisenhauer, 2016), the hypothesized nexus of habitat complexity, soil biodiversity, and ecosystem functioning is understudied.

Preliminary work

The applicants are soil ecologists with a strong history in the assessment of soil biodiversity and soil ecosystem functions in response to different environmental drivers, such as climate change (e.g., Cesarz et al., 2015; Eisenhauer et al., 2012; Thakur et al., 2018), plant diversity (e.g., Cesarz et al., 2013; Eisenhauer et al., 2018, 2013), and land use (e.g., Siebert et al., 2019; Smith et al., 2021). They have studied the temporal and spatial drivers of soil communities and ecosystem functions across ecosystems (e.g., Eisenhauer et al., 2011; Gottschall et al., 2019; Guerrero-Ramírez et al., 2017; Isbell et al., 2015; Smith et al., 2021) and have linked soil communities to ecosystem functions (e.g., Beugnon et al., 2021; Lange et al., 2015; Schwarz et al., 2017). A recent study conducted in an experimental forest system indicated the importance of microclimate (night temperature) for soil ecosystem functioning (Gottschall et al. 2019). And a global study on soil microbial properties in tree diversity experiments revealed that soil water is the main driver of soil functioning. More importantly, high soil water content was shown to alleviate unfavorable conditions of other important abiotic drivers (Cesarz et al. 2020). Above- and belowground tree traits on soil ecosystem functioning differ among spatial scales, ranging from tree-tree interactions to the neighborhood scale (Beugnon, Cesarz, Eisenhauer et al., unpubl. data), also suggesting impacts on the α-, β-, and γ-diversity. Moreover, a recent study on nematode communities in olive tree stands in southern Spain showed that the conversion from natural to agricultural systems and even moderate increases in land-use intensity caused a strong biotic homogenization by enhancing the functional similarities of nematode communities, represented by nematode body size (Archidona-Yuste et al., 2021).

Generally, the applicants use a wide range of methods to mechanistically understand multiple taxa and processes in the soil. In addition to comprehensive taxonomic assessments of soil biodiversity (e.g., Scherber et al. 2010; Cesarz et al. 2013; Eisenhauer et al. 2013), they commonly perform analyses of microbial respiration and biomass (e.g., Eisenhauer et al., 2018, 2010), soil enzymes (e.g., Thakur et al., 2019), nematodes as soil indicators (e.g., Cesarz et al., 2017; Eisenhauer et al., 2011a), PLFA analysis of the microbial community to obtain information on community structure (e.g., Kostin et al., 2021; Wagner et al., 2015), as well as proxies for bacterial and fungal biomasses (e.g., Beugnon et al., 2021; Eisenhauer et al., 2017). Furthermore, the applicants have expertise in different decomposition measurements (Vogel et al., 2013; Djukic et al., 2018; Gottschall et al., 2019, 2021) and the analysis of water-stable aggregates (Pérès et al. 2013; Eisenhauer et al. 2018). Based on this solid soil ecological background, the applicants are funding members of Soil BON, a global initiative to monitor soil biodiversity and ecosystem functioning (Guerra et al. 2021a), which will address critical gaps in soil ecological research (Eisenhauer et al. 2017a; Guerra et al. 2020). As expert in soil ecology, N Eisenhauer has contributed to important biodiversity reports (FAO et al. 2020; Pörtner et al. 2021).

In preparation of this proposal, baseline data for future investigations of soil biodiversity (nematodes), community structure (nematodes and microbial communities), and soil ecosystem functions (microbial respiration, biomass, and the respiratory quotient) were taken at the study site in Sailershausen every year in October since 2018 (Fig. 1). Therefore, five soil samples were randomly taken and pooled per patch. Similar samples were collected for microbial community analysis from the Mercator fellow Petr Baldrian which can be combined. In a nutshell, the available data (2018 [all done], 2019 [all done], 2020 [microbial analyses done, nematode analyses pending], and 2021 [to be performed in October 2021]) represents a great basis for the proposed project and already indicates promising results on significant

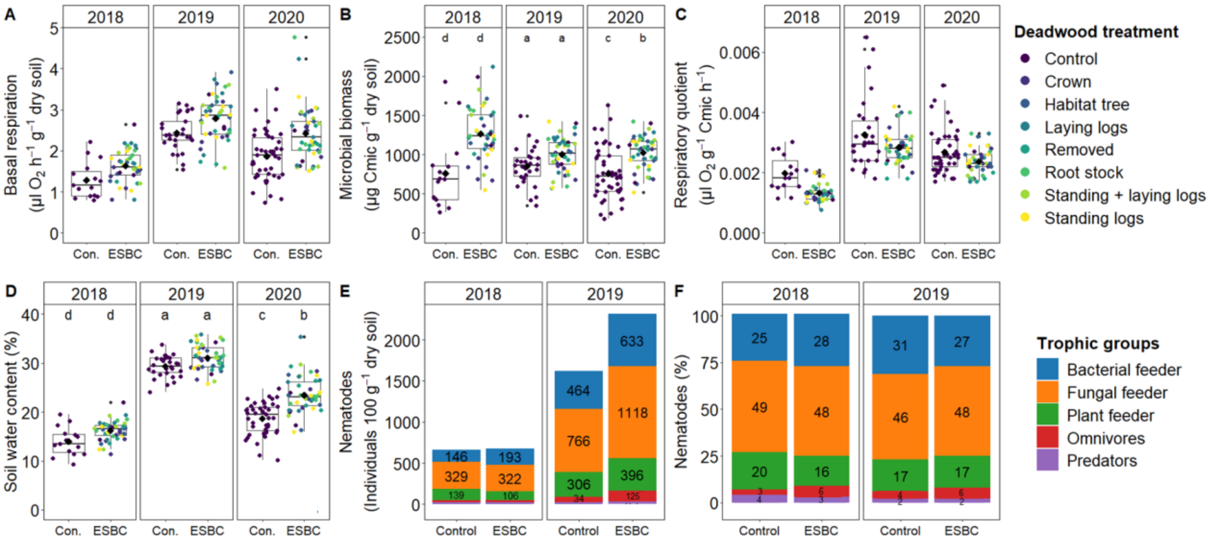


Figure 1: Preliminary results of baseline measurements of soil microbial properties in 2018-2020 (A-D) and nematode trophic group composition in 2018 and 2019 (E-F) as affected by ESBC and the control (Con.). Colored circles in boxplots highlight the single deadwood treatments. Letters above boxplots highlight significant interactions of Year x ESBC and significant differences among means for panel B and D, and fungal feeders and predators in panel E. In all other cases but relative proportions in panel F, the single factors year and ESBC are always significant. Numbers on bar graphs display the values for each trophic group.

ESBC (Enhancement of Structural Beta Complexity; see main proposal) on soil biodiversity and ecosystem functions. For the proposed research period, the goal is to proceed with the monitoring while also exploring the generality (gradient of different sites across Germany) and the underlying mechanisms of ESBC treatment effects via distinct changes at the patch level (Enhancement of Structural Alpha Complexity;ESC; see main proposal). To investigate if an increase of microhabitats generally increases soil biodiversity and ecosystem functioning, the sampling effort will be extended to include more microsites in a standardized way. In addition, different potential explanatory variables will be measured and linked to the distribution and type of deadwood to identify the main drivers of nematode diversity and microbial properties at the α-, β-, and γ-scale.

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. Gottschall F, **Cesarz S**, Auge H, Kovach KR, Mori AS, Nock CA, **Eisenhauer N** (2021) Spatio-temporal dynamics of abiotic and biotic properties explain biodiversity-ecosystem functioning relationships. Ecological Monographs, Accepted.

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

2. Archidona-Yuste A, Wiegand T, **Eisenhauer N**, Cantalapiedra-Navarrete C, Palomares-Rius JE, Castillo P (2021) Agriculture causes homogenization of plant-feeding nematode communities at the regional scale. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.14025
3. Beugnon R, Du J, **Cesarz S**, Jurburg SD, Pang Z, Singavarapu B, Wubet T, Xue K, Wang Y, **Eisenhauer N** (2021) Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning. ISME Communications 1:41.
4. **Cesarz S**, Ciobanu M, Wright AJ, Ebeling A, Vogel A, Weisser WW, **Eisenhauer N** (2017) Plant species richness sustains higher trophic levels of soil nematode communities after consecutive environmental perturbations. Oecologia 184, 715–728.
5. **Cesarz S**, Craven D, Auge H, Bruelheide H, Castagneyrol B, Hector A, Jactel H, Koricheva J, Messier C, Muys B, O’Brien MJ, Paquette A, Ponette Q, Potvin C, Reich PB, Scherer-Lorenzen M, Smith AR, Verheyen K, **Eisenhauer N** (2020) Biotic and abiotic drivers of soil microbial functions across tree diversity experiments. BioRxiv.
6. **Eisenhauer N,** Dobies T, **Cesarz S**, Hobbie SE, Meyer RJ, Worm K, Reich PB (2013) Plant diversity effects on soil food webs are stronger than those of elevated CO_2 and N deposition in a long-term grassland experiment. Proceedings of the National Academy of Sciences of the United States of America 110, 6889–6894.
7. **Eisenhauer N,** Hines J, Isbell F, van der Plas F, Hobbie SE, Kazanski CE, Lehmann A, Liu M, Lochner A, Rillig MC, Vogel A, Worm K, Reich PB (2018). Plant diversity maintains multiple soil functions in future environments. ELife 7, 1–20.
8. Gottschall F, Davids S, Newiger-Dous TE, Auge H, **Cesarz S, Eisenhauer N** (2019) Tree species identity determines wood decomposition via microclimatic effects. Ecology and Evolution 9, 12113–12127.
9. Guerra CA, Bardgett RD, Caon L, Crowther TW, Delgado-Baquerizo M, Montanarella L, Navarro LM, Orgiazzi A, Singh BK, Tedersoo L, Vargas-Rojas R, Briones MJI, Buscot F, Cameron EK, **Cesarz S**, Chatzinotas A, Cowan DA, Djukic I, van den Hoogen J, Lehmann A, Maestre FT, Marín C, Reitz T, Rillig MC, Smith LC, de Vries FT, Weigelt A, Wall DH, **Eisenhauer N** (2021). Tracking, targeting, and conserving soil biodiversity: A monitoring and indicator system can inform policy. Science 371, 239–241.
10. Guerra CA, Heintz-Buschart A, Sikorski J, Chatzinotas A, Guerrero-Ramírez N, **Cesarz S,** Beaumelle L, Rillig MC, Maestre FT, Delgado-Baquerizo M, Buscot F, Overmann J, Patoine G, Phillips HR., Winter M, Wubet T, Küsel K, Bardgett RD, Cameron EK, Cowan D, Grebenc T, Marín C, Orgiazzi A, Singh BK, Wall DH, **Eisenhauer N** (2020). Blind spots in global soil biodiversity and ecosystem function research. Nature Communications 11, 387.

1.2.3 Patents

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

4 years

2.2 Objectives

The main objective of this subproject is to explore the response of α-, β-, and γ-diversity of soil organisms and ecosystem functions, and multifunctionality to Enhancement of Structural Beta Complexity (ESBC) via small scale manipulation at the patch level (ESC). ESBC is expected to increase soil ecosystem multifunctionality due to ESC via i) increased habitat complexity/heterogeneity that will increase habitat space and thus ii) the taxonomical and functional diversity, which will enhance iii) multiple soil ecosystem functions. Three complementary working packages (WPs) will investigate these relationships, whereas a fourth WP focuses on time series analysis of soil microbial properties, including the measurements that started in 2018 in preparation for this proposal. Extensive collaboration and data exchange with other subprojects of the Research Unit (Fig. 2) will yield unique mechanistical insights into the generality and underlying mechanisms of relationships between structural complexity, soil biodiversity, and ecosystem functions at different spatial scales. With 15 replicates and three microsites per patch SP4 can investigate how small-scale changes cascade to the larger scale. Each WP will result in at least one publication in an international peer-reviewed journal.

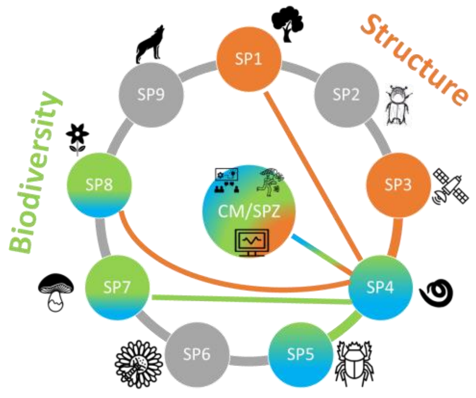


Figure 2: Close cooperation of SP4 with other subprojects, the color of arrows indicates the type of data exchanged; green: species data, blue: functions, brown: structure.

WP1: Community properties of soil organisms

H1: ESC increases nematode species richness, functional diversity, density, as well as bacterial and fungal biomass due to increased habitat complexity and resource availability.

H2: Increases in community properties on the small scale (α; ESC) cascade to the large scale (β, and γ; ESBC) due to specific treatment responses.

H3: ESC treatments induce shifts in microclimatic conditions leading to distinct communities at the small scale.

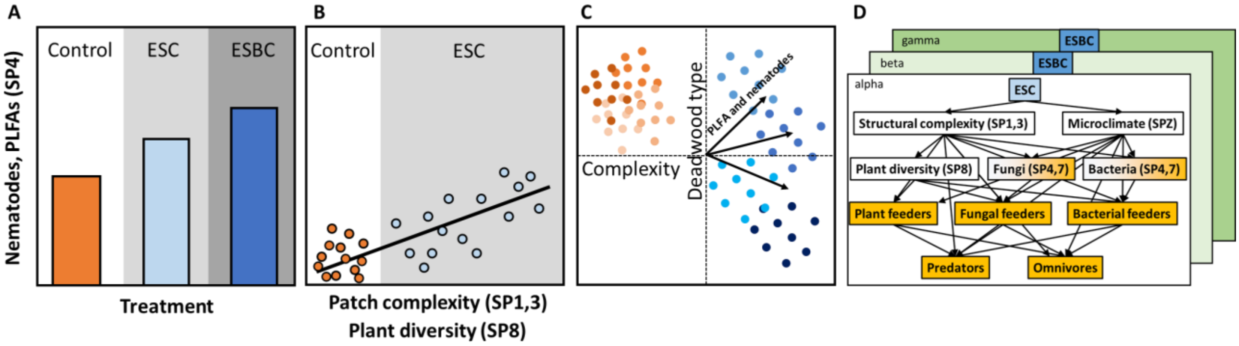


Figure 3*:* Overview of proposed analyses and hypothesized relationships in work package 1. A) Expected effect of ESB (light blue) and ESBC (dark blue) on nematode and microbial properties compared to the control (orange). B) Linking data from SP1, 3, and 8 to highlight the significance of habitat complexity in driving soil communities and functions. C) Multivariate analyses with distinct communities across deadwood types. D) SEM to test causal relationships and multiple, correlated mechanisms. Own measurements (SP4 in panel D) are highlighted in yellow.

WP1 will investigate if and how ESC affects nematode diversity (taxonomic and functional), the community composition of nematodes and microorganisms, as well as bacterial and fungal biomass (Fig. 3A,B). Although studies provide strong support that habitat and resource complexity increase diversity and functions for microorganisms (Jousset et al. 2011; Baldrian 2017) and higher trophic levels (Cardinale 2011; Dainese et al. 2019; Tscharntke et al. 2021), evidence for soil nematodes is lacking. However, microsites in terms of soil and litter (Kitagami et al. 2020), small-scale tree clusters (Cesarz et al. 2013), tree identity of deadwood (Moll et al. 2021), as well as light availability (Mueller et al. 2016) are known to lead to specific nematode and microbial communities (Fig. 3C). Light availability as increased by the aggregation treatment will increase plant diversity (Markgraf et al. 2020) which was shown to increase soil biodiversity (Scherber et al. 2010; Eisenhauer et al. 2013; Eisenhauer 2016). In combination, aggregation and different types of deadwood are suggested to lead to distinct changes in the microclimate and distinct plant and soil communities (Fig. 3C,D). In case no distinct nematode and microbial communities can be found across ESC treatments, the increase in resources due to deadwood addition may be the main driver for the diversity and community composition of microorganisms and nematodes.

WP2: Functional diversity of soil microorganisms

H4: ESC creates different microhabitats with distinct microbial communities that support diverse ecosystem functions and indicated by different substrate use.

H5: Distinct microbial communities at the α-(patch, ESC) level cascade to higher functional diversity on the β- and γ-level (ESBC).

Soil microorganisms are the main driver of soil ecosystem functions (van der Heijden et al., 2008) and have a wide range of metabolic pathways and enzymes that allow them to degrade a diversity of materials (Baldrian 2009). Although the majority of microorganisms can degrade a range of similar substrates and there is some evidence for functional redundancy in soil (Hättenschwiler et al. 2005), soil microorganisms can also have diversity effects on ecosystem

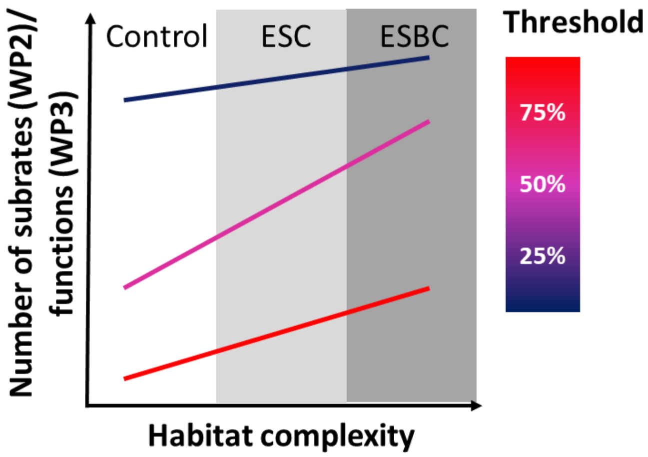


Figure 4: Microbial activity and biomass (WP2) or different multiple functions (WP3) are indicted by lines and are suggested to increase with habitat complexity. ESC, and therefore, ESBC will simultaneously lead to higher values of all functions as indicated as the percentage of reaching the maximum value of the microbial property (threshold).

functions (Tiunov and Scheu 2005; Wagg et al. 2014; Delgado-Baquerizo et al. 2016). Especially as substrates become more complex (e.g., leaf litter and wood), different enzymes and metabolic pathways are required for decomposition, and different soil microorganisms complement each other in the decomposition process (biotic interactions; Tiunov and Scheu (2005). As different types of deadwood represent a variety of different resources, and as they also occur under different microclimatic conditions induced by the aggregation treatment, functionally different soil microbial communities can be expected. Functionally different communities are likely to be a key mechanism explaining increased ecosystem multifunctionality (WP3; Jousset et al. 2011; Soliveres et al. 2016; Eisenhauer et al. 2018), which would be in line with the complementarity effect of biodiversity (Loreau and Hector 2001; Eisenhauer et al. 2019). Alternatively, a higher functioning can be achieved without any increase in functional diversity due to the dominance of specific high-performing species or optimal conditions, which is in line with the selection effect of biodiversity (Loreau and Hector 2001; Cardinale 2011; Eisenhauer et al. 2019). ESC is hypothesized to increase the taxonomic diversity of soil organisms (WP1), which is also likely to increase their functional diversity (WP2). Functional diversity exists, when more substrates can be used simultaneously at higher levels (blue line, Fig. 4). We will test this hypothesis by offering eleven substrates that span a gradient in substrate complexity to soil communities from three different microsites. With increasing habitat complexity, the magnitude of ecosystem functioning should increase due to more different communities.

WP3: Belowground multifunctionality

H6: ESC increases belowground ecosystem multifunctionality via distinct changes in the taxonomic and functional diversity of soil communities.

H7: High levels of multifunctionality at the α-level in ESC treatments cascade to higher multifunctionality on the β-and γ-level (ESBC).

Soil microorganisms drive multiple ecosystem functions simultaneously, such as nutrient cycling, decomposition, forming of stable soil aggregates, and carbon sequestration (Delgado-Baquerizo et al., 2020, 2016; Lange et al., 2015b; van der Heijden et al., 2008; Wagg et al., 2014). Accordingly, a previous study has shown that tree diversity and trait identity effects on ecosystem multifunctionality are mediated by a diverse soil community (Schuldt et al. 2018). However, such work has mostly focused on the α-diversity of soil organisms, while the role of the β-diversity of soil organisms and functions is unknown. At the same time, there is an increasing number of studies reporting that human activities homogenize soil communities at regional (Archidona-Yuste et al., 2021) to global (Guerra et al. 2021b) scales, with heretofore unknown consequences for ecosystem functioning. ESC-induced increases in the α-, β-, and γ-diversity of soil organisms are the prerequisite for enhanced levels of different soil ecosystem functions and ecosystem multifunctionality at different spatial scales. Increased substrate complexity and heterogeneity across forest patches will facilitate positive species interactions in the soil (i.e., complementarity and facilitation), and this enhances soil biodiversity effects on ecosystem functioning; while simple resources can cause antagonistic interactions and negative biodiversity effects (Jousset et al. 2011). In this WP, we will explore relationships between α-, β-, and γ-diversity of soil organisms with the simultaneous provisioning of ecosystem functions at different spatial scales. Enhanced taxonomic and – even more importantly – functional biodiversity of soil organisms are significant predictors of ecosystem multifunctionality. We will integrate measurements on microbial biomass and respiration, water stable aggregates, decomposition data of SP5, and enzyme analysis of the Mercator fellow Petr Baldrian (Fig. 4).

WP4: Time series analysis

H8: Differences in microbial properties between ESC and the control increase with time leading to higher properties at the β-and γ-level (ESBC).

Biodiversity-ecosystem functioning research suggests that biodiversity effects strengthen with time (Reich et al. 2012; Guerrero-Ramírez et al. 2017), likely due to increasing biotic interactions during community assembly processes (Eisenhauer et al. 2012b). Increased availability of deadwood and changes in the aggregation of deadwood can affect soil nutrient dynamics (Perreault et al. 2020). The nutrient content in coarse woody debris increases with time during decomposition in the first years (Herrmann and Bauhus 2018), providing also nutrients for soil organisms (Kappes et al. 2007), and stimulating enzyme activity (Perreault et al. 2020). In WP4, we will make use of the data of soil microbial properties (SIR method) that were sampled yearly since 2018 and will be continued throughout the project until 2025 following the same soil sampling approach (one microsite with five soil samples per patch) focusing on the sites of the University forest Sailershausen (Site 1-3). Soil water content, soil pH, and soil C measurements will also be further measured over time, partly covered by measurements of SPZ, whereas soil from 2018-2021 will be analyzed by SP4 and provided to the whole Research Unit.

2.3 Work programme including proposed research methods

General sampling (all WPs)

To reflect plot heterogeneity, we will conduct a targeted soil sampling with 15 samples per patch. These samples will be distributed across the patch in order to represent three microsites with five replicates each: 1) soil with light and dark spots reflecting the aggregation treatment, 2) soil directly under deadwood, and 3) in deadwood. This allows to test for within and between patch heterogeneity and the importance of scale. For WP1, and therefore the nematode and PLFA analysis, the soil of all 15 samples will be pooled by using similar portions. Keeping the microsites separated is not possible due to high laboratory work effort. For WP2 and WP3, the five replicates of each microsite will be pooled. Results from WP2 and WP3 can inform a more targeted analysis of nematodes and PLFAs in a potential second funding period. Generally, different methods/analyses will be used for the different working packages, including a different pooling of samples (Table 1). SP4 will take samples in all years (2022-2025) and all sites in October, as suggested by the overall sampling scheme, without differentiating between a comprehensive sampling and a rapid assessment (SPZ, Figure 1). However, SP4 will extend the sampling in that way that sites in the University forest Sailershausen (site 1-3) will be sampled each year. Although the sampling for the time-series analysis will also be performed in 2025, these additional data will not enter the analysis of WP1-3, but that of WP4.

WP1 (lead: Simone Cesarz): Community properties of soil organisms

Methods: Nematodes (1) (numbers in brackets refer to Table 1) will be extracted from ~25 g of the pooled samples following Cesarz et al. (2019). Nematodes will be identified based on morphological traits, allowing to assign them to functional groups (Bongers 1990; Yeates et al. 1993; Ferris et al. 2001). Nematodes will be identified by Marcel Ciobanu, the taxonomist who has identified the nematode samples since 2018, however, the PhD student will learn how to identify nematodes and their ecological relevance by attending an internationally well-known nematode course at Wageningen University in June 2022. Nematode communities in deadwood will be assessed using meta-barcoding approaches in close collaboration with SP7 and SPZ (where the funds for sequencing are requested). PLFAs and NLFAs (2) will be extracted from 4 g

Table 1: Overview of measurements per working package (WP) and the different pooling of samples according to the WPs in SP4. Numbers on the left side indicate measurements that will be done by SP4 and are referred to in the text. Microsites = samples of soil, soil under deadwood, and deadwood, respectively. Site 1-3: University forest Sailershausen.

Measurement		WP1	WP2	WP3	WP4
1	Nematodes	Pooled			
2	PLFA (community composition, bacterial and fungal biomass)	Pooled			
3	Soil respiration (activity)		Sites 1-11 + Microsites in Sites 1-3	Sites 1-11 + Microsites in Sites 1-3	Soil samples only
4	Soil microbial biomass		Sites 1-11 + Microsites in Sites 1-3	Sites 1-11 + Microsites in Sites 1-3	Soil samples only
5	Soil water content		Sites 1-11 + Microsites in Sites 1-3	Sites 1-11 + Microsites in Sites 1-3	Soil samples only
6	Water holding capacity			Sites 1-11 + Microsites in Sites 1-3	
7	Aggregate stability			Sites 1-11 + Microsites in Sites 1-3	
	Decomposition (SP5)			Site 1-11 + one litterbag in each microsite Site 1-3	
	Enzyme activity (Petr Baldrian)			Soil samples only	
	Soil C,N, pH, texture (SPZ)	Soil samples only	Sites 1-11 + Microsites in Sites 1-3	X	Soil samples only
	Microclimate (SPZ)	x	Sites 1-11 + Microsites in Sites 1-3	X	

of the pooled sample material following the protocols by Frostegård et al., (1991) and Frostegård and Bååth, (1996). Bacterial- and fungal biomass, as well as microbial community composition, will be assessed via PLFA and NLFA marker fatty acids following (Ruess and Chamberlain 2010) allowing the assignment to different microbial groups, i.e., bacteria, saprophytic and ectomycorrhizal fungi, and arbuscular mycorrhizal fungi, as commonly done in our lab (e.g., Beugnon et al., 2021; Kostin et al., 2021). ***Collaboration:*** Using data from SP1 about stand structural complexity, canopy openness, and understory complexity index, and SP3 about forest structure, will allow to more specifically link nematode properties to structural components (Fig. 1B). In addition, SP8 will provide data on the understory plant community composition that will be linked to nematode and microbial properties (Fig. 1B). To guarantee synergies, both projects will focus on the same sampling sites. In collaboration with SP7 (Deadwood microbial diversity), nematodes in deadwood will be linked to the microbial communities in deadwood. Here, metabarcoding approaches are used (supported by SPZ), whereas all other analyses are based on morphological analyses. The nutrient status of the soil (C and N), soil pH, and soil texture will be integrated by using this data from SPZ. In addition, data from microclimate loggers installed by SPZ will be used. To better reflect our microhabitats, we will work closely with SPZ and install three microclimate loggers per patch at sites 1-3, but use only one microclimate logger at the other sites. ***Statistical analyses:*** WP1 will test if the specific changes in the type of deadwood and aggregation vs. distribution, as well as interactions, have specific effects on nematode and microbial community composition using linear-mixed effects models and multivariate statistical methods (Fig. 1C). Finally, all data will be linked using an SEM approach to test multiple possible effect pathways (Fig. 1D). All variables will be additionally linked to factors known to influence soil microorganisms and nematodes, i.e., soil C and N, soil pH, soil water availability, and microclimate as recorded by SPZ (Serna-Chavez et al. 2013; Gottschall et al. 2019; Liu et al. 2019).

WP2 (lead: Simone Cesarz): Functional diversity of soil microorganisms

Methods: The substrate-induced respiration (SIR) method will be used to measure functional diversity via <u>microbial activity</u> (3) and <u>biomass</u> (4) (numbers in brackets refer to Table 1; Scheu 1992), which is well established in our lab (e.g., Eisenhauer et al. 2010b; Beugnon et al. 2021; Smith et al. 2021). By default, glucose is used as the common substrate, as most microorganisms are able to use it for their metabolism. For WP2, however, we will add further substrates reflecting a gradient in complexity and biochemical classes, i.e., wood of high and low density, litter of high and low CN, dung with high and low CN, low and fast decomposing tea (tea bags), filter paper, and wooden popsicles. Based on the elemental analyses of all substrates, we will use the same amount of substrate representing 3.2 mg carbon. All substrates will be ground, and the respiration curves will be followed for at least 48 h to differentiate responses of highly complex substrates, such as wood material. Due to the different substrate complexity levels, it is assumed that each substrate requires different enzymes during degradation. If ESC leads to different microbial communities and thereby functions, we can detect these differences by specific responses for each microsite and substrate. Since microorganisms are strongly related to water, soil water content will be measured before and all samples will be adjusted to the same soil water content. Sampling material represents the three different microsites (1) soil, (2) soil under deadwood, and (3) deadwood to get specific small-scale information that will allow to better understand changes at the β- and γ-scale. ***Collaboration:*** All substrates that will be used are the same substrates used for the decomposition assessment in SP5. SP5 will provide the material and elemental analyses for the substrate-induced respiration measured. Linking laboratory analyses of SP4 with measurements on-site of SP5 allows a more mechanistical evaluation of how ESC and ESBC affects ecosystem functioning. The nutrient status of the soil (C and N), soil pH, and soil texture will be integrated by using this data from SPZ. ***Statistical analyses:*** The data will be analyzed for functional diversity according to Byrnes et al. (2014) using the averaging and the multiple thresholds approach, as done previously (Eisenhauer et al. 2018).

WP3 (lead: Nico Eisenhauer): Belowground multifunctionality

Methods: WP3 will investigate the effect of ESB and ESBC on multiple soil functions and related soil biodiversity–multifunctionality relationships. In addition to soil microbial activity (2) and biomass (3) (numbers in brackets refer to Table 1), measured in WP2 (but with only glucose as substrate), WP3 will also include further variables: soil water holding capacity (6) is an important factor influencing soil water content, as previously shown in one of our previous studies (Smith et al. 2021). Similarly, water-stable soil aggregates (7) strongly affect soil water content and will be measured according to Kemper and Rosenau (1986), such as done in previous studies (e.g., Eisenhauer et al., 2018b). Decomposition and enzyme data will complement the set of functions (see below). ***Collaboration:*** In addition to the above-mentioned variables, SP5 will provide data on decomposition. Both projects agreed on the same microsites so that decomposition data from SP5 can be directly integrated into the spatial analysis of SP4. In addition, data of enzyme activity assessed by Petr Baldrian will be included. The nutrient status of the soil (C and N), soil pH, and soil texture will be integrated by using this data from SPZ. In addition, data from microclimate loggers installed by SPZ will be used. To better reflect our microhabitats, we will work closely with SPZ and install three microclimate loggers per patch in the University forest Sailershausen (Site 1-3), but use only one microclimate logger in the other sites. ***Statistical analyses:*** The data will be analyzed for multifunctionality according to Byrnes et al. (2014) using the averaging and the multiple thresholds approach, as done previously (Eisenhauer et al. 2018). The analysis of WP3 focuses on different functions, whereas in WP2 functional diversity of one function is assessed but responses are expected to be different due to the diversity of substrates.

WP4 (lead: Simone Cesarz): Time series analysis

Methods: WP4 will focus on the five pooled soil samples per patch that were already taken and analyzed since 2018 and will be continued annually until 2025. The data from WP4 allows us to provide also information about annual changes, which is especially important as all sites will be sampled mostly once and in different years. Thus, results of this time-series analysis will be provided to the whole Research Unit as a context. Samples will be analyzed for soil microbial activity (2) and biomass (3) as described before (Table 1).

Collaboration: The nutrient status of the soil (C and N), soil pH, and soil texture will be integrated by using this data from SPZ. ***Analyses:*** We will use mixed-effects models to test effects of ESC and ESBC, time, and the interaction of ESC and ESBC x time on soil microbial properties, as done previously (Eisenhauer et al. 2010; Strecker et al. 2016) to test the hypothesis that effects of environmental heterogeneity on soil properties increase over time.

Table 2: Time table of the work program by month for SP4.

	2022									2023												2024												2025												2026		
	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	O	N	D	J	F	M
Sampling SP4							■												■												■												■					
Technician (duration, 40 months)						■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■			
WP1 - Community properties																																																
Nematodes (course, extraction, counting, ID)			■				■	■	■	■	■	■	■						■	■	■	■	■	■	■						■	■	■										■	■	■			
PLFA (extraction, measurement)							■	■	■	■			■						■	■	■	■			■						■	■	■	■			■											
Manuscript Writing	■	■	■																							■	■	■	■	■	■	■	■	■	■													
WP2 - Functional diversity																																																
SIR 11 substrates (+ microsites)											■	■	■										■	■	■																							
Manuscript Writing				■	■																															■	■	■	■	■	■	■						
WP3 - Belowground multifunctionality																																																
SIR (+ microsites)							■	■											■	■																												
Water-stable soil aggregates (+microsites)														■	■	■										■	■	■																				
Water holding capacity (+microsites)							■	■	■										■	■	■																											
Manuscript Writing						■	■							■	■	■	■	■																									■	■	■	■	■	■
WP4 - Time series (by PIs)																																																
SIR (soil samples only)								■												■												■												■				
Manuscript Writing																																									■	■	■	■	■	■	

3 Bibliography concerning the state of the art, the research objectives, and the work programme

Baldrian P (2009) Microbial enzyme-catalyzed processes in soils and their analysis. Plant, Soil and Environment 55:370–378

Baldrian P (2017) Forest microbiome: Diversity, complexity and dynamics. FEMS Microbiology Reviews 41:109–130

Bardgett RD, van der Putten WH (2014) Belowground biodiversity and ecosystem functioning. Nature 515:505–511

Beugnon R, Du J, Cesarz S, et al (2021) Tree diversity and soil chemical properties drive the linkages between soil microbial community and ecosystem functioning. ISME Commun. https://doi.org/10.1038/s43705-021-00040-0

Bongers T (1990) The maturity index: an ecological measure of environmental disturbance based on nematode species composition. Oecologia 83:14–19

Briar SS, Fonte SJ, Park I, et al (2011) The distribution of nematodes and soil microbial communities across soil aggregate fractions and farm management systems. Soil Biology and Biochemistry 43:905–914

Byrnes JEK, Gamfeldt L, Isbell F, et al (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: Challenges and solutions. Methods in Ecology and Evolution 5:111–124

Cameron EK, Martins IS, Lavelle P, et al (2019) Global mismatches in aboveground and belowground biodiversity. Conservation Biology 33:

Cardinale BJ (2011) Biodiversity improves water quality through niche partitioning. Nature 472:86–91

Cesarz S, Ciobanu M, Wright AJ, et al (2017) Plant species richness sustains higher trophic levels of soil nematode communities after consecutive environmental perturbations. Oecologia 184:715–728

Cesarz S, Reich PB, Scheu S, et al (2015) Nematode functional guilds, not trophic groups, reflect shifts in soil food webs and processes in response to interacting global change factors. Pedobiologia 58:1–10

Cesarz S, Ruess L, Jacob M, et al (2013) Tree species diversity versus tree species identity: Driving forces in structuring forest food webs as indicated by soil nematodes. Soil Biology and Biochemistry 62:36–45

Cesarz S, Schulz AE, Beugnon R, Eisenhauer N (2019) Testing soil nematode extraction efficiency using different variations of the Baermann-funnel method. Soil Organisms 91:61–72

Dainese M, Martin E, Aizen M, et al (2019) A global synthesis reveals biodiversity-mediated benefits for crop production. Science Advances 5:eaax0121

De Deyn GB, Raaijmakers CE, Zoomer HR, et al (2003) Soil invertebrate fauna enhances grassland succession and diversity. Nature 422:711–3

Delgado-Baquerizo M, Maestre FT, Reich PB, et al (2016) Microbial diversity drives multifunctionality in terrestrial ecosystems. Nature Communications 7:1–8

Delgado-Baquerizo M, Reich PB, Bardgett RD, et al (2020) The influence of soil age on ecosystem structure and function across biomes. Nature Communications 11:1–14

Djukic I, Kepfer-Rojas S, Schmidt IK, et al (2018) Early stage litter decomposition across biomes. Science of the Total Environment 628–629:1369–1394

Eisenhauer N (2016) Plant diversity effects on soil microorganisms: Spatial and temporal heterogeneity of plant inputs increase soil biodiversity. Pedobiologia 59:175–177

Eisenhauer N, Antunes PM, Bennett AE, et al (2017a) Priorities for research in soil ecology. Pedobiologia 63:1–7

Eisenhauer N, Beßler H, Engels C (2010) Plant diversity effects on soil microorganisms support the singular hypothesis. Ecology 91:485–496

Eisenhauer N, Cesarz S, Koller R, et al (2012a) Global change belowground: impacts of elevated CO2, nitrogen, and summer drought on soil food webs and biodiversity. Global Change Biology 18:435–447

Eisenhauer N, Dobies T, Cesarz S, et al (2013) Plant diversity effects on soil food webs are stronger than those of elevated CO2 and N deposition in a long-term grassland experiment. Proceedings of the National Academy of Sciences of the United States of America 110:6889–6894

Eisenhauer N, Hines J, Isbell F, et al (2018) Plant diversity maintains multiple soil functions in future environments. eLife 7:1–20

Eisenhauer N, Lanoue A, Strecker T, et al (2017b) Root biomass and exudates link plant diversity with soil bacterial and fungal biomass. Scientific Reports 7:44641

Eisenhauer N, Migunova VD, Ackermann M, et al (2011a) Changes in plant species richness induce functional shifts in soil nematode communities in experimental grassland. PLoS ONE 6:e24087

Eisenhauer N, Milcu A, Allan E, et al (2011b) Impact of above- and below-ground invertebrates on temporal and spatial stability of grassland of different diversity. Journal of Ecology 99:572–582

Eisenhauer N, Reich PB, Scheu S (2012b) Increasing plant diversity effects on productivity with time due to delayed soil biota effects on plants. Basic and Applied Ecology 13:571–578

Eisenhauer N, Schielzeth H, Barnes AD, et al (2019) Chapter One - A multitrophic perspective on biodiversity–ecosystem functioning research. In: Eisenhauer N, Bohan DA, Dumbrell AJ (eds) Mechanisms underlying the relationship between biodiversity and ecosystem function. Academic Press, pp 1–54

FAO, ITPS, GSBI, et al (2020) State of knowledge of soil biodiversity - Status, challenges and potentialities

Ferris H, Bongers T, de Goede RGM (2001) A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Applied Soil Ecology 18:13–29

Frostegård A, Bååth E (1996) The use of phospholipid fatty acid analysis to estimate bacterial and fungal biomass in soil. Biology and Fertility of Soils 22:59–65

Frostegård Å, Tunlid A, Bååth E (1991) Microbial biomass measured as total lipid phosphate in soils of different organic content. Journal of Microbiological Methods 14:151–163

Gamfeldt L, Snäll T, Bagchi R, et al (2013) Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4:1340

Gołębiewski M, Tarasek A, Sikora M, et al (2019) Rapid Microbial Community Changes During Initial Stages of Pine Litter Decomposition. Microbial Ecology 77:56–75

Gottschall F, Davids S, Newiger-Dous TE, et al (2019) Tree species identity determines wood decomposition via microclimatic effects. Ecology and Evolution 9:12113–12127

Gray AN, Spies TA, Easter MJ (2002) Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. Canadian Journal of Forest Research 32:332–343

Guerra CA, Bardgett RD, Caon L, et al (2021a) Tracking, targeting, and conserving soil biodiversity: A monitoring and indicator system can inform policy. Science 371:239–241

Guerra CA, Delgado-Baquerizo M, Duarte E, et al (2021b) Global projections of the soil microbiome in the Anthropocene. Global Ecology and Biogeography 30:987–999

Guerra CA, Heintz-Buschart A, Sikorski J, et al (2020) Blind spots in global soil biodiversity and ecosystem function research. Nature Communications 11:387

Guerrero-Ramírez NR, Craven D, Reich PB, et al (2017) Diversity-dependent temporal divergence of ecosystem functioning in experimental ecosystems. Nature Ecology and Evolution 1:1639–1642

Hättenschwiler S, Tiunov A V., Scheu S (2005) Biodiversity and Litter Decomposition in Terrestrial Ecosystems. Annual Review of Ecology, Evolution, and Systematics 36:191–218

Hautier Y, Zhang P, Loreau M, et al (2020) General destabilizing effects of eutrophication on grassland productivity at multiple spatial scales. Nature Communications 11:1–9

Hector A, Bagchi R (2007) Biodiversity and ecosystem multifunctionality. Nature 448:188–90

Herrmann S, Bauhus J (2018) Nutrient retention and release in coarse woody debris of three important central European tree species and the use of NIRS to determine deadwood chemical properties. Forest Ecosystems 5:1–15

Hillebrand H, Matthiessen B (2009) Biodiversity in a complex world: consolidation and progress in functional biodiversity research. Ecology Letters 12:1405–1419

Hodda M, Peters L, Traunspurger W (2009) Nematode diversity in terrestrial, freshwater aquatic and marine systems. In: Wilson MJ, Kakouli-Duarte T (eds) Nematodes as Environmental Indicators. CABI, Oxfordshire, pp 45–93

Isbell F, Calcagno V, Hector A, et al (2011) High plant diversity is needed to maintain ecosystem services. Nature 477:199–202

Isbell F, Craven D, Connolly J, et al (2015) Biodiversity increases the resistance of ecosystem productivity to climate extremes. Nature 526:574–577

Jousset A, Schmid B, Scheu S, Eisenhauer N (2011) Genotypic richness and dissimilarity opposingly affect ecosystem functioning. Ecology Letters 14:537–545

Kappes H, Catalano C, Topp W (2007) Coarse woody debris ameliorates chemical and biotic soil parameters of acidified broad-leaved forests. Applied Soil Ecology 36:190–198

Kemper WD, Rosenau RC (1986) Aggregate Stability and Size Distribution. In: Klute A (ed) Methods of Soil Analysis, Part 1 Physical and Mineralogical Methods, 2nd edn. American Society of Agronomy, Madison, pp 425–442

Kitagami Y, Tanikawa T, Matsuda Y (2020) Effects of microhabitats and soil conditions on structuring patterns of nematode communities in Japanese cedar (Cryptomeria japonica) plantation forests under temperate climate conditions. Soil Biology and Biochemistry 151:108044

Kostin JE, Cesarz S, Lochner A, et al (2021) Land-use drives the temporal stability and magnitude of soil microbial functions and modulates climate effects. Ecological Applications 0:1–16

Kovalenko KE, Thomaz SM, Warfe DM (2012) Habitat complexity: Approaches and future directions. Hydrobiologia 685:1–17

Lange M, Eisenhauer N, Sierra CA, et al (2015) Plant diversity increases soil microbial activity and soil carbon storage. Nature Communications 6:6707

Le Provost G, Thiele J, Westphal C, et al (2021) Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. Nature Communications 12:

Liu T, Hu F, Li H (2019) Spatial ecology of soil nematodes: Perspectives from global to micro scales. Soil Biology and Biochemistry 137:

Loreau M, Barbier M, Filotas E, et al (2021) Biodiversity as insurance: from concept to measurement and application. Biol Rev. https://doi.org/10.1111/brv.12756

Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. Nature 412:72–76

Markgraf R, Doyon F, Kneeshaw D (2020) Forest landscape heterogeneity increases shrub diversity at the expense of tree seedling diversity in temperate mixedwood forests. Forests 11:1–18

Meyer ST, Ptacnik R, Hillebrand H, et al (2018) Biodiversity-multifunctionality relationships depend on identity and number of measured functions. Nature Ecology and Evolution 2:44–49

Moll J, Roy F, Bässler C, et al (2021) First evidence that nematode communities in deadwood are related to tree species identity and to co-occurring fungi and prokaryotes. Microorganisms 9:1–15

Mori AS, Isbell F, Fujii S, et al (2016) Low multifunctional redundancy of soil fungal diversity at multiple scales. Ecology Letters 19:249–259

Moyle PL, Kaya HK (1981) Dispersal and Infectivity of the Entomogenous Nematode, Neoaplectana carpocapsae Weiser (Rhabditida: Steinernematidae), in Sand. Journal of Nematologyematology 13:295–300

Mueller KE, Eisenhauer N, Reich PB, et al (2016) Light, earthworms, and soil resources as predictors of diversity of 10 soil invertebrate groups across monocultures of 14 tree species. Soil Biology and Biochemistry 92:184–198

Muscolo A, Bagnato S, Sidari M, Mercurio R (2014) A review of the roles of forest canopy gaps. Journal of Forestry Research 25:725–736

Pérès G, Cluzeau D, Menasseri S, et al (2013) Mechanisms linking plant community properties to soil aggregate stability in an experimental grassland plant diversity gradient. Plant Soil. https://doi.org/10.1007/s11104-013-1791-0

Perreault L, Forrester JA, Wurzburger N, Mladenoff DJ (2020) Emergent properties of downed woody debris in canopy gaps: A response of the soil ecosystem to manipulation of forest structure. Soil Biology and Biochemistry 151:108053

Piaszczyk W, Lasota J, Błońska E (2020) Effect of organic matter released from deadwood at different decomposition stages on physical properties of forest soil. Forests 11:

Pörtner HO, Scholes RJ, Agard J, et al (2021) PBES-IPCC co-sponsored workshop report synopsis on biodiversity and climate change

Ptatscheck C, Gansfort B, Traunspurger W (2018) The extent of wind-mediated dispersal of small metazoans, focusing nematodes. Scientific Reports 8:1–10

Ptatscheck C, Traunspurger W (2020) The ability to get everywhere: dispersal modes of free-living, aquatic nematodes. Hydrobiologia 847:3519–3547

Reich PB, Tilman D, Isbell F, et al (2012) Impacts of biodiversity loss escalate through time as redundancy fades. Science 336:589–592

Ruess L, Chamberlain PM (2010) The fat that matters: Soil food web analysis using fatty acids and their carbon stable isotope signature. Soil Biology and Biochemistry 42:1898–1910

Šamonil P, Daněk P, Baldrian P, et al (2020) Convergence, divergence or chaos? Consequences of tree trunk decay for pedogenesis and the soil microbiome in a temperate natural forest. Geoderma 376:114499

Scherber C, Eisenhauer N, Weisser WW, et al (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553–556

Scheu S (1992) Automated measurement of the respiratory response of soil microcompartments: active microbial biomass in earthworm faces. Soil Biology and Biochemistry 24:1113–1118

Schuldt A, Assmann T, Brezzi M, et al (2018) Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications 9:1–10

Schwarz B, Barnes AD, Thakur MP, et al (2017) Warming alters energetic structure and function but not resilience of soil food webs. Nature Climate Change 7:895–900

Seibold S, Bässler C, Brandl R, et al (2015) Experimental studies of dead-wood biodiversity - A review identifying global gaps in knowledge. Biological Conservation 191:139–149

Serna-Chavez HM, Fierer N, van Bodegom PM (2013) Global drivers and patterns of microbial abundance in soil. Global Ecology and Biogeography 22:1162–1172

Shen Y, Yang W, Zhang J, et al (2019) Forest gap size alters the functional diversity of soil nematode communities in alpine forest ecosystems. Forests 10:

Siebert J, Sünnemann M, Auge H, et al (2019) The effects of drought and nutrient addition on soil organisms vary across taxonomic groups , but are constant across seasons. Sci Rep. https://doi.org/DOI:10.1038/s41598-018-36777-3

Smith LC, Orgiazzi A, Eisenhauer N, et al (2021) Large- scale drivers of relationships between soil microbial properties and organic carbon across Europe. Global Ecology and Biogeography 1–14

Soliveres S, van der Plas F, Manning P, et al (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 1–16

Strecker T, Macé OG, Scheu S, Eisenhauer N (2016) Functional composition of plant communities determines the spatial and temporal stability of soil microbial properties in a long-term plant diversity experiment. Oikos 125:1743–1754

Thakur MP, Del Real IM, Cesarz S, et al (2019) Soil microbial, nematode, and enzymatic responses to elevated CO2, N fertilization, warming, and reduced precipitation. Soil Biology and Biochemistry 135:184–193

Thakur MP, Reich PB, Fisichelli NA, et al (2014) Nematode community shifts in response to experimental warming and canopy conditions are associated with plant community changes in the temperate-boreal forest ecotone. Oecologia 175:713–23

Thakur MP, Reich PB, Hobbie SE, et al (2018) Reduced feeding activity of soil detritivores under warmer and drier conditions. Nature Climate Change 8:75–78

Tiunov A V., Scheu S (2005) Facilitative interactions rather than resource partitioning drive diversity-functioning relationships in laboratory fungal communities. Ecology Letters 8:618–625

Tscharntke T, Grass I, Wanger TC, et al (2021) Beyond organic farming – harnessing biodiversity-friendly landscapes. Trends in Ecology & Evolution 1–12

Türke M, Lange M, Eisenhauer N (2018) Gut shuttle service: endozoochory of dispersal-limited soil fauna by gastropods. Oecologia 186:655–664

van den Hoogen J, Geisen S, Routh D, et al (2019) Soil nematode abundance and functional group composition at a global scale. Nature In press:

van der Heijden MGA, Bardgett RD, van Straalen NM (2008) The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11:296–310

Vogel A, Eisenhauer N, Weigelt A, Scherer-Lorenzen M (2013) Plant diversity does not buffer drought effects on early-stage litter mass loss rates and microbial properties. Global Change Biology 19:2795–2803

Wagg C, Bender SF, Widmer F, van der Heijden MGA (2014) Soil biodiversity and soil community composition determine ecosystem multifunctionality. Proceedings of the National Academy of Sciences of the United States of America 111:5266–5270

Wagner D, Eisenhauer N, Cesarz S (2015) Plant species richness does not attenuate responses of soil microbial and nematode communities to a flood event. Soil Biology and Biochemistry 89:135–149

Wall DH, Nielsen UN, Six J (2015) Perspective Soil biodiversity and human health. Nature 528:69–76

Wang S, Loreau M, de Mazancourt C, et al (2021) Biotic homogenization destabilizes ecosystem functioning by decreasing spatial asynchrony. Ecology 102:1–10

Yeates GW, Bongers T, De Goede RG, et al (1993) Feeding habits in soil nematode families and genera-an outline for soil ecologists. Journal of Nematology 25:315–331

Zavaleta ES, Pasari JR, Hulvey KB, Tilman GD (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. Proceedings of the National Academy of Sciences of the United States of America 107:1443–1446

4 Relevance of sex, gender and/or diversity

Next to the official advertisements that includes statements like "Women are expressly invited to apply; the same applies to people with disabilities", we will actively contact collaborators and ask to forward our advertisement to promising female master students (see *2.5 Measures to advance research careers* in the General Introduction of the Coordination Project). We fully

Project Description – Project Proposals

Michael Scherer-Lorenzen, Freiburg
Marcell K. Peters, Würzburg

SP5: After life - decomposition

Project Description

1 Starting Point

1.1 State of the art and preliminary work

Decomposition of organic material is a key processes in carbon and nutrient cycling of forest ecosystems: the physical, biological and chemical breakdown of organic matter during decomposition produces both humus and CO_2, and releases nutrients, the latter being again available for plant nutrition (Swift et al. 1979; Berg & McClaugherty 2003). The amounts of CO_2 released to the atmosphere as a consequence of decomposition are approximately in the same order of magnitude as photosynthetic assimilation (Berg & McClaugherty 2003). However, heterotrophic processes at the same time lead to the production of humic substances storing large amounts of carbon and nutrients and contributing to soil fertility. A large number of studies determine the factors controlling the process of litter and wood decomposition (reviews by e.g. Harmon et al. 1986; Aerts 1997; Coûteaux et al. 1995; Cadisch & Giller 1997; Seibold et al. 2021). The classical conceptualization of these controlling factors arrange environmental controls, litter and wood quality, and decomposer organisms into the ‘decomposition triangle’ (Bradford et al. 2016). According to this paradigm, decomposition of plant material is influenced by *environmental conditions*, with macro- but also microclimatic conditions being of paramount importance, together with soil factors and nutrient availability. In addition, decomposition rates depend on physico-chemical traits of litter (i.e. *substrate quality*: e.g. content of lignin and other phenolic compounds, lignin:nitrogen ratios, C:N ratios, morphology). Finally, the composition and activity of the *soil decomposer community* is also affecting decomposition rates. For a long time, it has been thought that these factors control decomposition processes in decreasing order of importance, with the role of litter/wood traits and the decomposer community mainly relevant at the local scale (Aerts 1997; Meentemeyer 1984). More recently, there has been some debate around the relative importance of these factors at different spatial scales, with the suggestion that litter traits related to the “leaf-economic spectrum” can be more important than climate even at global scales (Cornwell et al. 2008, Zhang et al. 2008). Finally, the role of decomposers has also been reassessed, finding a similar effect strength for the effect of soil fauna as for the quality of the plant matter (Garcia-Palacios 2013). Most importantly, all these studies suggest strong context-dependencies as well as interdependencies among these factors. For example, climate mainly influences decomposition processes via the detrital food web through strong effects of temperature and moisture on the metabolic activity of the component organisms (Seibold et al. 2021). In addition, climate also indirectly affects litter decomposition through changes in litter chemistry (Aerts 1997). During the last two decades, the effect of biodiversity was further included in the discussion about decomposition-controlling factors. Mixing of litter from different species or functional groups has profound effects on litter decomposition, with neutral, antagonist and synergistic effects being observable (see e.g. reviews Gartner & Cardon 2004; Hättenschwiler et al. 2005), although a more recent meta-analyses suggests overall positive litter mixing effects on decomposition rates (Mori et al. 2020; but see Porre et al. 2020). Litter and wood decomposition could be affected by plant species diversity due to differences among species in litter/woody debris quantity and quality, in timing of those inputs, but also due to the creation of different microclimatic conditions within a stand (Smith & Bradford 2003; Hobbie et al. 2006; Scherer-Lorenzen et al. 2007; Scherer-Lorenzen 2008, Seidelmann et al. 2016; Trogisch et al. 2016, Eichenberg et al. 2017; Kahl et al. 2017). These differences may also result in changes of the abundance and composition of the soil fauna and microbial community (Wardle & van der Putten 2002; De Deyn & Van der Putten 2005). Thus, we need further studies that focus on the influence of changing boundary conditions and contexts (e.g. forest management affecting tree composition, diversity and forest structure) on the entire ´decomposition triangle´.

Most decomposition studies only quantify different aspects of the process of decomposition as such (e.g. early-stage decomposition rates, factors controlling decomposition), and it is not entirely clear what ecological questions can really be answered by focusing on the rates of decomposition alone (Prescott 2005). Very few studies followed the flow of nutrients released from decomposing litter and subsequent uptake by plants, soil fauna or microbes (e.g. Zeller et al. 2000; Caner et al. 2004, Leppert et al. 2017). They showed that litter mass loss and N release are tightly linked in a 1:1 relationship, and that litter species identity is more important than litter diversity for such processes related to nutrient cycling. However, these studies were done at homogeneous abiotic conditions, neglecting potential microclimatic effects and thus the role of forest management.

In overlap with the decomposition of plant material, the decomposition of animal derived matter like dung or dead animals has also been associated with climate, organic matter quality and the species diversity of dung or carcass decomposers (Beynon et al. 2012; Kaartinen et al. 2013; Frank et al. 2017a; Peters et al. 2019). The relative strength of these effects is debated and could be related to the macroclimatic context, the pool of species available as decomposers and anthropogenic perturbation. In comparison to dead wood and leaf litter, dung and carcass decomposition rates are more strongly dependent on insects, particularly on beetles and flies, which typically decompose a large fraction of the total biomass within short periods of time (Hanski and Cambefort 1991). Because of the strong dependence of insect metabolism and of insect species pools on temperature (Brown et al. 2004), decomposition rates of dung and carcasses decline with seasonal, latitudinal or elevational decreases in temperature (Kaartinen et al. 2013, Frank et al. 2017b). The quality of the organic matter may also be of importance in determining the attractivity for decomposers: Dung of lower C:N ratio tends to attract more individuals of dung beetles but further studies are needed to underscore evidence for this effect (Frank et al. 2017a). Last, a couple of field and experimental studies in the framework of biodiversity-ecosystem functioning research could show that species diversity and functional diversity increase rates of dung decomposition (Beynon et al. 2012; own unpublished data). It has been a concern that land use and the loss of mammals from ecosystems causes an impoverishment of decomposer communities and correlated decreases in decomposition rates, for which evidence is mounting (Nichols et al. 2007; Nichols et al. 2008; Culot et al. 2013; Dirzo et al. 2014).

While the effects of differences in macroclimate across global or regional gradients have been studied for longer times, small-scale effects of forest canopy structure and its heterogeneity on microclimatic conditions in real-world ecosystems have received more attention only recently (e.g. Seidelmann et al. 2016, Ni et al. 2018, Gottschall et al. 2019, Gora et al. 2019). It is, however, the local or patch scale with its specific microclimate that is relevant for biodiversity and ecosystem functioning; hence there is a need to advance ‘microclimate ecology’ (De Frenne et al. 2021, Jucker et al. 2020). In forests, the microclimate at the soil surface strongly differs from the macroclimate (Zellweger et al. 2020), through canopy shading and insulation, and through transpiration, interception and stemflow (Schulze et al. 2019, De Frenne et al. 2021). Canopy effects are also responsible for the local distribution of litter differing in quantity and quality (Prescott 2002), and for plant regrowth and associated dynamics in the distributions of mammalian herbivores. Harvesting of trees from forest stands may also lead to a reduction in leaf production and total leaf biomass. In heterogeneous stands, litter is not evenly mixed on the forest floor so that local patches of highly degradable, more recalcitrant litter, or a mixture of both form a spatial mosaic with small-scale differences in nutrient dynamics (Burghouts et al. 1998). Therefore, changes in forest management practices that alter the forest canopy and associated changes in microclimate can largely affect decomposition processes and nutrient fluxes (Shorohova & Kapitsa 2014, Frank et al. 2017b).

Thus, by largely controlling the carbon and nutrient cycles, and hence indirectly also primary productivity and carbon storage, decomposition determines key ecosystem functions in forests. **However, the links between local forest management practices, affecting canopy structural heterogeneity and dead wood biomass, and the diversity of decomposers, decomposition and nutrient fluxes at different spatial scales remain poorly understood. Even unknown are the effects of changes in canopy structure and dead wood biomass – e.g. through Enhancement of Structural Alpha (ESC) and Beta (ESBC) Complexity in forests (see Cooperation project) – on between-patch β-diversity of decomposers and related decomposition processes, to our knowledge.**

Preliminary work

The subproject can build on an extensive sampling of communities of macrodetritivores and decomposition rates, which was conducted in the intensive sites in the Sailershausen forest both prior to ESBC treatments and after the ESBC treatments took place (i.e. in the winter of 2018/2019). In 2018, in the year before ESBC treatments, we collected on 60 study patches dung beetle communities with baited pitfall traps and quantified dung decomposition rates (loss of dry mass). Importantly, we did not find any significant differences in dung beetle abundance, species richness nor decomposition rates between the patches of future ESBC treatments (ANOVA, $P > 0.25$). We found that species richness, abundance and composition of dung beetle communities prior to the ESBC treatments were mainly driven by the natural variation in the openness of the vegetation and the distance to the forest edge (Fig. 1). Testing the biodiversity-ecosystem functioning relationship, we found stronger relationships between decomposition and the abundance of the decomposer community than for its species richness (Fig. 2).

In addition, we already quantified pre-treatment decomposition rates of tree leaf litter, wooden sticks (as a slow decomposing standard, data not shown) and filter paper (as a fast decomposing standard substrate) in all patches, with five replicates per patch each. The litter bags were composed of senescent leaf litter (2g dry weight) of the four dominant tree species of the sites, namely *Fagus sylvatica*, *Quercus robur*, *Carpinus betulus* and *Acer platanoides*, with the proportion of the species adjusted to their abundance at the site (*Fagus* 40%, *Quercus* 40%, *Carpinus* 10%, *Acer* 10%). In essence, decomposition rates of several substrates were not different among the patches where the ESBC treatments were applied afterwards, both for the spatial arrangement of the cuttings (aggregated vs. distributed, data not shown) as well as for the future deadwood structure (Fig. 3). The presence of *Vinca minor* in the understory of the patches increased decomposition rates of all substrates significantly (data not shown), suggesting that its abundance must be taken into account as a co-variable in future analyses.

Our data shows that there were no pre-treatment effects on litter decomposition rates nor on dung decomposition rates nor on the species richness and abundance of macrodetritivore communities. Thus, any future differences among patches must be due to our applied ESBC treatments.

In 2019, after the ESBC treatments were finished, we measured dung beetle diversity and abundance across the 60 study patches. First results indicate that ESBC treatments significantly influence decomposer diversity and abundance.

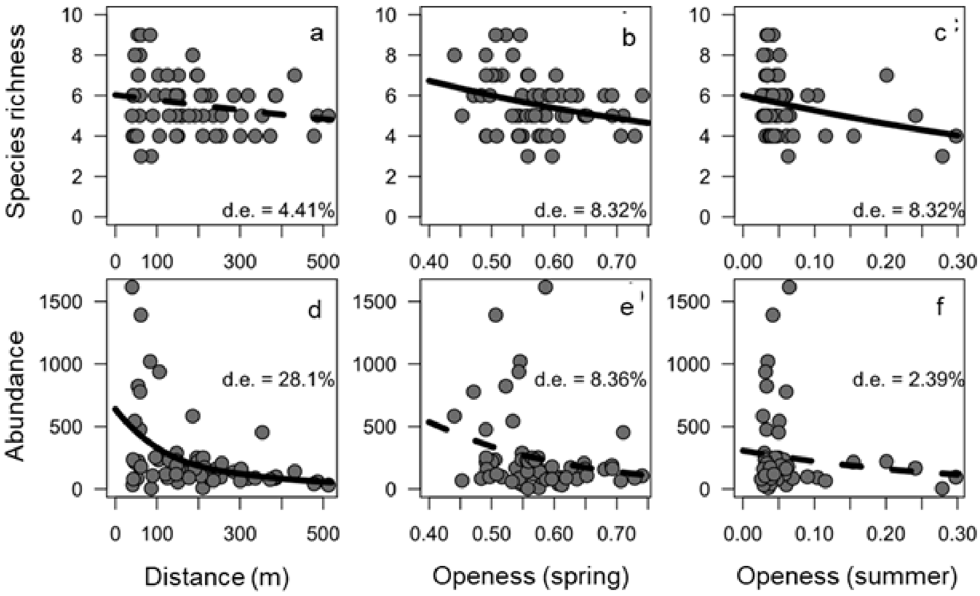


Fig. 1. Species richness (a-c) and abundance (d-f) of dung decomposing beetles varies with regard to the openness of the vegetation (relative values) and with regard to the distance to the forest edge, respectively. Lines show predictions of generalized additive models with significant effects ($p < 0.05$) shown by a continuous line and marginally significant effects ($p < 0.10$) indicated by an interrupted line. d.e. = explained deviance.

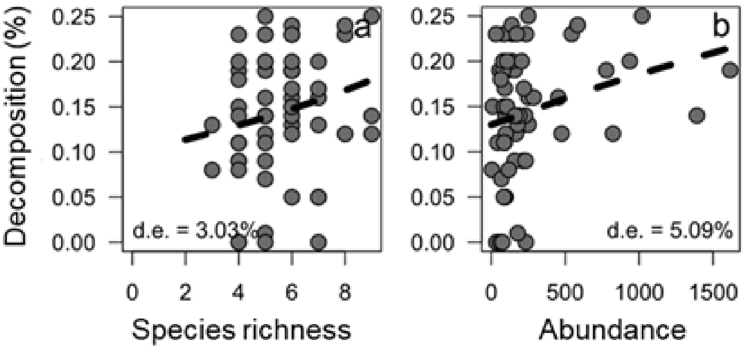


Fig. 2. The biodiversity effect on dung decomposition rates was more strongly driven by changes in abundance (number of individuals) than by changes in the species richness of dung decomposing communities. Lines show predictions of generalized additive models with marginally significant effects ($p < 0.10$) indicated by an interrupted line. d.e. = explained deviance.

Both PIs have long lasting expertise in community ecology and biodiversity-ecosystem functioning (BEF) research, with a focus on decomposition processes. MSL studies the mechanisms behind BEF relationships with a focus on plant litter decomposition and nutrient cycling, adopting litter bag approaches and tracer studies (e.g. Ristok et al. 2019, Joly et al. 2017, Scherer-Lorenzen 2008, Scherer-Lorenzen et al. 2007, Seidelmann et al. 2016, Trogisch et al. 2016; Leppert et al. 2017). He has also coordinated or participated in several large-scale forest ecology and BEF projects (coordination: FunDivEUROPE, Dr.Forest, TreeDivNet; participation: BEF China, SoilForEUROPE, MixForChange, ConFoBi, smallForest, BACCARA). MKP studies changes in biodiversity and ecosystem functions along climate and land use gradients with a focus on insects and their ecosystem functions and services in forests, applying a wide range of field, laboratory and statistical tools including field measurements of dung beetle diversity, and the decomposition of dung and carcasses under different exclosure treatments (Ross et al. 2018; Peters et al. 2019; Gebert et al. 2020; Albrecht, Peters et al. 2021). He coordinated or participated already in several research consortia (finished: BIOTA East Africa, FOR1246; current: UPSCALE, ANDIV).

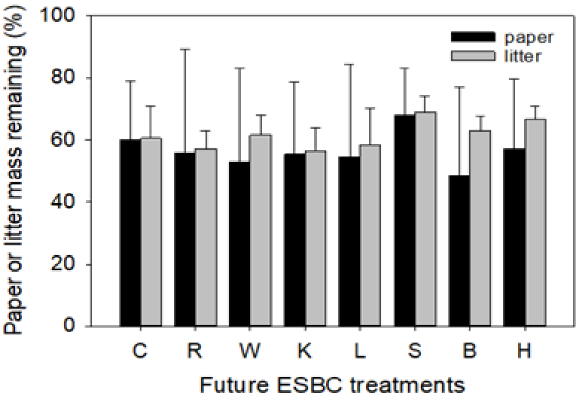


Fig. 3. Litter and paper decomposition rates among patches before ESBC management practises have been applied. Shown are the future deadwood structures (C: control; R: total tree removed; W: stumps remain; K: crowns remain; L: logs; S: snags; B: logs and snags; H: habitat trees; see Fig. 5 in cooperation project for more information about the treatments). Future treatments do not differ in decomposition rates (ANOVA). Litter bags and filter papers were in the field for 70 days in spring 2019.

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. Albrecht J*, **Peters MK***, Becker JN, Behler C, Classen A, Ensslin A, Ferger SW, Gebert F, Gerschlauer F, Helbig-Bonitz M, Kindeketa WJ, Kühnel A, Mayr AV, Njovu HN, Pabst H, Pommer U, Röder J, Rutten G, Schellenberger Costa D, Sierra-Cornejo N, Vogeler A, Vollstädt MGR, Dulle HI, Eardley CD, Howell KM, Keller A, Peters RS, Kakengi V, Hemp C, Zhang J, Manning P, Mueller T, Bogner C, Böhning-Gaese K, Brandl R, Hertel D, Huwe B, Kiese R, Kleyer M, Leuschner C, Kuzyakov Y, Nauss T, Tschapka M, Fischer M, Hemp A, Steffan-Dewenter I, Schleuning M (2021) Species richness is more important for ecosystem functioning than species turnover along an elevational gradient. *Nature Ecology and Evolution*. https://doi.org/10.1038/s41559-021-01550-9. ***equal contribution.**
2. Gebert F, Steffan-Dewenter I, Moretto P, **Peters MK** (2020) Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. *Journal of Biogeography* 47:371-381.
3. Joly F-X, Milcu A, **Scherer-Lorenzen M**, Jean L-K, Bussotti F, Dawud SM, Müller S, Pollastrini M Raulund-Rasmussen K, Vesterdal L, Hättenschwiler S (2017) Tree species diversity affects decomposition through modified micro-environmental conditions across European forests. *New Phytologist* 214: 1281-1293.
4. Leppert KN, Niklaus PA, **Scherer-Lorenzen M**. (2017) Does species richness of subtropical tree leaf litter affect decomposition, nutrient release, transfer and subsequent uptake by plants? *Soil Biology and Biochemistry* 115: 44-53.
5. **Peters MK**, Hemp A, Appelhans T, Becker JN, Behler C, Classen A, Cornejo NS, Detsch F, Ensslin A, Ferger SW, Frederiksen SB, Gebert F, Gerschlauer F, Gütlein A, Haas M, Helbig-Bonitz M, Hemp C, Kindeketa WJ, Kühnel A, Mayr A, Mwangomo E, Ngereza C, Njovu HN, Otte I, Pabst H, Renner M, Röder J, Rutten G, Schellenberger Costa D, Vollstädt MGR, Eardley CD, Keller A, Peters RS, Ssymank A, Kakengi V, Zhang J, Bogner C, Böhning-Gaese K, Brandl R, Hertel D, Huwe B, Kiese R, Kleyer M, Kuzyakov Y, Nauss T, Schleuning M, Tschapka M, Fischer M, Steffan-Dewenter I (2019) Climate-land-use interactions shape tropical mountain biodiversity and ecosystem functions. *Nature* 568:88-92.

6. Ristok C, Leppert KN, **Scherer-Lorenzen M**, Niklaus PA, Bruelheide H (2019) Soil macrofauna and leaf functional traits drive the decomposition of secondary metabolites in leaf litter. *Soil Biology and Biochemistry* 135, 429-437.
7. Ross SRP-J, Hita Garcia F, Fischer G, **Peters MK** (2018) Selective logging intensity in an East African rain forest predicts reductions in ant diversity. *Biotropica* 50: 768-778.
8. **Scherer-Lorenzen M** (2008) Functional diversity affects decomposition processes in experimental grasslands. *Functional Ecology* 22: 547-555.
9. **Scherer-Lorenzen M**, Bonilla J-L, Potvin C (2007) Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. *Oikos* 116: 2108-2124.
10. Seidelmann KN, **Scherer-Lorenzen M**, Niklaus PA (2016) Direct vs. microclimate-driven effects of tree species diversity on litter decomposition in young subtropical forest stands. *PLoS ONE* 11: e0160569.

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed not applicable

1.2.3 Patents not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

Four years

2.2 Objectives

We hypothesise that ESBC treatments influence the diversity and composition of macrofauna detritivores, decomposition rates of dead organic matter (leaf litter, wood, dung, and carcasses) and nutrient fluxes within forest patches. We specifically hypothesise that the diversity of ESBC management practises will translate into increases in β-diversity of macrofauna detritivores and β-functionality of decomposition processes between forest patches, which consequently positively influence diversity and ecosystem multifunctionality at the forest district level (γ-diversity, γ-multifunctionality) (Fig. 4). By linking data on decomposer communities, decomposition processes and nutrient fluxes collected by SP5 with collective data sampled by other SP's of the RU we test the following specific hypotheses:

At the local (α) patch level:

Hypothesis 1*: Those ESC treatments, which cause an opening of the vegetation, positively affect the species α-diversity of macrodetritivores*

Due to the positive effect of temperature on the species richness of insects, we expect that the species richness of macrofauna detrivores generally increases with soil temperature and in more open habitats (Peters et al. 2016; Gebert et al. 2020). Additionally, we expect the species richness and abundance of macrodetritivores to increase with increases in the availability of food resources.

Hypothesis 2: *a) Those ESC treatments maximizing relative humidity and, of secondary importance temperature, foster decomposition rates of plant-derived organic matter (leaf litter, dead wood, filter, tea bags), while decomposition rates of animal-derived organic matter will be maximized in habitats of high temperature (while relative humidity is less important). b) We expect that decomposition rates of all organic materials are positively related to the abundance, biomass and the diversity of decomposers.*

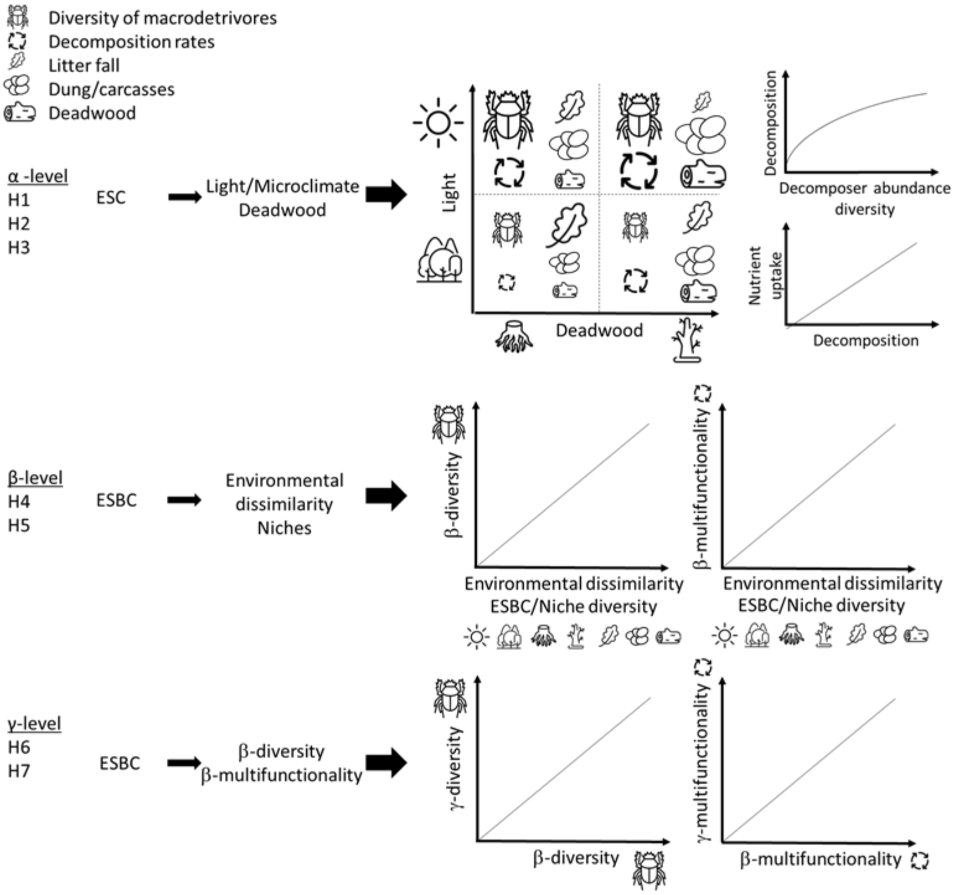


Fig. 4. Conceptual overview showing the expectations and hypotheses at the α-, β- and γ-level. Different ESC treatments vary in their effect on canopy closure, which influences the microclimate at the forest floor, and the amount and distribution of deadwood. These environmental changes are assumed to affect detritivore communities and decomposition rates of different types of organic matter in various ways. Environmental changes caused by ES(B)C are, thus, expected to affect the diversity of decomposers and decomposition rates at the α-level, and their dissimilarity at the β-level. In consequence, ESBC-managed forests will have a higher multifunctionality in decomposition processes than control forests with homogeneous management.

We assume that different ESC treatments lead to predictable differences in climatic conditions and decomposer diversity, abundance and biomass, which in turn influence decomposition rates. Importantly, ESC treatments effects may not be homogeneous across all types of organic materials. Instead, decomposition rates of different organic materials may be maximized under different ESC treatments. We assume that the difference between macroinvertebrate exclosures and the ‘control bags’ to be higher for organic material characterized by low C:N values. Furthermore, based on BEF theory, we assume that differences between exclosure treatments will be highest where ESC management treatments lead to predictable reduction in macrodetritivore diversity. Following predictions of BEF theory, we expect a general increase of decomposition rates of all organic materials with the species diversity, biomass and abundance of decomposer communities.

Hypothesis 3*: ESC practises influence resource availability and nutrient fluxes. a) Leaf litter mass available for decomposers declines, but dead wood and dung mass increases along the deadwood- and light-gradients of ESC treatments. b) Those ESC treatments maximising decomposition rates (cf. H2) will increase subsequent nutrient uptake by plants and animals.*

Nutrient availability in forest soils is influenced by organic matter mass entering the decomposition system, by climate-mediated changes in decomposer communities and decomposition rates, and increases with higher light and temperature conditions or soil moisture.

At the between-patch (β) level:

***Hypothesis 4**: Macrodetritivore communities are altered in predictable and different ways by different ESBC treatments, fostering β-diversity (by changes in both species richness and by species turnover) in ESBC districts.*

ESBC treatments influence the vegetation structure and soil microclimate. As different macrodetritivore species have specific habitat niche requirements, ESBC treatments will promote the establishment of different species communities.

***Hypothesis 5**: ESBC districts show stronger differences in decomposition rates (i.e. higher β-decomposition-multifunctionality) and in plant/animal nutrient uptake rates (i.e. β-nutrient-uptake-multifunctionality) than Control districts.*

Due to deterministic changes in microclimate and detritivore communities (diversity, abundance, species composition) along ESBC treatment gradients, decomposition rates of various organic materials and subsequent uptake of nutrients by plants and animals strongly differ among different ESBC treatments. In consequence, the average difference in decomposition rates of individual types of organic matter and β-multifunctionality (based on decomposition rates of multiple organic substrates or nutrient uptake rates) is higher in ESBC districts than in Control districts.

At the landscape (γ) level:

***Hypothesis 6**: The higher β-diversity among forest patches leads to a higher γ-diversity* of *macrodetritivores in ESBC districts in comparison to Control districts.*

Adopting our first, general approach of a multiplicative determination of β-diversity (β = γ/α, see Box 1 in cooperation project), we assume an increase of γ-diversity with increasing β-diversity.

***Hypothesis 7**: Decomposition rates across different types of organic material (decomposition multifunctionality) will overall be higher in ESBC districts than in Control districts.*

Differences in decomposition rates of different organic materials among ESBC treatments (β-decomposition-multifunctionality) and a more diverse species pool of decomposers will lead to a higher γ-decomposition multifunctionality in the ESBC districts.

Data exchange and collaboration within the consortium

For the whole RU and syntheses in SPZ, we provide data on the diversity of macrodetritivores and decomposition rates of various types of organic matter from all 234 patches (Fig. 5). We will depend on data of SPZ on microclimate, on SP1 and SP3 on the amount of dead wood and forest structure and on data of SP9 on mammal communities on the 234 patches. We will supply data on decomposition rates to SP4, data on leaf litter and seed rain (in leaf litter traps) to SP6, and data on dead wood decomposition on the forest floor to SP7. Together with SP4, SP6 and SP7 we will analyse the effects of different taxa of decomposers (SP4: invertebrate soil detritivores; SP6: snails; SP7: fungi and bacteria) on decomposition rates of different types of organic matter, from deadwood to carcasses. For analyses of multifunctionality and statistical analyses, we will closely collaborate with SPZ. Our analysis of nutrient composition of organic matter and nutrient fluxes will provide a better mechanistic understanding on the turnover of nutrients, which will also be used by SP4, SP7 and SPZ.

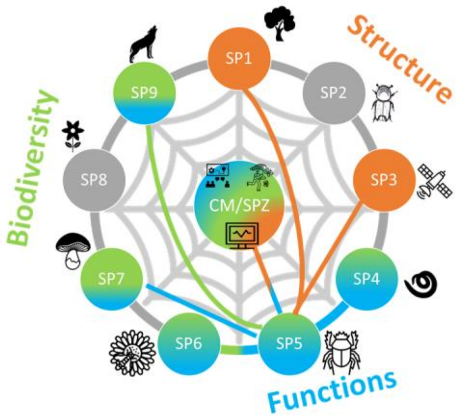


Fig. 5: Close cooperation of SP5 with other subprojects, the colour of arrows indicate the type of data exchanged; green: species data, blue: functions, brown: structure.

2.3 Work programme including proposed research methods

WP1: Effects of ES(B)C forest management on macrofauna detritivores (lead: Peters)

As dung and scavenger insects (mostly beetles and flies) search for food by smell and as they are typically highly mobile, they can be easily and accurately sampled with baited pitfall traps (Larsen and Forsyth 2005). Traps will consist of 500 cm^3 plastic cups, which are buried in the ground so that the upper rim is even with the soil surface hindering beetles from perceiving the trap as an obstacle (Fig. 6A, B). The cup will be filled with an 80% ethanol solution to approximately its half. The bait is wrapped in a tea-bag and fastened with a string to a stick positioned in the ground so that it will be suspended over the cups, simulating the odour of a natural dung pad. We use two kinds of baits to attract macrofauna detritivores: cattle dung and mouse carcasses. The two baited pitfall traps will be placed at the peak activity time of macrofauna insect decomposers (~May to June) in the centre of each patch, at an approximate distance of 5 m to each other. A rain cover placed at ca. 20 cm height protects traps from rain. The traps will be activated after finishing the dung and mouse carcass decomposition experiment, in order to exclude a potential influence of macrodetritivore sampling on decomposition. Traps will be left open for two days. After this time, captured specimens will be sieved and stored in Whirl-Paks filled with 95% ethanol. At the laboratory, individuals in each trap will be sorted into orders and the abundance and weight of each sample fraction will be determined (drained wet weight; → abundance and biomass of the dung beetle, dung fly, scavenger beetle and scavenger fly community). Insects will be mounted and identified to genera and species (or morphospecies) using identification literature and by consulting expert taxonomists for difficult genera. From the data of all patches we construct a species-abundance table, which will be used for determining various diversity measures.

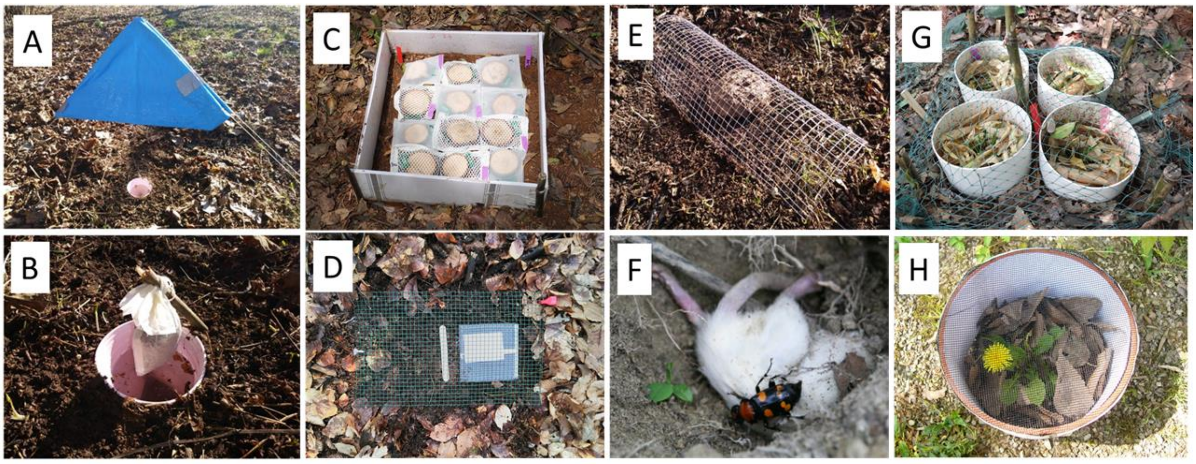


Fig. 6. Pictures illustrating some of the sampling done on study patches. (A) Pitfall trap with rain cover and dung bait (B) freely hanging over the trap. (C) Fine-mesh and coarse mesh exclosures of wood samples lying on the forest ground for measuring dead wood decomposition. (D) Filter paper and lolly stick in coarse-mesh exclosure, (E) dung pad with protection, (F) detail of mouse and burying beetle illustrating some types of organic matter used in SP5 for measuring decomposition rates. (G, H) Mesocosms for measuring nutrient fluxes.

WP2: Effects of ES(B)C forest management on decomposition rates of different types of organic matter (lead: Scherer-Lorenzen & Peters)

To quantify the effects of the ES(B)C treatments on decomposition of organic matter we will use a standard protocol on all patches (Fig. 6C-F). At the eight extensive sites (Coordination Project: Fig. 13), a total of five different organic materials will be used. At the three intensive sites, we will further use materials of different quality for some of the substrate types, differing regarding fibre content or wood density and C/N ratio, and which influences the overall digestibility for decomposers (marked with asterisks in the list below). This yields a total of eleven different substrates at the intensive sites. The following types of organic matter will be placed with the indicated dry masses, exposition times and in the corresponding microhabitats:

i 4 pieces of wood of high density, 300 g (dry weight), 2 years, ground*
ii 4 pieces of wood of low density, 300 g (dry weight), 2 years, ground
iii 4 bags of leaf litter with high C:N ratio, 5 g (dry weight), 180 days, ground*
iv 4 bags of leaf litter with low C:N ratio, 5 g (dry weight), 180 days, ground
v 4 pads of dung with high C:N ratio (cow, herbivore), 350 g (wet weight), 21 days, ground
vi 4 pads of dung with low C:N ratio (wild boar, generalist), 350 g (wet weight), 21 days, ground*
vii 4 complete mouse carcasses, ~20 g (wet weight), 21 days, ground
viii 4 tea bags with high C:N ratio (rooibos tea), 180 days, soil at 8 cm depth*
ix 4 tea bags with low C:N ratio (green tea), 180 days, soil at 8 cm depth
x 4 laboratory filter papers of 10 cm diameter, 90 days, ground*
xi 4 wooden (popsicle) sticks, 2.5 g (dry weight), 2 years, ground*

The tree species used to obtain wood and litter of different qualities do not occur at our study sites to avoid “home-field-advantage” effects depending on their abundance (see Table 1 in Coordination Project). Thus, we will use wood pieces of high density from *Aesculus hippocastanum* (wood density 650 kg/m³), and those of low density from *Populus tremula* (wood density 410 kg/m³). Leaf litter with high C:N ratio will be obtained from *Sorbus aucuparia* (C:N 54), and that with low C:N ratio from *Ulmus glabra* (C:N 28). Similarly, we will use both herbivore (cow) and generalist dung (wild boar).

In order to quantify the relative contribution of macro- and microdetritivores on decomposition (Seibold et al. 2021) one set of the above-mentioned units will be placed in a polyester mesh bag (1 mm mesh size) which excludes all macrodetritivores. The other set of units will be placed in a polyester mesh bag of 5 mm mesh size, which gives access to all microdetritivores and most macrodetritivores while still making it possible to sample the remaining substrate at the end of the exposition time (Seibold et al. 2021). Replicate units of all substrates will be placed together at randomly selected locations in the central area of patches and recollected after the above listed exposition times. At the intensive sites we will regularly measure fresh weight of dead wood, dung and mouse carcass samples at five times within the exposition period (at time 0, 0.25 quantile of the exposition time, 0.5, 0.75 and at the end). Upon final collection, remaining material will be cleaned and dried at 60°C for 48h and again weighted. Initial mass of the wood, litter, tea bag and filter paper samples will be determined with air-dry material, with subsamples additionally dried at 60°C until constant weight to obtain a 60°C dry mass correction factor. For relating the weight of the remaining cow dung to the weight at the start of the experiment, 10 fresh dung pads of each type will be directly dried and used for comparison. The weight of individual mouse carcasses will be determined before placing them in the field. For determining the dry weight of mouse carcasses at the start of the experiment, fresh and dry weight of 10 mouse carcasses of different sizes will be determined and related to each other in a linear model. Models will be used for predicting the dry weight of all mouse carcasses from the fresh weight at the start of decomposition experiments. The decomposition rate of samples will be determined as dry weight related mass loss.

WP3: Effects of ES(B)C forest management on resource availability and nutrient fluxes (lead: Scherer-Lorenzen)

The nutrient pool sizes of leaf litter, their temporal changes, and litter decomposition and the turnover of labile soil organic matter could be affected by the forest structure and heterogeneity due to differences in canopy cover, litter and deadwood production, and microclimatic conditions within a stand. From an ecosystem perspective, insights into nutrient-cycling and C-sequestration and into the effect of forest heterogeneity on these processes might not be gathered from short-term litter decomposition rates only (Prescott 2005). Hence, the quantification of mass and nutrient content of organic matter input should be an integral part of decomposition studies. Thus, a combination of both decomposition trials and quantification of organic matter inputs are needed to obtain a broad understanding of decomposition and nutrient cycling. Together with SPZ and SP1 we will therefore quantify temporal dynamics of leaf litter fall, as well as dead wood production, and corresponding nutrient fluxes from aboveground biomass to the soil. Replicate litter traps will be installed in each patch and the mass of trapped litter (separated by tree species and into leaves, twigs and reproductive organs) will be quantified monthly or bi-weekly (in times of huge litter production in autumn). Four times a year, we will analyse these samples for their C, N, P and cation concentrations and will use these data to calculate element fluxes with litter fall. Together with data on forest floor litter biomass (sampling of replicate forest floor frames of 25 x 25cm, four times per year; together with SP4) and its element concentrations, we will calculate turnover coefficients of forest floor mass (annual litterfall input/mean floor mass), and will thus have all data necessary to quantify litter pools and fluxes. For the extensive sites, we will not measure the chemical composition of all litter samples, but will use data from the intensive sites or from databases (such as TRY) on species-specific mean element concentrations.

Dung resource production will be approximated by using data on the species-occurrence of mammals on study patches. Data on the temporal occurrence of mammals on patches will be derived from camera trapping data of SP9. Making use of the known biomass of individual mammal species and the approximate scaling of dung production with the biomass$^{0.75}$ (~metabolic biomass), we calculate a relative measure of dung production by summing up the metabolic biomass values of camera-detected mammals over time (Gebert et al. 2020). The assumption here is that the probability of dung production of a mammal is directly, positively related to the time it spends on patches. A similar approach will be used to approximate the carcass biomass available to carcass decomposers.

To assess the nutritional consequences of different decomposition rates that might result from our ES(B)C treatments (see above), we will measure nutrient release from decomposing substrates, and subsequent uptake by plants (phytometers) and dung beetles, by adopting a tracer approach with ^{15}N and Lithium (as surrogate for potassium) enriched plant material (Leppert et al. 2017), and ^{15}N enriched dung (Nervo et al. 2017). Tracers are substances, which are present only in very low quantities in the ecosystems to be studied and are chemically equivalent to the nutrients of interest. To assess the uptake of potassium by plants, non-isotopic tracers have been effectively applied in the past and one of us (MSL) has actively used and developed such techniques (Gockele et al. 2014, Leppert et al. 2017). This tracer experiment can only be done in two replicates of the ESBC treatments at the intensive sites, with a total of 30 patches. Thus, it will focus on the α- and β-level.

In each patch, we will install eight mesocosms (Fig. 6 G, H) made of PVC (4 mesocosms for plant and 4 for dung material: 30 cm diameter x 12.5 cm height, lowered 10 cm into the soil). The position of the mesocosms within the patches will be randomized to account for a possible heterogeneity in soil conditions and due to the differences of the overstory species composition and canopy openings. Half of the mesocosms will be filled with 15 g of ^{15}N and Lithium labelled litter, the other half with 500 g of ^{15}N labelled dung, respectively. One hemicryptophyte phytometer plant (*Viola reichenbachiana*), originating from the same forest stand, will be transplanted in the centre. In those mesocosms with labelled dung, we will also insert 10 marked dung beetles (Beynon et al. 2012). We will confirm that the body sizes of beetles are similar across all mesocosms. Mesocosms will be covered with a 1.5 cm mesh to prevent litter input from surrounding trees. At the end of the experiment, after ~20 days, we will excavate the phytometer plants, collect the original, hatched and larval dung beetles, and remove the decomposing litter. The resulting samples of above- and belowground organs of the phytometers, of the dung beetles, of the remaining litter, and of the topsoil beneath the mesocosms (bulk soil) will be analysed for their ^{15}N and Lithium (the latter only in the phytometers) concentrations. Nutrient release from decomposing litter and uptake rates by plants and beetles will be calculated as done in similar, previous experiments (Gockele et al. 2014, Leppert et al. 2017, Nervo et al. 2017). In essence, we will calculate ^{15}N and Lithium excess rates based on comparisons between element concentrations before and after the experimental exposure.

Statistical analyses (sorted by manuscripts and hypotheses)

Manuscript 1: Hypothesis (H) 1, H4, H6 (PhD, lead supervisor MKP)

***H1**:* We will analyse the direct and indirect effects of ESC management practises, forest floor microclimate and food resources (diversity, biomass) on macrofauna detritivore diversity, abundance and biomass using Bayesian hierarchical structural equation models (Dainese et al. 2019). We expect that ESC management practices influence ground humidity and temperature and, by modifying the vegetation structure, the mean mammalian biomass and diversity. As response variables we will use the observed and chao1-estimated species richness, the abundance and biomass of dung beetles, dung flies (i.e. insects attracted to the dung trap), scavenger beetles and scavenger flies (i.e. insects attracted to the mouse carcass trap). We expect positive effects of temperature and food resource richness (approximated by the mammalian biomass/ metabolic biomass; see WP3) on insect diversity, abundance and biomass of dung-attracted insects and scavenger insects. This finding would suggest limitations of macrodetritivore communities in forests by both temperature and food resources.

H4*:* We will calculate β-diversity of detritivore communities among patches of the 11 Control and 11 ESBC districts. We will calculate different measures of β-diversity (Kraft et al. 2011) but base our major inference on the multiplicative beta in harmony with other SP's of the RU. We will use a simple paired-t-test or Bayesian hierarchical models to test if β-diversity among forest patches is higher in ESBC districts than in Control districts. In addition, we will calculate the between-patch Euclidean dissimilarity in environmental variables which are assumed to influence decomposer communities (e.g. temperature, humidity) and use linear models and null models to test if a higher dissimilarity in the environment of decomposers lead to higher dissimilarity in macrodetritivore communities (for individual types of organic matter and multifunctionality).

H6*:* First, we will use mean estimates of β-diversity per district and relate them to γ-diversity. Second, we test if ESBC districts have a higher mean γ-diversity in macrodetritivores than Control districts.

Manuscript 2: H2 (PhD, lead supervisor MSL & MKP)

H2: Using Bayesian hierarchical models (to adjust for the multiple measurements per patch) and only data from coarse-mesh matter samples, we will test for each type of organic matter how mean decomposition rates differ between ESC treatments. By adding data from macrodetritivore exclosures we test, if the contribution of macrodetritivores to decomposition rates (in relation to microdetritivores) varies among different types of organic material and with ESC management. For disentangling direct and indirect effects of ESC treatment, climate, macrodetritivore diversity and decomposition rates, Bayesian hierarchical structural equation models will be used.

The analyses described above will additionally be done for a multifunctionality decomposition index capturing the (standardized) rates of decomposition of all 11 types or 6 types (for intense site data and data from all sites, respectively) of organic matter (Byrnes et al. 2014, Lefcheck et al. 2015). The multifunctionality index will be calculated using different strategies, e.g. threshold based indices or average indices of multifunctionality (Lefcheck et al. 2015) and related to the diversity of different decomposer taxa (invertebrates, fungi, bacteria; from SP4, SP6, SP7).

Manuscript 3: H3 (PhD, lead supervisor MSL):

H3*:* We will use Bayesian hierarchical models to test the influence of ESC treatments on the amount of dead wood, leaf litter and dung production. Bayesian hierarchical structural equation models will be used to quantify the linkages between ESC treatment, decomposition rates and nutrient uptake by plants.

Manuscript 4: H5 + H7 (PhD, lead supervisor MSL & MKP)

***H5**:* In addition to the calculation of multifunctionality at the patch scale (see H2), we will calculate indices of β-multifunctionality of decomposition rates and of plant and animal uptake rates of nutrients in analogy to β-diversity (Mori et al. 2018) (see also Fig. 2 of Coordination Project). We will use a simple paired-t-test or Bayesian hierarchical models to test if *β*-multifunctionality among forest patches is higher in ESBC districts than in Control districts. In addition, we will calculate the between-patch Euclidean dissimilarity in environmental variables that are assumed to influence decomposer communities and decomposition (temperature, humidity, pH, amount of dead wood) and use linear models and null models to test if a higher dissimilarity in the environment of decomposers lead to higher dissimilarity in decomposition rates (for individual types of organic matter and multifunctionality).

***H7**:* We will use Bayesian hierarchical models to test if ESBC districts have a higher mean multifunctionality of decomposition rates. The multifunctionality index will be calculated using different strategies, e.g. threshold based indices or average indices of multifunctionality (Lefcheck et al. 2015).

Table 1. Time table of the work program by month.

	2022	2023	2024	2025	26
WP1 - Effects of ESBC forest management on macrofauna detritivores					
Macrodetritivore sampling	▨▨▨▨▨▨□□□	□□□□□□□□□□□□	□□□□□□□□□□□	□□□□□□□□□□□□	□□□
Processing and identification of samples	□□▨▨▨▨▨▨▨	▨▨▨▨▨▨▨□□□□□	□□□□□□□□□□□	□□□□□□□□□□□□	□□□
Set up of data tables	□□□□□□□□▨	▨▨▨▨▨▨▨▨□□□□	□□□□□□□□□□□	□□□□□□□□□□□□	□□□
WP2 - Effects of ESBC forest management on decomposition rates of various organic materials					
Measuring decomposition rates	▨▨▨▨▨▨▨▨▨	▨▨▨▨▨▨▨▨▨▨▨▨	▨▨▨▨□□□□□□□	□□□□□□□□□□□□	□□□
Laboratory processing of samples	□□▨▨▨▨▨▨▨	▨▨▨▨▨▨▨▨▨▨▨▨	▨▨▨▨▨□□□□□□	□□□□□□□□□□□□	□□□
Set up of data tables	□□□▨▨▨▨▨▨	▨▨▨▨▨▨▨▨▨▨▨▨	▨▨▨▨▨□□□□□□	□□□□□□□□□□□□	□□□
WP3- Effects of ESBC forest management on resource availability and nutrient fluxes					
Field work nutrient fluxes on intense study sites	□□□□□□□□□	□□□□□□□□□□□□	□□□▨▨▨□□□□□	□□□□□□□□□□□□	□□□
Laboratory analyses of samples	□□□□□□□□□	□□□□□□□□□□□□	□□□▨▨▨▨□□□□	□□□□□□□□□□□□	□□□
Set up of data tables	□□□□□□□□□	□□□□□□□□□□□□	□□□□□□▨▨▨□□	□□□□□□□□□□□□	□□□
Statistical analyses and manuscript writing					
Manuscript 1: Hypothesis1 + H4 + H6	□□□□□□□□□	□□□□□□▨▨▨▨▨▨	▨▨□□□□□□□□□	□□□□□□□□□□□□	□□□
Manuscript 2: H2	□□□□□□□□□	□□□□□□□□□□□□	□□□□□▨▨▨▨▨▨	▨□□□□□□□□□□□	□□□
Manuscript 3: H3	□□□□□□□□□	□□□□□□□□□□□□	□□□□□□□□□□□	▨▨▨▨▨▨▨▨□□□□	□□□
Manuscript 4: H5 + H7	□□□□□□□□□	□□□□□□□□□□□□	□□□□□□□□□□□	□□□□□□▨▨▨▨▨▨	▨▨▨

3 Bibliography concerning the state of the art, the research objectives, and the work programme

Aerts R (1997) Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: a triangular relationship. Oikos 79:439.

Berg B, McClaugherty C (2003) Plant Litter. Springer Berlin Heidelberg, Berlin, Heidelberg

Beynon SA, Mann DJ, Slade EM, Lewis OT (2012) Species-rich dung beetle communities buffer ecosystem services in perturbed agro-ecosystems. Journal of Applied Ecology 49:1365–1372.

Bradford MA, Berg B, Maynard DS, et al. (2016) Understanding the dominant controls on litter decomposition. Journal of Ecology 104:229–238.

Brown JH, Gillooly JF, Allen AP, et al. (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789

Burghouts TBA, Straalen NMV, Bruijnzeel LA (1998) Spatial heterogeneity of element and litter turnover in a Bornean rain forest. Journal of Tropical Ecology 14:477–506.

Byrnes JEK, Gamfeldt L, Isbell F, et al. (2014) Investigating the relationship between biodiversity and ecosystem multifunctionality: challenges and solutions. Methods in Ecology and Evolution 5:111–124.

Cadisch G, Giller KE (eds) (1997) Driven by nature: plant litter quality and decomposition. CAB International, Wallingford, Oxon, UK

Caner L, Zeller B, Dambrine E, et al. (2004) Origin of the nitrogen assimilated by soil fauna living in decomposing beech litter. Soil Biology & Biochemistry 36:1861-1872.

Cornwell WK, Cornelissen JHC, Amatangelo K, et al. (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecology Letters 11:1065–1071.

Coûteaux M-M, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. Trends in Ecology & Evolution 10:63–66.

Culot L, Bovy E, Zagury Vaz-de-Mello F, et al. (2013) Selective defaunation affects dung beetle communities in continuous Atlantic rainforest. Biological Conservation 163:79–89.

Dainese M, Martin EA, Aizen MA, et al. (2019) A global synthesis reveals biodiversity-mediated benefits for crop production. Science Advances 5:eaax0121

Dirzo R, Young HS, Galetti M, et al. (2014) Defaunation in the Anthropocene. Science 345:401–406.

De Deyn G, Van der Putten W (2005) Linking aboveground and belowground diversity. Trends in Ecology & Evolution 20:625–633.

De Frenne P, Lenoir J, Luoto M, et al. (2021) Forest microclimates and climate change: Importance, drivers and future research agenda. Global Change Biology 27:2279-2297.

Eichenberg D, Pietsch K, Meister C, et al. (2017) The effect of microclimate on wood decay is indirectly altered by tree species diversity in a litterbag study. Journal of Plant Ecology 10:170–178.

Frank K, Brückner A, Hilpert A, et al. (2017a) Nutrient quality of vertebrate dung as a diet for dung beetles. Scientific Reports 7:12141.

Frank K, Hülsmann M, Assmann T, et al. (2017b) Land use affects dung beetle communities and their ecosystem service in forests and grasslands. Agriculture, Ecosystems & Environment 243:114–122.

García-Palacios P, Maestre FT, Kattge J, Wall DH (2013) Climate and litter quality differently modulate the effects of soil fauna on litter decomposition across biomes. Ecology Letters 16:1045–1053.

Gartner TB, Cardon ZG (2004) Decomposition dynamics in mixed-species leaf litter. Oikos 104:230–246.

Gebert F, Steffan-Dewenter I, Moretto P, Peters MK (2020) Climate rather than dung resources predict dung beetle abundance and diversity along elevational and land use gradients on Mt. Kilimanjaro. Journal of Biogeography 47:371–381.

Gockele A, Weigelt A, Gessler A, Scherer-Lorenzen M (2014) Quantifying resource use complementarity in grassland species: A comparison of different nutrient tracers. Pedobiologia 57:251–256.

Gora EM, Lucas JM, Yanoviak SP (2019) Microbial composition and wood decomposition rates vary with microclimate from the ground to the canopy in a tropical forest. Ecosystems 22:1206-1219.

Gottschall F, Davids S, Newiger-Dous TE, et al. (2019) Tree species identity determines wood decomposition via microclimatic effects. Ecology and Evolution 9:12113-12127.

Hanski I, Cambefort Y (eds) (1991) Dung beetle ecology. Princeton University Press, Princeton, N.J

Harmon ME, Franklin JF, Swanson FJ, et al. (1986) Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research, pp 133-302, Academic Press, New York

Hättenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. Annual Review of Ecology, Evolution, and Systematics 36:191–218.

Hobbie SE, Reich PB, Oleksyn J, et al. (2006) Tree species effects on decomposition and forest floor dynamics in a common garden. Ecology 87:2288–2297.

Jucker T, Jackson TD, Zellweger F, et al. (2020) A research agenda for microclimate ecology in human-modified tropical forests. Frontiers in Forests and Global Change 2, Art. 92:1-11

Kaartinen R, Hardwick B, Roslin T (2013) Using citizen scientists to measure an ecosystem service nationwide. Ecology 94:2645–2652

Kahl T, Arnstadt T, Baber K, et al. (2017) Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. Forest Ecology and Management 391:86–95.

Kraft NJB, Comita LS, Chase JM, et al. (2011) Disentangling the drivers of diversity along latitudinal and elevational gradients. Science 333:1755–1758.

Larsen TH, Forsyth A (2005) Trap spacing and transect design for dung beetle biodiversity studies. Biotropica 37:322–325.

Lefcheck JS, Byrnes JEK, Isbell F, et al. (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature Communications 6:6936.

Leppert KN, Niklaus PA, Scherer-Lorenzen M (2017) Does species richness of subtropical tree leaf litter affect decomposition, nutrient release, transfer and subsequent uptake by plants? Soil Biology & Biochemistry 115:44–53.

Meentemeyer V (1984) The geography of organic decomposition rates. Annals of the Association of American Geographers 74:551–560.

Mori AS, Cornelissen JHC, Fujii S, et al. (2020) A meta-analysis on decomposition quantifies afterlife effects of plant diversity as a global change driver. Nature Communications 11:4547.

Nervo B, Caprio E, Celi L, et al. (2017) Ecological functions provided by dung beetles are interlinked across space and time: evidence from ^{15}N isotope tracing. Ecology 98:433–446.

Ni XY, Berg B, Yang WQ, et al. (2018) Formation of forest gaps accelerates C, N and P release from foliar litter during 4 years of decomposition in an alpine forest. Biogeochemistry 139:321-335.

Nichols E, Larsen T, Spector S, et al. (2007) Global dung beetle response to tropical forest modification and fragmentation: A quantitative literature review and meta-analysis. Biological Conservation 137:1–19.

Nichols E, Spector S, Louzada J, et al. (2008) Ecological functions and ecosystem services provided by Scarabaeinae dung beetles. Biological Conservation 141:1461–1474.

Peters MK, Hemp A, Appelhans T, et al. (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nature Communications 7:13736.

Porre RJ, van der Werf W, De Deyn GB, et al. (2020) Is litter decomposition enhanced in species mixtures? A meta-analysis. Soil Biology and Biochemistry 145:107791.

Prescott CE (2002) The influence of the forest canopy on nutrient cycling. Tree Physiology 22:1193–1200.

Prescott CE (2005) Do rates of litter decomposition tell us anything we really need to know? Forest Ecology and Management 220:66–74.

Scherer-Lorenzen M (2008) Functional diversity affects decomposition processes in experimental grasslands. Functional Ecology 22:547–555.

Scherer-Lorenzen M, Luis Bonilla J, Potvin C (2007) Tree species richness affects litter production and decomposition rates in a tropical biodiversity experiment. Oikos 116:2108–2124.

Schulze ED, Beck E, Buchmann N, et al. (2019) Plant Ecology, 2nd edition. Springer, Berlin, Heidelberg

Seibold S, Rammer W, Hothorn T, et al. (2021) The contribution of insects to global forest deadwood decomposition. Nature 597:77–81.

Seidelmann KN, Scherer-Lorenzen M, Niklaus PA (2016) Direct vs. microclimate-driven effects of tree species diversity on litter decomposition in young subtropical forest stands. PLoS ONE 11:e0160569.

Shorohova E, Kapitsa E (2014) Influence of the substrate and ecosystem attributes on the decomposition rates of coarse woody debris in European boreal forests. Forest Ecology and Management 315:173–184.

Smith VC, Bradford MA (2003) Litter quality impacts on grassland litter decomposition are differently dependent on soil fauna across time. Applied Soil Ecology 24:197–203.

Swift MJ, Heal OW, Anderson JM (1979) Decomposition in terrestrial ecosystems. University of California Press, Berkeley

Trogisch S, He J-S, Hector A, Scherer-Lorenzen M (2016) Impact of species diversity, stand age and environmental factors on leaf litter decomposition in subtropical forests in China. Plant Soil 400:337–350.

Wardle DA, van der Putten WH (2002) Biodiversity, ecosystem functioning and above-ground-below-ground linkages. In: Loreau M, Naeem S, Inchausti P (eds.) Biodiversity and ecosystem functioning: Synthesis and perspectives. Oxford University Press, Oxford, New York, pp 155-168

Zhang D, Hui D, Luo Y, Zhou G (2008) Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. Journal of Plant Ecology 1:85–93.

Zeller B, Colin-Belgrand M, Dambrine E, et al. (2000) Decomposition of ^{15}N-labelled beech litter and fate of nitrogen derived from litter in a beech forest. Oecologia 123:550-559

Zellweger F, Frenne PD, Lenoir J, et al. (2020) Forest microclimate dynamics drive plant responses to warming. Science 368:772-775.

4 Relevance of sex, gender and/or diversity

The participating institutions are committed to the goal of actively supporting career perspectives of female scientists, diversity and internationalization in academia (see 2.5 Measures to advance research careers in the Coordination Project). The applicants will make their graduate students aware of the support and workshops provided in their institutions and by this research unit (3.2.4 Gender Equality Measures in Research Networks Module).

Project Description – Project Proposals

Prof. Dr. Heike Feldhaar, Bayreuth (PI)
Prof. Dr. Ingolf Steffan-Dewenter, Würzburg (PI)
Dr. Alice Classen, Würzburg (PI)

SP6: Plant-animal interactions - pollination, parasitism, and seed dispersal

---

Project Description

1 Starting Point

1.1 State of the art and preliminary work

1.1.1 State of the art

The richness and composition of local communities depends on habitat structure, resource availability, top-down regulation, assembly processes, and the regional species pool. Community structure, in turn, strongly influences ecosystem functioning as the rate at which ecosystem functions are locally performed depends on the richness, abundance and identity of species present (Soliveres et al. 2016). Biodiversity increases the performance and stability of ecosystem functioning through functional complementarity and redundancy (Schuldt et al. 2019). Across trophic levels the abundance and diversity of organisms at lower trophic level may drive abundance and diversity of organisms at higher trophic level and their ecosystem functions (Scherber et al. 2010). While the mostly positive relationship among local α-diversity and ecosystem functioning has been demonstrated in several systems (Weisser et al. 2017), the drivers of β-diversity and its impact on ecosystem functioning in natural or anthropogenically modified ecosystems is little understood (Mori et al. 2018). Local differences in habitat heterogeneity result in higher species turnover among communities (Keeton 2006, Sobek et al. 2009). Differences in structural complexity and microclimate between habitat patches should pose a stronger habitat filter and an altered spectrum of resources to species and will thus determine which species are present to perform a particular ecosystem function (Simons et al. 2021). Plant regeneration, an essential component of maintaining biodiversity and ecosystem functions of forests, largely depends on animal-mediated functions such as pollination and seed dispersal (Neuschulz et al. 2016). Both functions have been shown to be sensitive to forest management and disturbance (Neuschulz et al. 2016), suggesting that more diverse animal communities increase resilience and performance of these functions.

Seeds of most herbaceous understory plants and a large proportion of tree species in temperate forests are dispersed by different groups of animals (Howe and Smallwood 1982). Thus, small scale structural heterogeneity within forests (e.g. due to Enhanced Structural Beta Complexity (ESBC) treatments) may drive the abundance and species richness of seed dispersing animals. In turn, their functional traits will affect the rates and distances at which seeds are dispersed as important parameters for plant recruitment on local scale and regional scale. Seed-disperser networks depend on matching of consumer and resource traits (Schleuning et al. 2020), with e.g. larger seeds being preferentially dispersed by animals with larger body size (Munoz et al. 2017; Türke and Weisser 2013), different animal species being attracted to seeds (or fruits) of different nutritional quality (Reifenrath et al. 2012; Türke and Weisser 2013) or on aligned plant phenology and animal activity patterns

(Gordon et al. 2019). Dispersal distance as well as potential damage to seeds through handling or consumption by animals and thus plant recruitment may strongly depend on the identity of seed-dispersers (Schupp et al. 2010; Türke and Weisser 2013) and competitive interactions among dispersers (Prior et al. 2020). Ants (Howe and Smallwood 1982; Reifenrath et al. 2012; Kiel et al. 2020) but also gastropods (Türke et al. 2010b; Prior et al. 2020) are important seed dispersers of spring geophytes in temperate forests. Both groups are often attracted to seeds bearing elaiosomes, nutrient-rich appendages of seeds (Türke et al. 2010b; Reifenrath et al. 2012). Seed dispersal by ants benefits plants through escape from predation by rapid removal and burial of seeds, and directed dispersal to microsites suitable for seedling establishment (Giladi 2006). Seeds swallowed by gastropods (especially slugs) may be dispersed further than by ants (Türke et al. 2010b), and after gut passage seeds can often still germinate (Türke and Weisser 2013) and are less attractive to seed predators such as rodents (Türke et al. 2010b). Likewise, the dispersal (or consumption) of larger seeds of trees in autumn by different vertebrate groups will depend on the traits of the animal removing the seeds. Seed predation has been shown to be high by wild boars (Focardi et al. 2000). In contrast, a larger proportion of seeds may successfully germinate when collected by scatter-hoarding corvids and small mammals when caches are forgotten (Pesendorfer et al. 2016; Lichti et al. 2017). Also, habitat preferences of seed dispersers can strongly affect seed-seed disperser interactions. Species richness and abundance of ants correlates with a warmer microclimate found in forests stands with a more open canopy (Grevé et al. 2018; Georgiev et al. 2021). In contrast, forest-associated gastropods and especially slugs tend to be found in more humid and shaded forest habitats (Kappes 2006) and benefit from the presence of dead wood (Kappes 2006; Kirchenbaur et al. 2017). The abundance of rodent species tends to increase in dense understory vegetation (Pérez-Ramos and Marañón 2008; Stephens et al. 2021) due to a reduced predation risk (Lichti et al. 2017), while richness and abundance of forest birds is more driven by canopy density and variability of vertical structures within forests (Bae et al. 2018).

About 78% of flowering plants in temperate ecosystem rely on pollination for reproduction and the maintenance of genetic diversity (Ollerton et al. 2011). Similar to seed disperser communities, pollinator communities are composed by taxa and species, which strongly differ in life history traits (e.g. overwintering stage, nest location), morphological traits (e.g. body size, proboscis length) (Ball and Morris 2015; Westrich 2019) and/or physiological traits (e.g. thermal tolerance (Peters et al. 2016b)). Such traits inform, for instance, about species environmental requirements, movement and dispersal abilities, but also about their probability of interactions in ecological networks (Schleuning et al. 2020). Active interventions in the forest management, as conducted in our RU, cause alterations in e.g. microclimate, vegetation structure, the diversity and abundance of certain nectar and pollen resources, or the availability of different nesting sites. Some taxonomic groups and pollinator traits have been found to respond to such changes and become more abundant under certain management forms (Fortuin and Gandhi 2021). However, the possible mechanisms behind community assembly processes and the consequences for species interactions with resources and/or higher trophic levels remains understudied, particularly in temperate forest ecosystems (Ashman et al. 2004; Knight et al. 2005; Braun-Reichert et al. 2021). Even less complete is our understanding about the impact of forest management and heterogeneity on pollination functions: Pollination success does not only depend on pollinator abundances or visitation rates, but also on pollinator diversity and the functional composition of pollinators (Hoehn et al. 2008; Garibaldi et al. 2013). Different pollinator groups complement each other, e.g. by interacting with different plant species or different flowers within plant individuals, by foraging under different weather conditions, seasons or times of the day, or by modifying each other's foraging behavior through species interactions (Brittain et al. 2013b, a). However, whether the expected turnover in community compositions and functional traits caused by different forest management strategies results in a predictive turnover of pollination types, and finally in an increase of pollination services on a γ-scale in heterogeneous environments, remains to be explored.

1.1.2 Preliminary work

The applicants and their research groups have long-lasting and complementary experience in the study of ant, bee and wasp diversity, the design of empirical and experimental field studies in various ecosystems and geographical regions, and the use of a broad spectrum of methods to assess biotic interactions, and ecosystem functions.

The **Feldhaar** group has comprehensive experience in studying ant-plant interactions in tropical rainforests (Feldhaar et al. 2005; Jürgens et al. 2006; Türke et al. 2010a), the effects of forest management and conversion on ant-plant interactions (Houadria et al. 2020), and on ant communities in temperate forests (Grevé et al. 2018; Georgiev et al. 2021). We previously analysed the impact of land use intensification on ant species richness and functional diversity in grasslands (Heuss et al. 2019) and the entailing effects on herbivore predation as ecosystem function of ants and other groups (Meyer et al. 2019). In recent years, we have intensively studied the potential role of dispersal limitation of myrmecophytic ants and saproxylic beetles in disturbed or managed forests using population genetic analyses (Türke et al. 2010a; Schauer et al. 2018a). We currently study the influence of forest management and microhabitat structure on saproxylic insect communities and population genetic structure of specific saproxylic species in tree hollows (Schauer et al. 2018a; Schauer et al. 2018b).

In the intensively studied site Sailershausen we already collected data on seed removal by vertebrates, by comparing removal rates of smaller seeds (sunflower seeds) to acorns in late summer in 2019, after the establishment of ESBCs. On all patches, seeds were removed after 24 hours. Using 15 camera traps we analysed seed remover identity on a subset of patches per week (see Fig. 1). Seeds were mostly removed by mice (n=194 observations) and relatively few by squirrels (n=2) or birds (n=6). Ant abundance and species richness will be determined from pitfall trap samples from 2018 (before the establishment of ESBCs) as well as from the years 2019 and 2020. Gastropod samples will be extracted and determined from pitfall traps of the 2020 sampling campaign.

Fig.1: Documentation of animals removing seeds in the intensively studied site Sailershausen in 2019. Seeds were sometimes removed by squirrels during daytime (left) but mostly by mice at night (right) (Pictures BSc project of M. Dahlem under supervision of H. Feldhaar).

The **Steffan-Dewenter group** has extensive experience in the study of bee and wasp diversity, plant-pollinator interactions and plant reproduction in forest and grassland ecosystems. Past research focused on α- and β-diversity of different functional groups in temperate and tropical forest ecosystems (Sobek et al. 2009; Peters et al. 2016a). Further research addressed the structure of plant-pollinator and host-antagonist interaction networks in fragmented habitats (Grass et al. 2018) and the specialization and network robustness plant-pollinator networks along elevational gradients (Classen et al. 2020). To increase pollinator network completeness, we have successfully developed the metabarcoding of mixed pollen samples and established the laboratory workflow in the Department (Keller et al. 2013, 2015). Trap-nesting bees and wasps and their natural antagonists are used as a long-term model system to assess the diversity, multitrophic interactions and environmental responses of bees and wasps (Steffan-Dewenter 2003; Steffan-Dewenter and Schiele 2008; Dainese et al. 2018). In secondary tropical forests, we used trap-nesting Hymenoptera to assess the effects of fragmentation and microclimate-related vertical stratification on hymenopteran communities, but also on interaction rates in Costa Rica (Stangler et al. 2015, 2016). We revealed complex interactive effects of forest fragment size, location (forest border, forest center) and temperature on parasitism rates. In a recent project, we studied the species richness, abundance and biotic interactions of trap-nesting bees, wasps and their natural enemies along the elevation gradient at Mt. Kilimanjaro and reveal complex, climate and resource-driven seasonal responses of different taxa (Mayr et al. 2020).

For the 60 intensively studied patches in Sailershausen, we already collected data with 120 trap nest (2 per patch) before the establishment of ESBC in 2018, and after the establishment in 2019 and 2021. These data will be used as reference data and starting points for evaluating longer-term temporal shifts in the richness, composition, traits and biotic interactions of trap-nesting bees and wasps. The data set will be immediately available to the PhD student for a first publication.

Classen leads an independent junior research group in the Department of Animal Ecology and Tropical Biology. Besides our experience in quantifying and explaining broad scale biodiversity, interaction and ecosystem function patterns (Classen et al. 2014, 2015, 2020; Peters et al. 2020), we have a strong interest in the analyses of functional trait shifts in space and time (Classen et al. 2017; Schellenberger Costa et al. 2017). We recently showed e.g. that the parallel assessment of intraspecific trait variation and community-level trait means can reveal even contrasting responses of community and species traits, suggesting different processes such as physiological and resource-related factors that drive diversity and functionality (Classen et al. 2017) (Fig. 2).

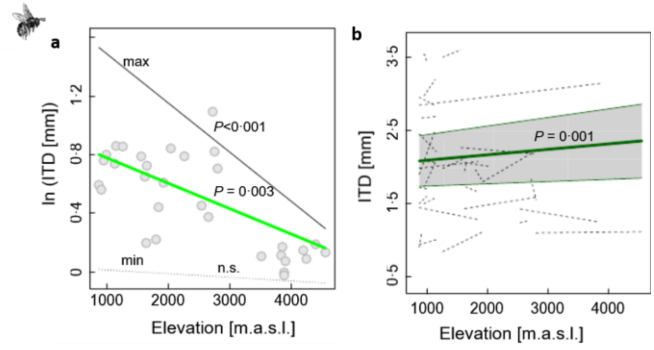


Fig. 2: Change in mean intertegular distance (ITD), as a measure for body size with elevation at the community level (a) and within species (b). At the community level, ITD decreased with elevation (light green line). Upper and lower grey lines represent the trends of maximal and minimal community trait values. Within species, ITD on average increased with increasing elevation (dark green line, with confidence interval (b)) with species-level responses (dotted lines) varying. Figure rearranged from Classen

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. **Classen A**, Eardley CD, Hemp A, Peters MK, Peters RS, Ssymank A, **Steffan-Dewenter I** (2020) Specialization of plant–pollinator interactions increases with temperature at Mt. Kilimanjaro. Ecol Evol 10:2182–2195
2. Dainese M, Riedinger V, Holzschuh A, Kleijn D, Scheper J, **Steffan-Dewenter I** (2018) Managing trap-nesting bees as crop pollinators: spatiotemporal effects of floral resources and antagonists. J Appl Ecol 55:195-204
3. Mayr AV, Peters MK, Eardley CD, Renner MR, Röder J, **Steffan-Dewenter I** (2020). Climate and food resources shape species richness and trophic interactions of cavity-nesting Hymenoptera. J Biogeogr 47:854-865
4. Heuss L, Grevé ME, Schäfer D, Busch V, **Feldhaar H** (2019) Direct and indirect effects of land-use intensification on ant communities in temperate grasslands. Ecol Evol 9:4013-4024
5. Georgiev K, Beudert B, Bässler C, **Feldhaar** H, Heibl C, Karasch P, Müller J, Perlík M, Weiss I, Thorn S (2021) Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity. For Ecol Manag 495:119354
6. **Classen A**, **Steffan-Dewenter I**, Kindeketa WJ, Peters MK (2017) Integrating intraspecific variation in community ecology unifies theories on body size shifts along climatic gradients. Func Ecol 31: 768–777
7. Grevé ME, Hager J, Weisser WW, Schall P, Gossner MM, **Feldhaar** H (2018) Effect of forest management on temperate ant communities. Ecosphere 9: e02303
8. Meyer ST, Heuss L, **Feldhaar H**, Weisser WW, Gossner MM (2019) Land-use components, abundance of predatory arthropods, and vegetation height affect predation rates in grasslands. Agric Ecosyst Environ 270:84-92
9. Schauer B, Steinbauer MJ, Vailshery LS, Müller J, **Feldhaar** H*, Obermaier E* (2018) Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. Biodiv Conserv 27:853-869 *equally contributing
10. Sobek S, Tscharntke T, Scherber C, Schiele S, **Steffan-Dewenter I** (2009) Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? For Ecol Manag 258:609–615

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.2.3 Patents

Not applicable

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

April 2022 to March 2026

2.2 Objectives

Within forest patches, we first aim to understand the impact of forest management (Enhancement of Structural Alpha complexity, ESC), nesting and food resources and microclimate on the diversity and composition of seed dispersers and pollinators, on their interactions with plants and higher trophic levels, and on related ecosystem functions, such as seed removal rates, pollination, and parasitism. The study framework of the RU gives us the unique possibility to test our **main hypothesis**, in which we predict that **high heterogeneity in forest management practices**, as experimentally introduced by ESBC, **increases the turnover of invertebrate species and/or functional groups, and translates into complementary species interactions, seed dispersal, pollination and parasitism events at the landscape scale**. If this main hypothesis holds true, we expect to find a higher γ-diversity and, importantly, a higher γ-multifunctionality in landscapes with ESBC practices, than in control districts. By investigating two crucial functions in plant reproduction, our subproject will substantially contribute to our understanding on what kind of forest management is needed to counteract ongoing species and ecosystem function losses at local and landscape scales. More specifically, we will test the following hypotheses:

***H1**: On a local scale, forest management practises which lead to a reduction in the canopy cover and increases in dead wood amount, will have differential effects on different species groups and lead to altered communities and trait compositions under different ESCs.* The main drivers of species richness differ between animal taxa: While the richness of bees, aculeate wasps and ants is mainly driven by temperature by a reduced canopy cover, the richness of hoverflies, parasitoid wasps and gastropods peaks in more humid environments (Peters et al. 2016, Grevé et al. 2018). Within taxa, all species relying on dead wood for reproduction will be favoured by management practises that increase the amount of this resource. Bees will likely profit from reduced canopy cover, as lighter and warmer conditions increase the abundance and diversity of flowering resources in the understorey plant community. We will disentangle the most important drivers of diversity and composition of all investigated invertebrate groups (WP1, 2), as well as community- and intraspecific trait responses within and across taxa (WP6).

***H2:** On a local scale, differences in species and/ or trait composition caused by ESCs (=H1) is linked to differences in species interactions and related ecosystem functions.* Species prefer different interaction partners and differ in quantity, quality and identity of ecosystem services: E.g., vertebrates, such as mice or squirrels remove larger seeds than gastropods or ants. Consequently, the group profiting most from certain ESCs, determines the dominant size of removed seeds on a local scale (WP3). Similarly, plants with deeper tubes should show higher seed sets in bee-dominated pollinator communities, while short-tubed plants might produce more seeds in hoverfly-dominated communities (WP4). Forest patches with management forms favouring parasitoid wasps, but not bees (e.g. dense canopy cover – humid), should show higher parasitism rates of stem-nesting bees, than canopy-reducing management strategies (WP5).

H3*: On a between-patch scale, the different, but predictive responses of seed disperser, pollinator and parasitoid communities to forest management (H1), will lead to higher taxonomic and/or functional turnover rates within ESBC districts, than within control districts.* We further predict that the taxonomic turnover (WP1, 2) is higher than the turnover in functional traits (WP6), due to functional trait redundancy in species communities.

H4*: The turnover in functional traits is a better predictor of ecosystem function turnover, than (taxonomic) β-diversity.* This hypothesis relies on the assumption that functional traits that respond to environmental changes (= responsive traits) are directly linked to traits that are needed to execute a certain function (= effect traits).

H5*: If heterogeneous forest management causes higher turnover rates in seed disperser, pollinator and parasitoid species and/or community traits (H3), then districts with ESBCs should show a higher γ-diversity than control districts (landscape scale).*

H6: *Higher turnover rates in ecosystem functions caused by functional β-diversity, leads to a higher multifunctionality in ESBC districts than in control districts..*

Integration of SP6 within the research unit: SP6 has strong links with six other SPs of the RU (Fig. 3): From SP1 and SP3 we will receive data on temporal dynamics of forest structure at different spatial scales as input variable to explain diversity and activity patterns of groups studied in this SP. We provide data on gastropod feeding activity to SP5 to complement leaf litter decomposition experiments and in turn will receive data on leaf litter fall from SP5 as explanatory variable for gastropod diversity. Data on understory plant communities from SP8 will enable us to assess the diversity and abundance of myrmecochorous flowering plants and resources for pollinators. In turn, this SP delivers data to SP8 on pollination and seed dispersal as important drivers for plant community structure. We will collaborate closely with SP9 and will receive abundance and diversity data of small mammals and birds, which will complement vertebrate species activity data of this SP and delivered to SP9. Together with the data on ant, bee, wasp and gastropod diversity and abundances, this will allow us to calculate multidiversity within the RU. This SP will receive important baseline data on forest stand structure, microclimate and soil properties from SPZ. We will deliver data on pollination, parasitism and seed dispersal as important ecosystem functions for synthesis of

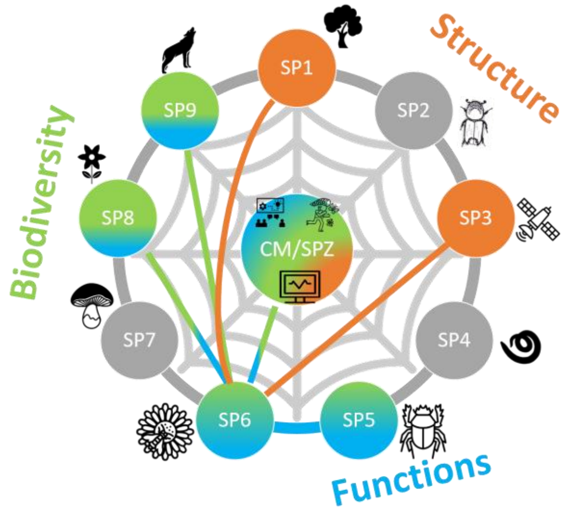


Fig. 3: Close cooperations of SP6 with other subprojects. The colour of arrows indicates the type of data exchanged; green: species data, blue: functions, brown: structure.

results over all SPs. In the 2nd phase of the RU, SP6 plans to assess (1) successional dynamics of functional diversity, network characteristics, and pollination and seed dispersal functions, and (2) perform experimental exclosure and removal experiments of different functional groups.

2.3 Work programme including proposed research methods

The work programme will be realised by two PhD students. PhD student 1 (Feldhaar) will focus on the characterisation of α- and β-diversity of seed dispersers (WP1) and the entailing seed removal rates (WP3). PhD student 2 (Steffan-Dewenter) will concentrate on the assessment of α- and β-diversity of bees, wasps, and hoverflies (WP2), record understory plant-pollinator interactions, quantify plant reproduction (WP4), and characterise multitrophic interactions (WP5). Functional traits (WP6) will be mainly assessed by student assistants and analysed by both PhD students (Classen).

WP 1: Diversity and abundance of potential invertebrate seed dispersers (H. Feldhaar)

Objective: Quantify impacts of local microclimate, dead wood enrichment, forest heterogeneity and successional changes on α-, β-, and γ-diversity of ant and gastropod communities.

We expect an increase in ant diversity and abundance in patches with canopies that are more open and a warmer and drier microclimate (Grevé et al. 2018). In contrast, we expect a higher gastropod (especially slug) abundance and diversity in patches with a more humid microclimate on the ground and larger amounts of dead wood (Kappes 2006, Kirchenbaur et al. 2017) (see H1).

Methods: We will determine the (functional) diversity and abundance of ants and gastropods (especially slugs) as important seed dispersers of spring geophytes on all 234 patches of the RU in the eleven sites. **Ant diversity** will be determined using pitfall traps (2 per patch; installed by SP9). Since the number of ants per pitfall trap is strongly dependent on the distance to the nests we will use the incidence (n traps x n months) where an ant species is found per patch as abundance measure (see Grevé et al. 2018). Morphological traits will be measured and life history traits will be taken from the literature (see Grevé et al. 2018). **Gastropods** will likewise be extracted from pitfall traps. In addition, we will sample gastropods in a standardised way by laying out pieces of cardboard on the forest floor (size 30cm X 30cm; Kirchenbaur et al. 2017) from May to September. Two pieces of cardboard per patch will be laid out close to pieces of dead wood (max. 15 cm away) and another two ~ 1.7 m away from the respective first cardboard. After retrieval of cardboards all gastropods found on or underneath the cardboard will be collected. Cardboards will then be dried and scored for gastropod feeding behaviour (counting the number of squares 5cm x 5cm from both sides of the cardboards with signs of gastropod feeding behaviour as a proxy for feeding activity of gastropods; Kirchenbaur et al. 2017). This data allows the estimation of gastropod feeding activity in the leaf litter per patch as a link to SP5. We will also take four leaf litter samples per patch (25 x 25 cm each including the first 2 cm of soil; two from within the enclosure, 2 from outside) and will directly extract larger slugs and snails (> 1cm) by hand sampling before drying and sieving the samples to extract smaller (shelled) individuals. Slugs and larger snails will be transferred to boxes and their faeces screened for seeds. This leaf litter sampling will be conducted once in spring and autumn.

Data analysis: We will use generalised additive models to estimate responses to local and landscape scale forest heterogeneity and will apply a multi-model inference approach in combination with piecewise structural equation models to test for direct and indirect effects of microclimate, dead wood amount and type, and forest structure determining ant and gastropod α-diversity and abundance on local and regional scales (Grevé et al. 2018). We will calculate β-diversity among patches of the 11 control and ESBC districts using a unified statistical framework based on Hill numbers (Hsieh et al. 2016). This framework provides coverage-based standardisations of diversity, including taxonomic, phylogenetic, and functional diversity (Chao et al. 2020). Differences in within-treatment β-diversity between control patches and structurally enhanced patches per region will be assessed using t-tests.

WP 2: Pollinator diversity (I. Steffan-Dewenter / A. Classen)

Objectives: Quantify impacts of local microclimate, dead wood enrichment, forest heterogeneity and successional changes after experimental ESBC on α-, β-, and γ-diversity of pollinator communities.

Methods: We will perform standardised samplings of bees, aculeate and parasitoid wasps and hoverflies with pan traps and trap nests on all 234 patches of the RU in the eleven sites. In each study patch, we will place three clusters of colored pan traps and trap nests for bees and wasps. The used pan trap colors (yellow, white, blue) are UV-reflecting which is increasing their attraction factor (Westphal et al. 2008). All clusters will be placed at about 1.5 m above ground. After 48 hours, pan traps will be emptied and all insects will be transferred to collecting containers in the field and stored in 85% ethanol. To cover different seasons and collect species with different phenologies, four pan trap sampling rounds at three-weekly intervals will be performed. Trap nests, providing nesting space for aboveground nesting bees and wasps, are a unique method to study species richness and biotic interactions with floral or other food resources and natural enemies (Steckel et al. 2014, Staab et al. 2018). We will use the trap-nest system to quantify the species richness, community composition and spatiotemporal turnover of bees, wasps and their natural enemies. Further, trap nests allow for a fine-grained evaluation of microclimatic effects on colonizing bees, wasps, and antagonists along a vertical tree canopy gradient (Stangler et al. 2015). In each patch we will place two trap nests at two different vertical strata (ca 1.5 m and at tree canopy level) for one season. Trap nests consist of bundles of reed internodes of different diameters placed into PVC tubes for rain shelter (Sobek et al. 2009). All occupied nests will be transported to the lab. Here, individual nests will be dissected and reared for identification at species level. Further analyses to reveal biotic interactions and interaction networks are described in WP5.

Data analysis: For the analyses of environmental drivers of taxonomic and phylogenetic diversity, we will combine bee, hoverfly and wasp data from pan trap sampling, trap nests and transect walks (WP4). The data set will allow to analyse α-, β-, and γ-diversity, species abundance, and phylogenetic diversity in relation to potential drivers of biodiversity (e.g. temperature, canopy cover, proportion of dead wood, etc). We will use generalised additive models with a poisson error distribution (quasi-poisson in case of overdispersed data) to estimate responses to local and landscape scale forest heterogeneity and will apply a multi-model inference approach in combination with piecewise structural equation models to test the support for direct and indirect effects of microclimate, dead wood, and floral resources as determinants of bee, hoverfly and wasp community abundance and richness on local patch and landscape scales (Classen et al. 2015, Peters et al. 2016a).

WP 3: Seed – animal interactions and seed removal rates (H. Feldhaar)

Objective: Assess seed-animal interactions and seed removal rates on α-, β-, and γ- scales and identify the underlying drivers on this ecosystem function.

We expect that seed-animal interactions are strongly driven by abundance effects. Currently it is not yet clear whether specific groups of seed removing animals are functionally redundant or complementary. Seed removal should be determined by functional traits of communities of seed removing animals, with e.g. ant species with small workers being limited by their mandible size.

Methods: We will conduct two seed removal experiments, one in spring offering seeds of myrmecochorous plants and one in late summer / early autumn offering larger seeds. In both experiments, we will measure seed removal rate and will document the respective animals responsible for seed removal using camera traps. For the **spring seed removal experiment** we will collect diaspores of myrmecochorous plants flowering in early spring (e.g. *Anemone nemorosa*, *Allium ursinum*) and commonly found in forests around Bayreuth. Diaspores will be collected just before ripening (between April and June) and frozen at -20°C until used in experiments. Diaspore dimensions (maximum width, length, and thickness) will be measured of 20 randomly chosen diaspores per species to relate diaspore traits with traits of seed removing animals. Diaspores will be exposed in batches of ten on 10cm x 10cm wooden plates. We will present four seed batches per patch. We will present diaspores of two different plant species and will exclude small mammals from one batch each with a wire mesh cage. Seed removal will be documented using camera-traps (Wild Vision Full HD 5.0) in time-lapse mode (taking one picture every 15 seconds) over a period of 3 days. In **late summer / autumn** when trees are fruiting (oak, beech) we will conduct another seed removal experiment. Due to larger seed sizes, seed removal by vertebrates should be more important than by arthropods or gastropods. We will collect seeds (acorns, beechnuts or other smaller seeds that are commercially available) and will offer those on round plastic trays (20 acorns and 50 smaller seeds). Due to the fast removal by vertebrates we will lay out one set of seeds in the morning and a second set at dusk to capture day and night-active seed removing animals. We will again use camera trapping to document which species remove seeds.

Seed rain will be measured in autumn over a period of two weeks in parallel to the seed removal experiments. We will set out two foldable boxes (comparable setup to SP5 for leaf litter trapping) per patch and will lay out a similar sized piece of gauze flat on the ground. We assume that most animals will not enter the boxes while having access to the gauze on the ground, and thus fewer seeds should be found on the gauze on the ground due to seed removal by animals.

Data analysis and output: We will model seed removal probability via a generalized additive mixed model for binomial data, selecting removed/not removed as binary response variable, and exposure time, plant species, abundance of seed dispersing organisms, environmental factors and ESBC treatment, as predictors. To account for our nested study design, we will add experimental block, patch-identity, and site as random effects.

WP 4: Plant-pollinator interactions and seed set (I. Steffan-Dewenter / A. Classen)

Objective: Assess plant-pollinator interactions and plant reproduction on α-, β-, and γ-scales and identify the underlying drivers and mechanisms

Only few studies address heterogeneity-driven shifts in pollinator networks and even fewer studies on pollinator networks are based on experimental manipulations (Hoiss et al. 2015) and link network data to plant reproduction. Similarly, the spatiotemporal dynamics of plant-pollinator networks and direct responses to climate, resource diversity and functional traits of involved species have been rarely studied (Wende et al. 2017, Grass et al., 2018). Most ecological network studies are based on observational data and are often biased due to incomplete sampling, particularly for rare pollinator species (Rivera-Hutienel et al. 2012). More complete information can be gained by supplementing observational data with the analysis of pollen loads carried by pollinators or stored pollen in bee nests (Dorado et al. 2011, Danner et al. 2017).

Methods: On each patch in the three intensive sites we will perform a minimum of five random transect walks. Random transect walks are standardised by the total transect length and the transect time but have no fixed route. A large-scale comparison of methods to assess bee diversity has demonstrated that random transects are more efficient than fixed transects, particularly in habitats with patchy distribution of floral resources (Westphal et al. 2008). Transect walks will be equally distributed over one year to cover seasonal variation in species composition and abundance in relation to resource availability. Each transect walk will have a duration of 80 minutes and will be subdivided into eight subunits á 10 minutes to later calculate species accumulation curves and sampling completeness (Colwell et al. 2012). Flower cover on each patch will be quantified on five subpatch of 5 x 4 m by recording flowering herbaceous and shrub plant species and counting (or estimating in case of large numbers) the number of flowers or flower units (Classen et al. 2015). Further, during the transect walks flowering trees within the 50 x 50 m patch will be noted and the amount of floral resources estimated. For each plant species flower colour, size and corolla length will be measured for latter network analysis (Albrecht et al., 2018, Classen et al. 2020). During the transect walks, flower-visiting bees and further potentially pollinating insects will be caught. Transect walks will focus on ground vegetation up to 2 m height. To improve the completeness of plant-pollinator network data, we will collect pollen from the body hair of each caught individual for pollen metabarcoding (samples will be pooled after barcoding per species (BIN), site and season (Keller et al. 2015, Danner et al. 2017). Recent observations indicate that this approach provides a more complete estimate of used floral resources compared to the use of pollen baskets or only direct flower visitor observations (Pornon et al. 2017). Observational studies will be complemented by experimental pollinator exclusion and supplementary pollination in the second and third study year. Based on vegetation mapping and occurrence of understorey herbs in the study patches, we will select three plant species with contrasting floral traits and flowering phenology. For each plant species we will select at least five separate individuals and apply the following treatments: open pollination (positive control), supplementary hand pollination and pollinator exclusion for spring, summer and autumn flowering forest understorey herbs. Plants and treatments will be permanently marked and seed set and quality will be measured by harvesting fruit stands, counting seeds and taking seed weights in the laboratory.

Data analysis: We will use these data to (1) analyse pollinator-plant interaction networks in relation to forest heterogeneity and resource gradients (Classen et al. 2020, Albrecht et al. 2018), (2) to link the structure of plant-pollinator networks to richness and functional traits of interacting species (Grass et al. 2018) (3) to analyse the spatial and seasonal variation of pollinator-plant networks (Burkle & Alarcón 2011), and (4) to link network structure and forest heterogeneity with pollination limitation. Plant-pollinator interaction data will be compiled from transect observations and also from trap nest data (see WP 5). Quantitative interaction networks will be analysed and visualised by using the R-package bipartite (Dormann et al. 2014). We will focus on ecologically meaningful network metrics such as nestedness, modularity, robustness, H_2' (Blüthgen et al. 2008, Grass et al. 2018). As almost all network metrics depend to some degree on network size, all metrics will be standardised to null models in order to compare the networks along the environmental gradients (Dormann et al. 2014, Sebastián-González et al 2015). Pollination limitation data will be analysed in relation to local environmental conditions, plant density, flower visitation rates, and network metric and forest heterogeneity. We will use generalised additive and linear models and the R packages mgcv, ape, FD, piecewiseSEM, phytools and bipartite for analyses of network and functional data sets.

WP 5: Resource-host-antagonist interactions of trap-nesting bees and wasps (I. Steffan-Dewenter / A. Classen)

Objective: Assess the impacts of local microclimate and resource conditions and landscape-level forest heterogeneity and unravel the underlying drivers of resource-host-antagonist interactions.

Methods: Pollen and arthropod food resources in nest chambers of bees and wasps will be identified by using metabarcoding to reveal biotic interactions and construct tritrophic mutualistic and antagonistic interaction networks (Grass et al. 2018). The number of intact brood chambers, dead brood chambers and of chambers attacked by natural enemies will be noted to calculate species- and site-specific parasitism and mortality rates (Steffan-Dewenter 2003, Steckel et al. 2014, Stangler et al. 2016). From each nest, pollen samples from brood cells in case of bee nests, or other food sources, e.g. beetle larvae, flies, spiders in case of wasp nests (Steckel et al. 2014) will be taken and later pooled per patch and species. Pollen and prey samples will be transferred into a DNA preservation buffer for further metabarcoding (Keller et al. 2015).

Data analysis: Mortality rates and parasitism rates will be analysed in relation to local habitat conditions (microclimate, dead wood, plant diversity) using linear mixed effects models. Further, turnover of interaction strength at the landscape level and density-dependent effects will be analysed. Tritrophic interaction networks obtained from (meta)barcoding data will be analysed as outlined in WP4.

WP 6: Intra and interspecific species traits and phylogeny (A. Classen)

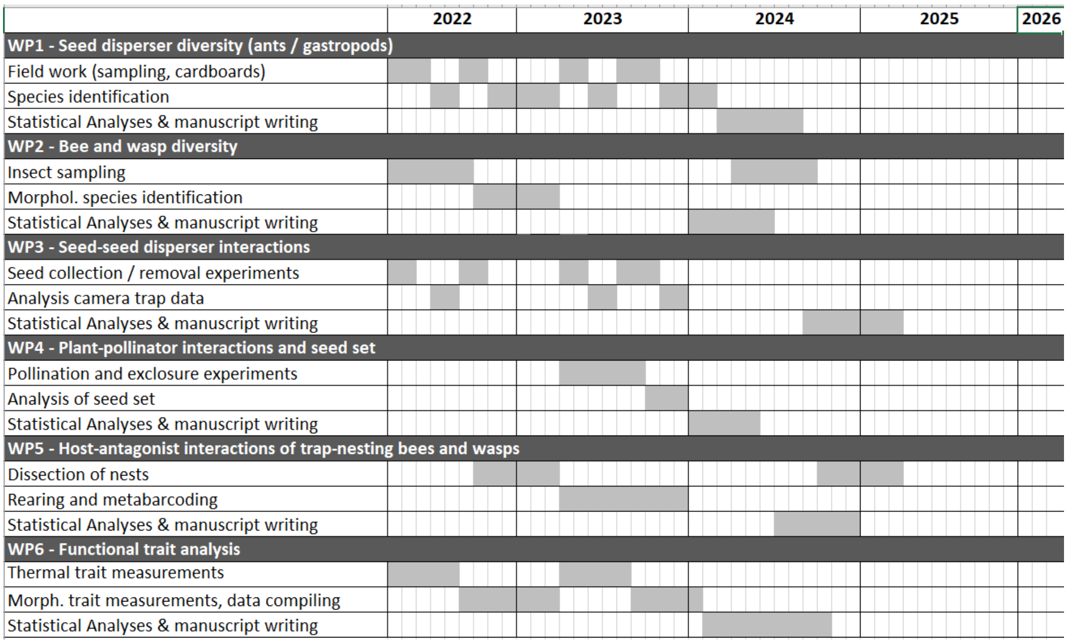
Objective: Community trait responses – especially those with weak phylogenetic signal - or intraspecific trait shifts are particularly informative concerning the mechanisms how single ES(B)Cs shape pollinator communities and turnover (Violle et al. 2012; Classen et al. 2017). Here, we aim to understand such trait responses to ESCs and ESBCs on α-,β- and γ-scales and under consideration of phylogeny.

Methods: We will measure functional traits of arthropod groups, recorded in WP2, 4 and 5 (bees, wasps, hoverflies) on both community- and intraspecific level, and receive respective morphological measurements for ants from WP1 (and WP3). For bees we will measure the intertegular distance, as a proxy for bee body size (Cane 1987). To allow a more accurate comparison of body mass across taxa, we will determine the body mass of dried insects with a fine scale. For bees, wasps, and hoverflies, we will further measure the proboscis lengths, as a rough indicator for preferred corolla depths in flowers (Albrecht et al. 2018), and relative forewing length (forewing length / body mass), as an indicator for flight performance (Dillon et al. 2006), by using a binocular microscope with a calibrated ocular micrometer. Ten individuals per species and patch will be measured, allowing the parallel and integrative analysis of both community trait means, intraspecific trait changes and inter- and intraspecific trait variances. After species identification, we will gather species-specific information from literature and databases on multiple life history traits, such as nesting behaviour, larval food, and overwintering stages.

To test, whether microclimate structures community assemblies of mobile organisms according to their thermal tolerances, we will determine thermal limits of flower visiting insects and ants directly in the field (Peters et al. 2016b). Insects, collected along transect walks in intensively studied patches will be exposed to decreasing and increasing temperatures generated with a battery-powered, programmable thermoblock (Eppendorf ThermoStatC). Temperatures under which we observe the loss of motoric control are recorded for each individual.

Data analysis: To analyse trait distributions and their dependence on management and environmental variables, we will conduct Fourth Corner and RQL analyses to fit predictive models for species abundance as a function of environmental variables, species traits and their interaction (Albrecht et al. 2018) (H1). We cross-validated relationships with phylogenetic multilevel models, which allow the consideration of phylogenetic non-independencies (*brms* package in R) (Nakagawa and Santos 2012; Albrecht et al. 2018). Linear regressions will be used to test whether a higher environmental heterogeneity increases the functional β-diversity in pollinator communities (H3), under consideration of geographic distance. The contribution of functional turnover and functional nestedness-resultant to functional β-diversity and ecosystem functions will be disentangled and compared to taxonomic turnover rates (Villéger et al. 2013) (H4). Non-independence in the pairwise comparisons between patches will be considered by bootstrapping sampling replicates; sampling effects of local functional diversity on β-diversity will be estimated by null-model approaches (Karp et al. 2012). Finally, we will use ordination analyses combined with β-dispersion tests to investigate on a regional scale whether functional diversity is higher under ESBC, than in control districts (H5).

Table 1: Overview of work programme and schedule. Sampling schedule will be in accordance with the schedule in the Coordination Module. In the 3rd and 4th year we will continue sampling (other group members and Master-students).



	2022									2023												2024												2025											2026		
WP1 - Seed disperser diversity (ants / gastropods)																																															
Field work (sampling, cardboards)	▨	▨	▨			▨	▨						▨	▨			▨	▨	▨																												
Species identification				▨	▨			▨	▨	▨	▨	▨			▨	▨				▨	▨	▨	▨																								
Statistical Analyses & manuscript writing																								▨	▨	▨	▨	▨	▨																		
WP2 - Bee and wasp diversity																																															
Insect sampling	▨	▨	▨	▨	▨	▨																			▨	▨	▨	▨	▨	▨																	
Morphol. species identification							▨	▨	▨	▨	▨	▨																																			
Statistical Analyses & manuscript writing																						▨	▨	▨	▨	▨	▨																				
WP3 - Seed-seed disperser interactions																																															
Seed collection / removal experiments	▨	▨				▨	▨						▨	▨			▨	▨	▨																												
Analysis camera trap data				▨	▨										▨	▨				▨	▨																										
Statistical Analyses & manuscript writing																														▨	▨	▨	▨	▨	▨	▨											
WP4 - Plant-pollinator interactions and seed set																																															
Pollination and exclosure experiments													▨	▨	▨	▨	▨	▨																													
Analysis of seed set																			▨	▨	▨																										
Statistical Analyses & manuscript writing																						▨	▨	▨	▨	▨																					
WP5 - Host-antagonist interactions of trap-nesting bees and wasps																																															
Dissection of nests							▨	▨	▨	▨	▨	▨																			▨	▨	▨	▨	▨	▨											
Rearing and metabarcoding													▨	▨	▨	▨	▨	▨	▨	▨	▨																										
Statistical Analyses & manuscript writing																												▨	▨	▨	▨	▨	▨														
WP6 - Functional trait analysis																																															
Thermal trait measurements	▨	▨	▨	▨	▨								▨	▨	▨	▨	▨																														
Morph. trait measurements, data compiling						▨	▨	▨	▨	▨	▨	▨						▨	▨	▨	▨	▨																									
Statistical Analyses & manuscript writing																							▨	▨	▨	▨	▨	▨	▨	▨	▨																

3 Bibliography concerning the state of the art, the research objectives, and the work programme

Albrecht J, Classen A, Vollstädt MRG, et al (2018) Reciprocal effects of plant and animal functional diversity on mutualistic network assembly. Nat Commun 9:3177

Ashman T-L, Knight TM, Steets JA, et al (2004) Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. Ecology 85:2408–2421

Bae S, Müller J, Lee D, et al (2018) Taxonomic, functional, and phylogenetic diversity of bird assemblages are oppositely associated to productivity and heterogeneity in temperate forests. Remote Sens Environ 215:145-156

Ball SG, Morris RKA (2015) Britain’s hoverflies: a field guide, Second edition. Princeton University Press, Princeton, New Jersey

Blüthgen N, Fründ J, Vázquez DP & Menzel F (2008) What do interaction network metrics tell us about specialization and biological traits? Ecology 89: 3387–3399

Braun-Reichert R, Rubanschi S, Poschlod P (2021) The importance of small natural features in forests—How the overgrowth of forest gaps affects indigenous flower supply and flower-visiting insects and seed sets of six *Campanula* species. Ecol Evol 11:11991–12002

Brittain C, Kremen C, Klein A-M (2013a) Biodiversity buffers pollination from changes in environmental conditions. Glob Chang Biol 19:540–547

Brittain C, Williams N, Kremen C, Klein A-M (2013b) Synergistic effects of non-*Apis* bees and honey bees for pollination services. Proc Roy Soc B 280:20122767–20122767

Burkle LA, Alarcón R (2011) The future of plant-pollinator diversity: understanding interaction networks across time, space, and global change. Am J Bot 98:528-538

Cane JH (1987) Estimation of bee size using intertegular span (Apoidea). J Kansas Entomol Soc 60:145–147

Chao AN, Kubota Y, Zelený D, et al. (2020) Quantifying sample completeness and comparing diversities among assemblages. Ecol Res 35:292-314

Classen A, Peters MK, Ferger SW, et al. (2014) Complementary ecosystem services provided by pest predators and pollinators increase quantity and quality of coffee yields. Proc Roy Soc B 281:20133148

Classen A, Peters MK, Kindeketa WJ, et al (2015) Temperature versus resource constraints: which factors determine bee diversity on Mount Kilimanjaro, Tanzania? Glob Ecol Biogeogr 24:642-652

Classen A, Steffan-Dewenter I, Kindeketa WJ, Peters MK (2017) Integrating intraspecific variation in community ecology unifies theories on body size shifts along climatic gradients. Func Ecol 31: 768–777

Classen A, Eardley CD, Hemp A, et al. (2020) Specialization of plant–pollinator interactions increases with temperature at Mt. Kilimanjaro. Ecol Evol 10:2182–2195

Colwell RK, Chao A, Gotelli NJ, et al. (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. J Plant Ecol 5:3-21

Dainese M, Riedinger V, Holzschuh A, et al. (2018) Managing trap-nesting bees as crop pollinators: spatiotemporal effects of floral resources and antagonists. J Appl Ecol 55:195-204

Danner N, Keller A, Härtel S, Steffan- Dewenter I (2017) Honey bee foraging ecology: Season but not landscape diversity shapes the amount and diversity of collected pollen. PLoS ONE 12:e0183716

Dillon ME, Frazier MR, Dudley R (2006) Into thin air: Physiology and evolution of alpine insects. Integr Comp Biol 46:49–61

Dorado J, Vázquez D, Stevani EL, Chacoff NP (2011) Rareness and specialization in plant–pollinator networks. Ecology 92:19-25.

Dormann CF & Strauss R (2014) A method for detecting modules in quantitative bipartite networks. Methods Ecol Evol 5:90–98.

Feldhaar H, Fiala B, Hashim RB, Maschwitz U (2003) Patterns of the *Crematogaster-Macaranga* association: The ant partner makes the difference. Insect Soc 50:9-19

Focardi S, Capizzi D, Monetti D (2000) Competition for acorns among wild boar (*Sus scrofa*) and small mammals in a Mediterranean woodland. J Zool 250:329-334

Fortuin CC & Gandhi KJK (2021) Functional traits and nesting habitats distinguish the structure of bee communities in clearcut and managed hardwood & pine forests in Southeastern USA. For Ecol Manag 496:119351

Garibaldi LA, Steffan-Dewenter I, Winfree R, et al. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608–1611

Georgiev KB, Beudert B, Bässler C, Feldhaar H, et al. (2021) Forest disturbance and salvage logging have neutral long-term effects on drinking water quality but alter biodiversity. Forest Ecol Manag 495:119354

Giladi I (2006) Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. Oikos 112:481–492

Gordon SCC, Meadley-Dunphy SA, Prior KM, Frederickson ME (2019) Asynchrony between ant seed dispersal activity and fruit dehiscence of myrmecochorous plants. Am J Bot 106:71–80

Grass I, Jauker B, Steffan-Dewenter I, Tscharntke T, Jauker F. (2018) Past and potential future effects of habitat fragmentation on structure and stability of plant-pollinator and host-parasitoid networks. Nat Ecol Evol 2:1408-1417

Grevé ME, Hager J, Weisser WW, Schall P, Gossner MM, Feldhaar H (2018) Effect of forest management on temperate ant communities. Ecosphere 9:e02303

Heuss L, Grevé ME, Schafer D, Busch V, Feldhaar H (2019) Direct and indirect effects of land-use intensification on ant communities in temperate grasslands. Ecol Evol 9:4013-4024

Hoehn P, Tscharntke T, Tylianakis JM, Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. Proc Roy Soc B 275:2283–2291

Hoiss B, Krauss J, Potts SG, et al. (2012) Altitude acts as an environmental filter on phylogenetic composition, traits and diversity in bee communities. Proc Roy Soc B 279:4447–4456

Hoiss B, Krauss J, Steffan-Dewenter I (2015) Interactive effects of elevation, species richness and extreme climatic events on plant-pollinator networks. Glob Chang Biol 21:4086–4097

Houadria MYI, Feldhaar H, Fiala B, et al (2020) Reduced benefits of ant occupation for ant-trees in oil palm compared with heavily logged forest. Symbiosis 81:79-91

Howe HF & Smallwood J (1982) Ecology of Seed Dispersal. Annu Rev Ecol Syst 13:201–228

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol 7:1451-1456

Jürgens A, Feldhaar H, Feldmeyer B, Fiala B (2006) Chemical composition of leaf volatiles in *Macaranga* species (Euphorbiaceae) and their potential role as olfactory cues in host-localization of foundress queens of specific ant partners. Biochem Syst Ecol 34:97-113

Kappes H (2006) Relations between forest management and slug assemblages (Gastropoda) of deciduous regrowth forests. For Ecol Manag 237:450–457

Karp DS, Rominger AJ, Zook J, et al (2012) Intensive agriculture erodes β-diversity at large scales. Ecol. Lett. 15:963–970.

Keeton WS (2006) Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. For Ecol Manag 235:129-142.

Keller A, Grimmer G, Steffan-Dewenter I (2013) Diverse microbiota identified in whole intact nest chambers of the Red Mason bee *Osmia bicornis* (Linnaeus 1758). PLoS ONE 8:e78296.

Keller A, Sickel W, Ankenbrand M, Steffan-Dewenter I (2015) NGS pollen metabarcoding and automatic taxonomic classification. Genome 58: 237

Kiel NG, Griffiths GR, McGee GG (2020) Can disruption of an ant–plant mutualism explain a lack of recovery of forest herbs in post-agricultural forests of New York? Northeast Nat 27:215

Kirchenbaur T, Fartmann T, Bässler C, et al (2017) Small-scale positive response of terrestrial gastropods to dead-wood addition is mediated by canopy openness. Forest Ecol Manag 396:85-90

Knight TM, Steets JA, Vamosi JC, et al (2005) Pollen limitation of plant reproduction: Pattern and process. Annu Rev Ecol Evol Syst 36:467–497

Le Provost G, …., Feldhaar H, ….I, Steffan-Dewenter I, et al. (2021) Contrasting responses of above- and belowground diversity to multiple components of land-use intensity. Nat Commun 12:3918

Lichti NI, Steele MA, Swihart RK (2017) Seed fate and decision-making processes in scatter-hoarding rodents. Biol Rev 92:474-504

Mayr AV, Peters MK, Eardley CD, Renner MR, Röder J, Steffan-Dewenter I (2020). Climate and food resources shape species richness and trophic interactions of cavity-nesting Hymenoptera. J Biogeogr 47:854-865

Meyer ST, Heuss L, Feldhaar H, Weisser WW, Gossner MM (2019a) Land-use components, abundance of predatory arthropods, and vegetation height affect predation rates in grasslands. Agr Ecosyst Environ 270-271:84-92

Mori AS, Isbell F, Seidl R (2018) beta-diversity, community assembly, and ecosystem functioning. Trends Ecol Evol 33:549-564.

Munoz MC, Schaefer HM, Böhning-Gaese K, Schleuning M (2017) Importance of animal and plant traits for fruit removal and seedling recruitment in a tropical forest. Oikos 126:823-832

Nakagawa S & Santos ESA (2012) Methodological issues and advances in biological meta-analysis. Evol Ecol 26:1253–1274.

Neuschulz EL, Mueller T, Schleuning M, Böhning-Gaese K (2016) Pollination and seed dispersal are the most threatened processes of plant regeneration. Sci Rep 6 29839

Ollerton J, Winfree R and Tarrant S (2011) How many flowering plants are pollinated by animals? Oikos 120: 321-326

Pérez-Ramos IM, Marañón T (2008) Factors affecting post-dispersal seed predation in two coexisting oak species: Microhabitat, burial and exclusion of large herbivores. For Ecol Manag 255:3506–3514.

Pesendorfer MB, Sillett TS, Koenig WD, Morrison SA (2016) Scatter-hoarding corvids as seed dispersers for oaks and pines: A review of a widely distributed mutualism and its utility to habitat restoration. Condor 118:215-237

Peters MK, Hemp A, Appelhans T, et al (2016a) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nat Commun 7:13736

Peters MK, Peisker J, Steffan-Dewenter I, Hoiss B (2016b) Morphological traits are linked to the cold performance and distribution of bees along elevational gradients. J Biogeogr 43:2040–2049

Peters MK, Classen A, Müller J, Steffan-Dewenter I (2020) Increasing the phylogenetic coverage for understanding broad-scale diversity gradients. Oecologia 192:629–639

Pornon A, Andalo C, Burrus M, Escaravage N. (2017) DNA metabarcoding data unveils invisible pollination networks. Sci Rep 7:16828

Prior KM, Meadley-Dunphy SA, Frederickson ME (2020) Interactions between seed-dispersing ant species affect plant community composition in field mesocosms. J Anim Ecol 89:2485–2495

Reifenrath K, Becker C, Poethke HJ (2012) Diaspore trait preferences of dispersing ants. J Chem Ecol 38:1093–1104

Rivera-Hutinel A, Bustamante RO, Marin VH, Medel R (2012) Effects of sampling completeness on the structure of plant-pollinator networks. Ecology 93: 1593-1603

Schauer B, Bong J, Popp C, Obermaier E, Feldhaar H (2018a) Dispersal limitation of saproxylic insects in a managed forest? A population genetics approach. Basic Appl Ecol 32:26-38

Schauer B, Steinbauer MJ, Vailshery LS, Müller J, Feldhaar H, Obermaier E (2018b) Influence of tree hollow characteristics on saproxylic beetle diversity in a managed forest. Biodivers Conserv 27:853-869

Schellenberger Costa D, Classen A, Ferger S, et al. (2017) Relationships between abiotic environment, plant functional traits, and animal body size at Mount Kilimanjaro, Tanzania. PLoS ONE 12:e0174157

Scherber C, Eisenhauer N, Weisser WW, et al (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553–556

Schleuning M, Neuschulz EL, Albrecht J, et al. (2020) Trait-Based Assessments of Climate-Change Impacts on Interacting Species. Trends Ecol Evol 35:319–328

Schuldt A, Eberling A, Kunz M, et al. (2019) Multiple plant diversity components drive consumer communities across ecosystems. Nat Commun 10: 1460

Schupp EW, Jordano P, Gómez JM (2010) Seed dispersal effectiveness revisited: a conceptual review. New Phytol 188:333–353

Sebastián-González E, Dalsgaard B, Sandel B & Guimarães PR (2015) Macroecological trends in nestedness and modularity of seed-dispersal networks: Human impact matters. Glob Ecol Biogeogr 24: 293–303

Simons NK, Felipe-Lucia MR, Schall P, et al (2021) National Forest Inventories capture the multifunctionality of managed forests in Germany. For Ecosyst 8:5

Sobek S, Tscharntke T, Scherber C, Schiele S, Steffan-Dewenter I (2009) Canopy vs. understory: Does tree diversity affect bee and wasp communities and their natural enemies across forest strata? For Ecol Manag 258:609–615

Soliveres S, van der Plas F, Manning P, et al. (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459

Staab M, Pufal G, Tscharntke T & Klein AM (2018) Trap nests for bees and wasps to analyse trophic interactions in changing environments - a systematic overview and user guide. Meth Ecol Evol 9:2226-2239

Stangler ES, Hanson PE, Steffan-Dewenter I (2015) Interactive effects of habitat fragmentation and microclimate on trap-nesting Hymenoptera and their trophic interactions in small secondary rainforest remnants. Biodivers Conserv 24:563–577

Stangler ES, Hanson PE, Steffan-Dewenter I (2016) Vertical diversity patterns and biotic interactions of trap-nesting bees along a fragmentation gradient of small secondary rainforest remnants. Apidologie 47:527–538

Steckel J, Westphal C, Peters MK, et al (2014) Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. Biol Cons 172: 56–64

Steffan-Dewenter I (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. Cons Biol 17: 1036-1044

Steffan-Dewenter I & Schiele S (2008) Do resources or natural enemies drive bee population dynamics in fragmented habitats? Ecology 89: 1375-1387

Stephens RB, Frey SD, D'Amato AW, Rowe RJ (2021) Functional, temporal and spatial complementarity in mammal-fungal spore networks enhances mycorrhizal dispersal following forest harvesting. Func Ecol 35:2072–2083

Türke M, Andreas K, Gossner MM, et al. (2012) Are gastropods, rather than ants, important dispersers of seeds of myrmecochorous forest herbs? Am Nat 179:124–131

Türke M, Fiala B, Linsenmair KE, Feldhaar H (2010a) Estimation of dispersal distances of the obligately plant-associated ant *Crematogaster decamera*. Ecol Entomol 35:662-671

Türke M, Heinze E, Andreas K, et al. (2010b) Seed consumption and dispersal of ant-dispersed plants by slugs. Oecologia 163:681–693

Türke M, Weisser WW (2013) Species, diaspore volume and body mass matter in gastropod seed feeding behavior. PLoS ONE 8:e68788

Villéger S, Grenouillet G, Brosse S (2013) Decomposing functional β-diversity reveals that low functional β-diversity is driven by low functional turnover in European fish assemblages: Decomposing functional β-diversity. Glob Ecol Biogeogr 22:671–681

Violle C, Enquist BJ, McGill BJ, et al. (2012) The return of the variance: intraspecific variability in community ecology. Trends Ecol Evol 27:244-52

Weisser WW, Roscher C, Meyer ST, et al. (2017) Biodiversity effects on ecosystem functioning in a 15-year grassland experiment: Patterns, mechanisms, and open questions. Basic Appl Ecol 23:1-73

Wende B, Gossner MM, Grass I, et al. (2017) Trophic level, successional age and trait matching determine specialization of deadwood-based interaction networks of saproxylic beetles. Proc Roy Soc B 284:20170198

Westphal C, Bommarco R, Carré G, et al. (2008) Measuring bee diversity in different European habitats and biogeographical regions. Ecol Monogr 78:653-671

Westrich P (2019) Die Wildbienen Deutschlands, 2., aktualisierte Auflage. Verlag Eugen Ulmer, Stuttgart

4 Relevance of sex, gender and/or diversity

The participating institutions are committed to the goal of actively supporting career perspectives of female scientists, diversity and internationalization in academia (see *2.5 Measures to advance research careers* in the General Introduction). The applicants will make their graduate students aware of the support and workshops provided in their institutions and by this research unit (*3.2.4 Gender Equality Measures in Research Networks Module*).

Project Description – Project Proposals

Prof. Dr. Claus Bässler, Frankfurt am Main

SP7: Effects of enhanced structural complexity on dead-wood microbial diversity and wood decomposition

---

Project Description

1 Starting Point

1.1 State of the art and preliminary work

State of the art

The diversity of wood-inhabiting organisms suffers strongly from forest management, particularly due to the reduction of dead-wood amount and heterogeneity in production forests (Grove 2002; Stokland et al. 2012). Wood-inhabiting fungi and bacteria are among the most species-rich lineages within forests and contribute substantially to decomposition and thus to ecosystem functioning (Baldrian 2017; Seibold et al. 2021). However, our understanding of the drivers of the fungal and bacterial diversity (termed in the following “microbial diversity”) in dead wood and how this diversity relates to the ecosystem processes they perform is still rudimentary, preventing efficient forest conservation concepts.

From object-level studies (where the sampling unit is the dead-wood object), we learned that host tree species characterized by differences in physico-chemical properties is an important determinant for microbial diversity at α- and β-level (Hoppe et al. 2015; Purahong et al. 2017; Krah et al. 2018; Moll et al. 2018). Host specificity seems more strongly pronounced for fungal compared to bacterial communities (Moll et al. 2021). A few studies indicate that dead-wood types (e.g., snags, logs) are related to different diversity pattern, however, available studies focused on fungi but not bacteria (Heilmann-Clausen and Christensen 2004; Pasanen et al. 2018). Besides dead-wood characteristics, the abiotic environment affects microbial diversity. At landscape scale, the variation in canopy cover affects microclimatic conditions and subsequently fungal diversity (Krah et al. 2018). However, the sensitivity to microclimate seems more pronounced for fungal compared to bacterial communities (Müller et al. 2020). Further, fungal fruiting communities seem more sensitive than the mycelium communities in response to environmental conditions (Müller et al. 2020). Observed effects of dead-wood resources in the surrounding on the diversity of a dead-wood object are inconsistent and only explored for fungal fruiting communities. While Edman et al. (2004) found increasing fungal species richness of dead-wood objects with an increasing amount of dead wood in the surrounding, Krah et al. (2018) found no such effects.

However, from survey studies and based only on fruiting bodies, it has been shown that dead-wood amount, dead-wood heterogeneity (e.g., different dead-wood types, tree species), and microclimate (e.g., canopy cover variation) are important factors to explain microbial diversity within and among forest patches (Bässler et al. 2010; Abrego and Salcedo 2013). Knowledge about the responses of mycelium (based on molecular data) fungal communities changes with resource amount and diversity and microclimate at patch level are scarce (Purahong et al. 2014) and, to the best of our knowledge, absent for bacterial communities.

Hence, we have a limited understanding of the independent effects of microbial α-diversity drivers (resource-related and abiotic microclimate factors) at patch level and how variability among patches contributes to explain β-diversity and, finally, γ-diversity at district level (small forest landscape). The patch and district level are also especially important for conservation strategies because it is the major scale of decision making in forestry; at patch level via decision directly of the forest manager (e.g., by selecting specific trees for cutting) and at district level via the decadal forest inventory planning ("Forsteinrichtung").

Temperature and moisture are important determinants of wood decomposition (Crockatt and Bebber 2015; Seibold et al. 2021). Low temperature and reduced moisture availability decrease wood decomposition rates, with moisture being more important at a smaller spatial scale in temperate ecosystems (Crockatt and Bebber 2015; Eichenberg et al. 2017). Therefore, factors affecting the microclimate conditions in a forest patch via changes in canopy cover should influence wood decomposition processes. Furthermore, the high diversity of microbial species within dead wood suggest that microbial diversity is linked to wood decomposition. However, results are inconsistent and experimental studies focusing on effects of fungal diversity on wood decomposition at object-level reported neutral, negative, and positive effects (e.g., Kahl et al. 2017, Fukami et al. 2010, and references therein). Finally, the prevalence of key decomposer fungal species might play a pivotal role in decomposition and hence might be a better predictor than overall diversity (Leonhardt et al. 2019). Those key decomposer species showed a prevalence under benign microclimate conditions, which suggests stronger decomposition rates under closed canopies and/or on dead-wood objects in moisture conditions (e.g., lying logs with soil contact vs. standing snags without soil contact) (Vogel et al. 2017; Hagge et al. 2019). Therefore, if microclimate and dead-wood object types change across forest patches the microbial community and its structure (e.g., prevalence of key decomposer species) might influence decomposition processes. To summarize, from previous studies, one might expect direct (abiotic microclimate) and indirect (via microbial community structure affected by microclimate) effects driving wood decomposition processes within and among patches.

To maintain forest biodiversity, Keeton (2006) developed the concept of enhancing structural complexity by increasing the variation in vertical and horizontal canopy density and in different types of dead wood within stands. We here ask whether the Enhancement of Structural α (ESC) and β (ESBC) Complexity in forests by silviculture or natural disturbances increases microbial diversity and modifies ecosystem processes (decomposition) in former homogeneous production forests. More specifically, we will disentangle the factors provided by ESB/ESBC, that is, variability in resource characteristics and microclimate conditions driving microbial diversity at patch level, and particularly ask how this translates into β-diversity at district level. For this reason, we contrast effects among patches of districts characterized by ESBC versus among patches of "state-of-the-art" homogenous forest districts. This will allow us to (i) gain a deeper mechanistic understanding of microbial diversity patterns and related assembly processes and (ii) evidence-based recommendations to maintain microbial diversity and subsequent decomposition processes in production forests at spatial scale highly relevant in forest management.

In addition to our research questions, this proposal will provide valuable data to reach the overall aim of the consortium (e.g., multidiversity and multifunctionality effects of ESBC) and will fuel several other SPs. Also, many SPs will provide important predictor variables to address our questions but also allows insights into important ecosystems compartments while considering cross-taxa approaches and related processes. Particularly, all major dead-wood-related taxa will be considered by several SPs, allowing broad inferences about the response of saproxylic diversity to ESBC. Also, cross-taxa inventories and related processes of the dead wood – soil interface will allow a deeper understanding of the nutrient cycling in forests, dependent on ESBC strategies (see below 2.2., Data exchange and collaboration within the consortium).

Preliminary work

We have experience in using microbial diversity in the context of forest ecology and conservation (e.g., Bässler et al. 2014). To address our research objectives, we use different microbial sampling techniques, which will also be used within this project. Specifically, we used fruiting body and metabarcoding inventories to characterize fungal and bacterial communities (Bässler et al. 2010; Krah et al. 2018; Moll et al. 2018; Seibold et al. 2019). Further, we used cross-taxonomic approaches and built collaborations with experts from other saproxylic taxa (see below project-related publications). Finally, to improve our mechanistic understanding of diversity response to changes in forest structure, we increasingly use experimental settings. With these studies, we also increasingly focus on the link between saproxylic diversity and decomposition (Seibold et al. 2021). Besides these references, we here briefly highlight three ongoing studies and one DFG project that are in strong context of the application:

Disentangling the importance of space and host on β-diversity for beetle, fungi, and bacteria: Lessons from a large dead-wood experiment (Rieker, D. … and Bässler, C. submitted to Conservation Biology)

Using fungal fruiting and molecular, bacterial, and beetle communities, we aim to disentangle the relative importance of space vs. host. Further, we aim to disentangle the levels country (among regions) vs. region (among forest stands/patches) and host clades (broad-leafed, conifer trees) vs. host tree species. Results suggest inconsistent diversity response of saproxylic groups to space and host. However, within the spatial scale, the between patch variability contributed most to explain saproxylic β-diversity, which is the focus of this RU.

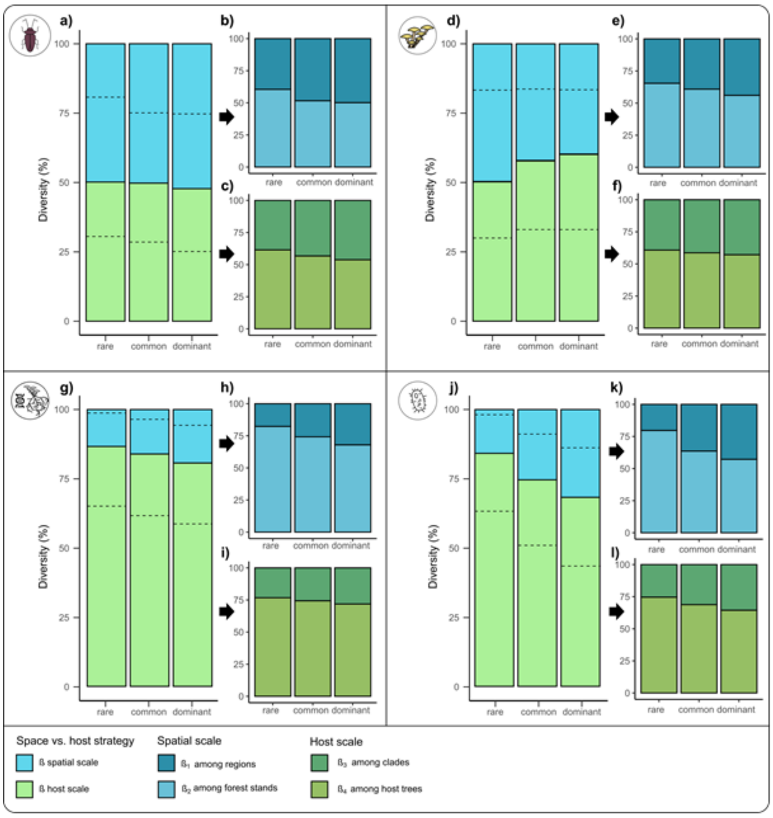


Fig. 1: Stacked barplots of multiplicative diversity partitioning comparing the relative importance of different scales for total diversity (a, d, g, j) of saproxylic beetles (a-c), fungal sporocarps (d-f), fungal mycelium (g-i), and bacteria (j-l). For a better overview, the joint results of all four scales, β1, among three different climatic regions; β2, among 27 forest stands/patches of three different management types; β3, among the two clades conifers and deciduous trees; β4, among logs of eleven different tree species (297 logs in total) were grouped into two superordinate scale groups spatial and host and again scaled to 100% diversity within this scale. Displayed are the relative importance of β-diversity of spatial- vs. host-scale (a, d, g, j), spatial-scale β1 vs. β2 (b, e, h, k), and the host-scale β3 vs. β4 (c, f, i, l). Calculated are the number equivalents of species richness (rare, q = 0), Shannon entropy (common, q = 1), and Simpson diversity (dominant, q = 2).

Relative importance of dead-wood types and microclimate on saproxylic diversity – a cross-taxonomic, experimental approach (Britta, U., … and Bässler, C., prepared for Biological Conservation)

Using fruiting and molecular fungal as well as beetle communities, we aim to disentangle the relative importance of different dead-wood types (stumps, logs, and snags) under various microclimates on saproxylic diversity. Results suggest that dead-wood type is more important than microclimate variability, and effects are more pronounced for fungi than beetles. This suggests that fungi have a stronger host association compared to beetles.

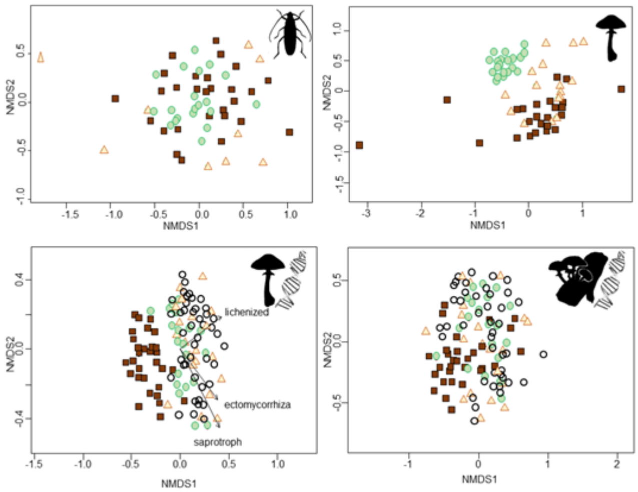


Fig. 2: NMDS ordinations for main saproxylic groups. Different symbol represents different dead-wood types (square=cut stump, triangle=snag, circle=log, open circle = living tree).

Assembly of bacteria in dead wood - effects of microclimate and host tree species (Krah, F. … and Bässler, C., resubmission to Molecular Ecology)

We ask whether bacterial communities in dead wood are phylogenetically structured by microclimate, host tree species, and succession to learn more about assembly processes. Results indicate that harsher microclimates will not substantially alter bacterial richness and assembly processes, but richness differs between host tree species. Integrity of the decomposition process seems to be of major importance for bacterial diversity.

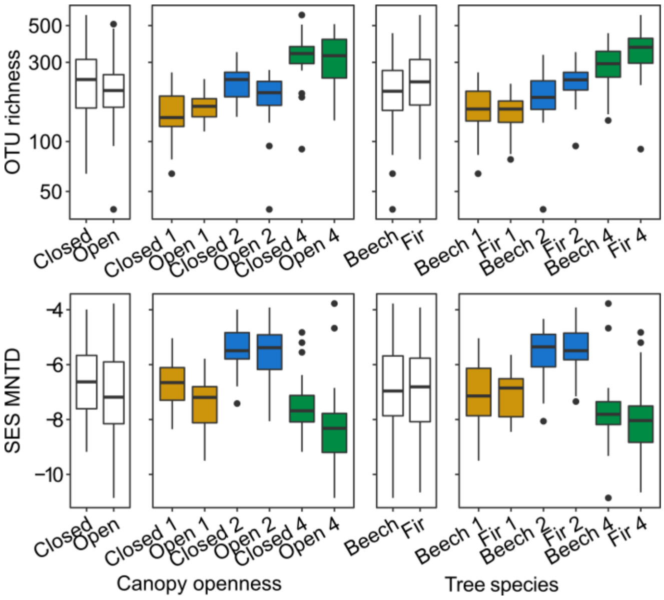


Fig. 3. Bacterial richness and phylogenetic α-diversity along with canopy openness and host tree species for different successional years. OTU richness is the number of OTUs based on the rarefied community matrix with 48 plots. Phylogenetic α-diversity is the standardized effect size (SES) of the mean nearest taxon distance (MNTD) based on a null model that randomizes taxon names.

Linking microclimate, dead-wood microbial diversity, adaption mechanisms, and ecosystem processes (GAČR-DFG Cooperation: Joint German-Czech Project Proposals, together with Vendula Brabcová, Petr Baldrian, and Harald Kellner)

Within this project and consortium, we aim to deepen our mechanistic understanding of the response of fungal and bacterial communities to microclimate change using molecular methods to determine diversity and metatranscriptomics (c.f. Krah et al. 2021). A particular focus of this project is also the microbial diversity – ecosystem processes (here: wood decomposition) relationship.

Based on the described ongoing studies and the DFG project, we investigate how the forest environment shapes microbial communities. However, all these studies have a strong focus on α- and β-level at object scale. With this application, we intend to extend the sampling to the patch level to address appropriately how forest districts (landscapes) with ESBC shape wood-inhabiting microbial communities and related ecosystem processes (wood decomposition).

Since the experiment has been established (please see Coordination project), we already gathered data: (i) We exposed two objects of standardized wood (1x *Fagus sylvatica*, 1x *Pinus sylvestris*, branches, 5-10 cm diameter) to allow colonization by fungal and bacterial communities in April 2018 in the center of each patch (1.50 m distance to the soil surface) in the intensive sampling sites. A slice has been cut before manipulation and after one growing season for later molecular community determination. (ii) In all patches of the three treatment and two control blocks at the intensive sampling sites, we took wood samples (before data) in 2018 for later molecular community determination (via drilling) and determination of mass loss (via cut slices). We stratified the sampling to include always one tree of each of the main tree species per patch. Among these trees, we randomly selected one tree per species per patch of those trees which were supposed to be cut or to be manipulated (habitat trees). In the patches AW and DW, we additionally sampled randomly one tree per species of the remaining stand. In total, we sampled 346 trees before the treatment. The sample trees are the same as included in bryophyte and lichen epiphyte community sampling in SP8. A subset of these data will be used to evaluate how existing fungal endophytes in still living trees affect subsequent microbial communities after die-off (priority effect).

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. **Bässler, C**., R. Ernst, M. Cadotte, C. Heibl, and J. Müller. 2014. Near-to-nature logging influences fungal community assembly processes in a temperate forest. Journal of Applied Ecology 51:939-948.
2. **Bässler, C**., J. Müller, M. W. Cadotte, C. Heibl, J. H. Bradtka, S. Thorn, and H. Halbwachs. 2016. Functional response of lignicolous fungal guilds to bark beetle deforestation. Ecological Indicators 65:149-160.
3. Peura, M., R. S. Gonzalez, J. Müller, M. Heurich, L. A. Vierling, M. Mönkkonen, and **C. Bässler**. 2016. Mapping a 'cryptic kingdom': Performance of lidar derived environmental variables in modelling the occurrence of forest fungi. Remote Sensing of Environment 186:428-438.
4. Baber, K., P. Otto, T. Kahl, M. M. Gossner, C. Wirth, A. Gminder, and **C. Bässler**. 2016. Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi. Forest Ecology and Management 377:161-169.
5. Krah, F. S., S. Seibold, R. Brandl, P. Baldrian, J. Müller, and **C. Bässler**. 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. Journal of Ecology 106:1428-1442.
6. Seibold, S., J. Müller, P. Baldrian, M. W. Cadotte, M. Stursova, P. H. W. Biedermann, F. S. Krah, and **C. Bässler**. 2019. Fungi associated with beetles dispersing from dead wood - Let's take the beetle bus! Fungal Ecology 39:100-108.
7. Hagge, J., **Bässler, C**., Gruppe, A., Hoppe, B., Kellner, H., Krah, F.-S., Müller, J., Seibold, S., Stengel, E., Thorn, S. Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. 2019. Proceedings B. 286: 20191744.
8. Krah, F.S., Büntgen, U., Schaefer, H., Müller, J., Andrew, C., Boddy, B., Diez, J. Egli, S., Freckleton, R., Gange, A.C., Halvorsen, R., Heegaard, E., Heideroth, A., Heibl, C., Heilmann-Clausen, J. Høiland, K., Kar, R. Kauserud, H., Kirk, P.M., Kuyper, T.W., Krisai-Greilhuber, I., Norden, J., Papastefanou, P., Senn-Irlet, B. and **Bässler, C**. 2019. European mushroom assemblages are darker in cold climates. Nature Communications 10:2890.
9. Thorn, S., A. Chao, M. Bernhardt-Römermann, Y.-H. Chen, K. B. Georgiev, C. Heibl, J. Müller, H. Schäfer, and **C. Bässler**. 2020. Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. Ecology 101.
10. Moll, J., A. Heintz-Buschart, **C. Bässler**, M. Hofrichter, H. Kellner, F. Buscot, and B. Hoppe. 2021. Amplicon Sequencing-Based Bipartite Network Analysis Confirms a High Degree of Specialization and Modularity for Fungi and Prokaryotes in Deadwood. mSphere 6.

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.2.3 Patents

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work program

2.1 Anticipated total duration of the project

Four years

2.2 Objectives

1. Alpha (α) patch-level

Diversity

Two basic factors of the ESC treatment might particularly affect the α-diversity of microbial communities at patch level; variability in dead-wood diversity (e.g., lying vs. standing dead-wood objects, host tree species) and microclimate (open vs. closed canopies). Microclimate has a marginal effect on both fungal and bacterial richness, as indicated by object-based studies (see Section 1.1). This might translate to patch level, and we, therefore, expect microclimate to have a subordinated effect on overall microbial species richness. In contrast, dead wood of different types harbors different fungal communities (Pasanen et al. 2018; Pasanen et al. 2019) (Uhl et al. in prep, see Section 1.1). Further, bacteria respond to different host characteristics, also suggesting sensitivity to dead-wood types (Tlaskal et al. 2017; Moll et al. 2018). We, therefore, expect an increase of microbial richness with increasing dead-wood diversity. If host specificity is stronger for fungal communities compared to bacterial communities as recently suggested (Moll et al. 2021, Rieker et al. in prep, see Section 1.1), the strength of response should be more pronounced for fungi compared to bacteria. Based on these assumptions, we, therefore, expect an overall positive relationship between microbial species richness with ESC.

H1: ESC increases microbial species richness caused by dead-wood diversity and not microclimate. This effect is more pronounced for fungi compared to bacteria.

Decomposition

We expect that the variability of decomposition within patches can be explained by direct and indirect environmental factors caused by ESC.

Moisture is a critical abiotic factor of decomposition rates in temperate forests (see Section 1.1). Open canopies are characterized by less buffered vapor pressure deficit compared to closed canopies, and hence, moisture availability is lower (Arx et al. 2013; Davis et al. 2019; Thom et al. 2020). Standing dead-wood objects (e.g., snags) are less directly exposed to the soil and therefore dryer compared to lying dead wood (e.g., logs) (Gora et al. 2019). We, therefore, expect a negative relationship of decomposition rates with increasing canopy openness and with an increasing proportion of snags within the dead-wood type treatments. However, the strength of the response is expected to be more pronounced for the microclimate than for the dead-wood type treatment because we expect microclimate to affect moisture to a stronger extend than dead-wood type.

We further expect that microbial species richness is correlated with decomposition. However, whether the relationship is synergistic (e.g., niche complementary, i.e., species richness is positively correlated with decomposition) or antagonistic (e.g., competition, i.e., species richness is negatively correlated with decomposition) is unclear (see Section 1.1).

Evidence is scarce; however, the prevalence of key decomposer fungal species seems to dominate in benign moisture conditions (Vogel et al. 2017; Hagge et al. 2019). It is therefore plausible that the abundance of key decomposer species is higher under closed canopies and patches dominated by logs which would favor decomposition rates. We, therefore, will also use the abundance and proportion of a priori selected key decomposer species (e.g., *Fomes fomentarius)* (Lustenhouwer et al. 2020).

H2: ESC affects decomposition rates directly via microclimate change and dead-wood types and indirectly via microbial richness and the prevalence of key decomposer species. Microclimate change contributes most strongly to decomposition.

2. Beta (β) patch-level

Diversity

We expect that the β-diversity among patches is determined by both microclimate and dead-wood diversity. From object-based studies, it has been suggested that microclimate affects fungal communities but not bacterial communities (see Section 1.1). Further, fungal communities seem to differ between different dead-wood types (Pasanen et al. 2018), but studies of bacterial communities are scarce. However, bacterial communities seem related to specific hosts even though to a lesser extent than fungi (Moll et al. 2021). Due to host specificity, we expect a stronger effect of dead-wood diversity on microbial β-diversity compared to microclimate among patches. However, the effect of dead-wood diversity on β-diversity is expected to be more pronounced for fungi. Based on these assumptions, we expect an overall positive relationship between microbial β-diversity and ESBC.

H3: ESBC increases microbial β-diversity mainly due to dead-wood diversity distance, and this response is stronger for fungi than bacteria.

Decomposition

If decomposition is driven by microclimate and dead-wood diversity as outlined above, we would expect an increase of decomposition rate distance with microclimate and dead-wood diversity distance, that is, an increase in pairwise patch decomposition rate differences with differences in pairwise patch microclimates or dead-wood diversities. We expect the strength of response to be more pronounced for microclimate distance than dead-wood diversity distance since moisture availability is more strongly driven by canopy than dead-wood type (see above).

We further expect that the microbial community distance is correlated with the decomposition rate distance. If the assumption holds true that key dominant decomposer species play a vital role in the decomposition process, a weighting of dominant species within the community via Hill numbers (Hill 1973) should better explain decomposition compared to a weighting of rare and common species.

H4: ESBC increases distance of decomposition rates due to microclimatic distance, dead-wood type distance, and abundance of key decomposer distance. Microclimatic distance explains most strongly decomposition distance.

3. Gamma (γ)-level

According to the hypothesized effects at α- and β-level, we expect a translation to the γ-level as indicated in Fig. 4. Hence, we expect γ-diversity at district level to be higher for ESBC than control and the opposite for decomposition rate. We further highlight β-patch-level treatments contributing to overall gamma (Fig. 4).

H5: γ-diversity is higher and decomposition rates lower for ESBC compared to the control.

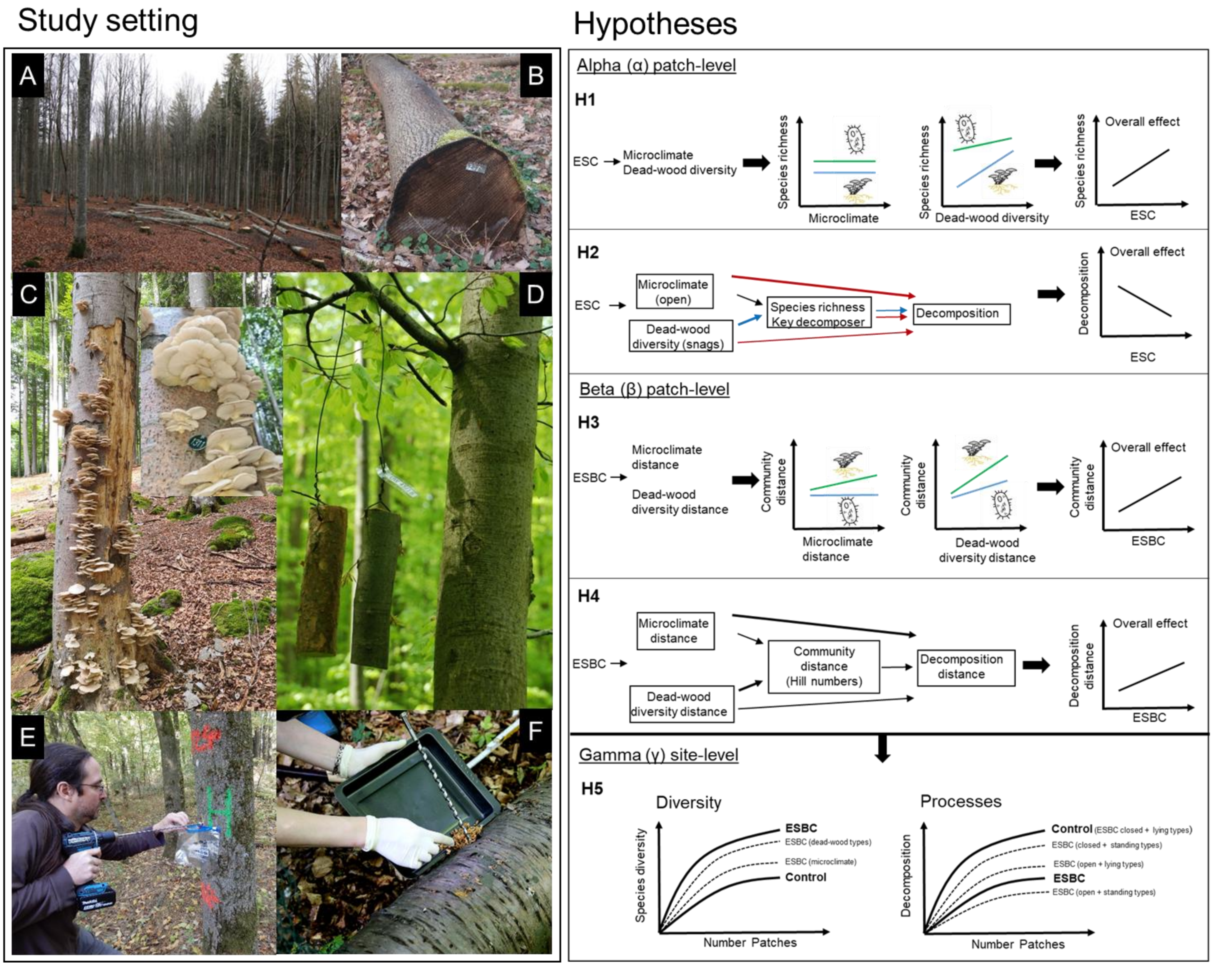


Fig. 4: Left: Study setting (A. patch with lying dead wood under an open canopy, B., and C. examples for dead wood objects in different successional stages, B. with fruiting bodies which will be considered within the fruiting body sampling, D. exposed dead wood of beech and pine which will be subjected for microbial and decomposition analyses, E. and F: sampling for molecular microbial communities.
Right: Conceptual overview about the derived expectations and related hypotheses.

Data exchange and collaboration within the consortium

(i) We provide basic data (microbial diversity, wood decomposition) to address the overall question of how multidiversity is linked to multifunctionality via ESBC (SPZ, SP9). (ii) We will link microbial diversity with decomposition directly in dead wood. Thereby, we provide complementary decomposition data, which will be used by SP5. Hence, the SP5 and SP7 will consider all main decomposition categories related to forests allowing a unified, in-depth decomposition analysis based on a common study setting. (iii) Together with SP2, we will use the exposed standardized wood and will link microbial diversity, bark beetle diversity, volatile expression, and decomposition. With these data, we will analyze the influence of co-existing taxa (interactions) on diversity and decomposition rates (Biedermann et al. 2019; Seibold et al. 2021). (iv) Together with SP8, we selected the trees for sampling fungi and bacteria (this SP) as well as bryophytes and lichens (SP8). In combination with the insect data from SP9, we will cover the most important organisms involved in the assembly and decomposition processes on dead wood, which allows cross-taxonomic analyses (Müller et al. 2020, see preliminary work). (v) Together with SP4, we will link microbial diversity and related processes of wood with soil. This allows testing of the importance and interactions of fungi and bacteria (this SP), bryophytes and lichens (SP8), and insects (SP9) for community assembly and decomposition processes (SP5) across ecosystems' compartments (soil and wood) via effects of ESBC (Baldrian 2017). (vi) We will use data provided by SP1 to calculate our predictor set (dead-wood amount, heterogeneity, and microclimate). We will link vertical microclimate measurements from SP1 to predict microbial diversity response to the vertical position of dead-wood objects (lying dead wood close to the soil, snags, uplifted exposed dead wood). (vii) Variables related to the environmental conditions at each patch (e.g., vigor, water content) sampled via earth observations from all wavelengths applied within SP3 and the basic meteorological background data from SPZ will be used as important predictors in our models. (viii) Structural measures at different scales from remote sensing provided by SP3 can be used as additional co-variables and to account for off-set effects in our models (e.g., tree species composition in the surrounding at larger scale). Remote sensing data can properly predict fungal diversity offering additional collaborating papers (Peura et al. 2016). (ix) SP5 will help to analyze wood chemical properties (e.g., use of C/N ratio analyzer). (x) We will use the moisture measurements organized by SPZ and the bryophyte and lichen cover of the dead-wood objects as additional predictors in our models (Abrego et al. 2015). (xi) A close collaboration with Petr Baldrian (Mercator Fellow) will ensure the application of cutting-edge microbial sampling methods (see also SP4) and help to implement bioinformatics analyses at the Goethe University. (xi) Finally, to reduce the sampling effort, we will harmonize sampling across SPs mentioned here and particularly use sampling support from SPZ.

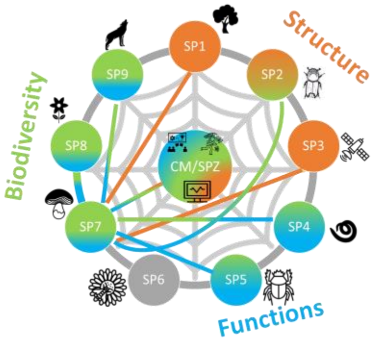


Fig. 5: Cooperation of SP7 with other Sps. The colors of connecting indicate the type of data exchange.

2.3 Work program including proposed research methods

Work packages

WP1 Sampling of microbial communities: The aim of the sampling approaches is to gather data that represents the diversity of microbial species with ECS/ESBC treatment and control at the patch level to test our hypotheses. We plan three sampling strategies: (i) We will continue the exposition of standardized dead wood on each patch at the intensive sampling sites (see above preliminary work, started with before treatments in 2018) and plan to analyze the samples to determine the molecular microbial communities (2018, 2020, 2022). Further, we will expose new standardized wood on each patch at all sites in 2022 and analyze them in 2023 as well as in 2024 for the time-series sites (Table 1, see Coordination project). For the time-series sites, we will also sample in 2025 but subject samples for further analyses to the 2nd Phase if funded. We will use one standardized dead wood object at each patch (*F. sylvatica,* similar to that already used during set up the experiment in 2018; this will be organized together with SP2, which will also use these objects). Sampling will be carried out by the Ph.D. student, the research assistant, and with the help of SPZ. Processing of samples will be carried out in the lab of C. Bässler. All molecular work will be done in close collaboration with the Mercator Fellow P. Baldrian. (ii) We first will use the samples from each patch gathered in 2018 (before data) from the intensive sites to determine the microbial species pool for each patch (except those patches characterized by total tree removal, AR, DR). Second, for all patches of the intensive and extensive sites, we will consider the following object types for sampling: Stumps, crowns, logs, snags, habitat trees, and branches. We will randomly select one object type of each of the main tree species per patch and for branches two. We will take wood samples via drilling for the determination of the molecular communities. The number of drillings per object type is as follows: snags: 2x at 0.50 m, 2.00 m height; logs: 0 to 5m 2x, 5-10m 3x, >10m 5x, stumps (cut): 1 x in the middle; crowns: 0 to 5m 2x, 5-10m 3x. Branches: similar to logs. Logs, crown, and branch drilling positions will be equally distributed. We will label each sampled object and assign the following information: dead-wood type, tree species, stage of decomposition, and estimates of length and diameter. For molecular community determination, we will pool all drillings to patch level. We will sample the intensive sites and the Bavarian Forest sites in 2022 and the remaining extensive sites in 2023 (Table 1). We will furthermore repeat sampling in 2024 and 2025 for the time-series sites (2025 samples will be subjected to lab analyses in the 2nd phase if funded to warrant consecutive sampling). Sampling will be carried out by the Ph.D. student, the research assistant, and with the help of SPZ. In 2025, sampling will be supported and co-financed by the National Park Bavarian Forest (not calculated below, 7. Budget). Processing of samples will be carried out in the lab of C. Bässler. All molecular work will be done in close collaboration with the Mercator Fellow P. Baldrian. (iii) To characterize the fungal fruiting community, we will carry out one standardized sampling campaign across the dead-wood objects used for molecular sampling on all patches (Table 1). As above, we will sample Sailershausen and the Bavarian Forest in 2022 and all others in 2023. In addition, we will sample in 2024 and 2025 at the time-series sites. We will use the main fruiting season and standardize sampling to macromycetes (>5mm fruit body size) with an emphasis on species that can be directly determined in the field (for details of methods, see Baber et al. 2016). Sampling will be carried out by the Ph.D. student and in 2025 by the research assistant and with the help of SPZ. Critical taxa will be stored and determined via a Microscope in the lab and with the help of experts.

Output: Community matrices for bacteria (molecular) and fungi (molecular and fruiting body-based). Data from WP1i and WP1iii are on object level (can be aggregated to patch level) and data from WP1ii on patch level. Dead-wood structural data matrix from WP1ii inventory on object level (can be aggregated to patch level).

WP2 Measuring decay and explanatory variables: For all samples from the exposed objects, we cut slices at the time of sampling described above and determine mass loss and wood chemical properties (C/N, pH, in collaboration with SP5) (WP1i, Table 1). For the patch samples based on the selected objects (WP1ii), we will analyze microbial biomass (Ergosterol, qPCR, Frankfurt lab and in collaboration with Mercator Fellow P. Baldrian – use of HPLC) and wood chemical properties (C/N, pH in collaboration with SP5) as suitable proxies of decomposition processes. Further, we will continue (before data, see above preliminary work) taking wood samples (cut slices) from the existing dead wood of each patch to measure mass loss). This sampling will be carried out with the help of SPZ. All decomposition data will also be used from SP5. For a subset of the sampled objects, we will measure temperature and humidity within dead wood using sensors complementary to microclimate data by SPZ. These data loggers are already available at Goethe University.

Output: Corresponding environmental matrices for objects and patches in relation to the bacterial and fungal communities (molecular and fruiting body-based) data (see WP1).

WP3-5 Hypotheses testing

In our models, we will use microbial diversity measures and decomposition rate measures at α- and β-level as response variables for each patch. As predictors, we will use variables related to dead-wood amount and diversity and microclimate conditions (see section 2.2) for each patch. To control for off-set effects, we will use covariates provided by the consortium (see Section 2.2). The analyses and the related manuscripts will be conducted by the Ph.D. student under the supervision of C. Bässler in close collaboration with the Mercator Fellow P. Baldrian.

WP3 Microbial diversity at α-, β- and γ- level (H1, H3, H5)

H1: We will use a generalized linear mixed-effects model with species richness as response and microclimate and dead-wood diversity as predictors and dead-wood amount as a covariate. We will use the microbial guild (fungi vs. bacteria) as an interaction term to test for different responses. We will account for the nested design and random effects in the case of repeated measurements in our models. H3: We will use multiple regressions on distance matrices (MRM) using the community distance as response and microclimate and dead-wood diversity distances as predictors. We will consider dead-wood amount and the spatial distance as covariates. We will compare the effects between microbial guilds via the strength of response (standardized coefficients) and the model r^2s since MRM allows not specifying interaction terms. To test for robustness, we will also apply a PERMANOVA based on the same response, predictors, and covariates. In addition, we will ordinate the microbial community, extract the relevant scores (e.g., NMDS scores from two dimensions assessed based on the stress value) and assign each vector (scores) the microbial guild. We will use the scores as responses and run models as described for species richness. Even though not straightforward, this allows testing for microbial guild interactions. H5: To compare γ-diversity across scales (patches or districts), a standardization approach via size- and coverage-based rarefaction and extrapolation will be applied (Hsieh et al. 2016).
Output: Paper 1 – Effects of ESC on microbial diversity (target journal: e.g., Journal of Applied Ecology).

WP4 Direct and indirect drivers of wood decomposition at α-, β- and γ- level (H2, H4, H5)

H2: To test for direct (environment) and indirect (via microbial richness) effects on decomposition, we will use structural equation models (SEM). We will consider the covariates, account for the nested design and random effects in case of repeated measures as described for H1. H4: To test for direct (environmental distances) and indirect (via microbial community distance) effects, we will use structural equation models (SEM). We are not aware of SEM frameworks using directly distances matrices. We, therefore, will use three approaches to test H4. (i) We will transform the distance matrices into vectors and apply an SEM as described in H2. We will account for repeated measures (pairwise comparisons among all patches) via a random effect in SEM. (ii) We will ordinate the microbial community and extract the scores (vectors) as described in H3. Based on these vector response variables, we can run SEMs as described in H2. (iii) We will run an MRM with decomposition distance as response and community and environmental distances as predictors. In all models, random effects and covariates will be implemented as outlined above. To test for the expectation that dominant species are crucial for decomposition, we apply all models based on Hill numbers. To compare γ-decomposition rates across scales (patches or districts), a standardization approach via size- and coverage-based rarefaction and extrapolation will be applied (Hsieh et al. 2016).

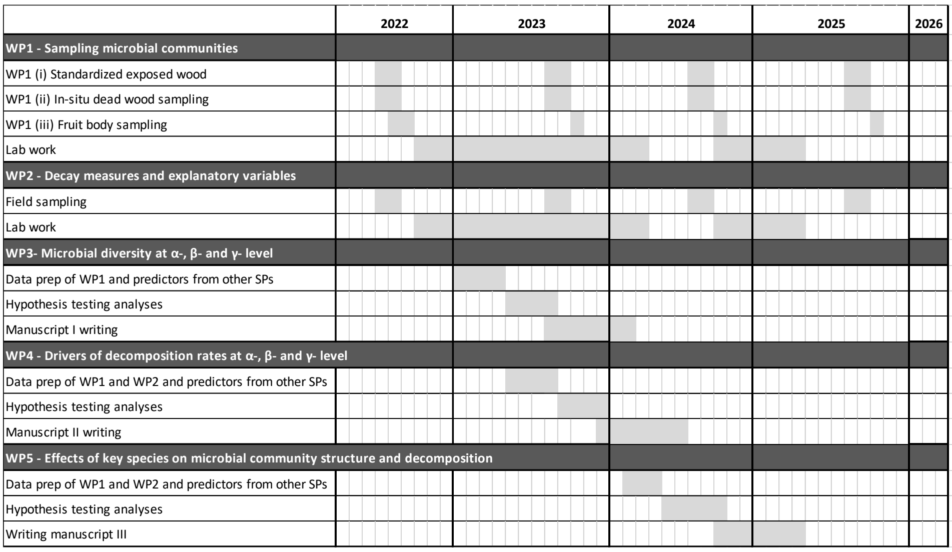
Output: Paper 2 – Relative importance of environment and microbial diversity on wood decomposition (target journal: e.g., Ecosystems, Global Change Biology)

WP5 Effects of key performing species on microbial community structure and decomposition (H2, H4)

To approach this paper, we will also apply SEMs as described above using abundance, the proportion of a priori key decomposer, and Hill Numbers (particularly weighting of dominant species) as predictors in the model described in H2 and H4. In addition, we will carefully explore rank-abundance curves to focus on how ESC/ESBC treatments mediate the relationship between abundant and rare species in communities. Further, bipartite network analyses and null modeling (Dormann et al. 2009) will provide further insights into how key species affect communities depend on ESC/ESBC treatments.

Output: Paper 3 - Effects of key species on microbial community structure and decomposition (target journal: e.g., ISME, Molecular Ecology)

Table 1: Time table of the work program by month.



	2022									2023												2024											2025												2026		
WP1 - Sampling microbial communities																																															
WP1 (i) Standardized exposed wood				▨	▨												▨	▨										▨	▨											▨	▨						
WP1 (ii) In-situ dead wood sampling				▨	▨												▨	▨										▨	▨											▨	▨						
WP1 (iii) Fruit body sampling					▨	▨													▨											▨													▨					
Lab work							▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨						▨	▨	▨	▨	▨	▨	▨											
WP2 - Decay measures and explanatory variables																																															
Field sampling				▨	▨												▨	▨										▨	▨											▨	▨						
Lab work							▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨						▨	▨	▨	▨	▨	▨	▨											
WP3- Microbial diversity at α-, β- and γ- level																																															
Data prep of WP1 and predictors from other SPs										▨	▨	▨	▨																																		
Hypothesis testing analyses														▨	▨	▨	▨																														
Manuscript I writing																	▨	▨	▨	▨	▨	▨	▨																								
WP4 - Drivers of decomposition rates at α-, β- and γ- level																																															
Data prep of WP1 and WP2 and predictors from other SPs														▨	▨	▨	▨																														
Hypothesis testing analyses																		▨	▨	▨	▨																										
Manuscript II writing																					▨	▨	▨	▨	▨	▨	▨																				
WP5 - Effects of key species on microbial community structure and decomposition																																															
Data prep of WP1 and WP2 and predictors from other SPs																							▨	▨	▨																						
Hypothesis testing analyses																										▨	▨	▨	▨	▨																	
Writing manuscript III																														▨	▨	▨	▨	▨	▨	▨											

3 Bibliography

Abrego N, Salcedo I (2013) Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages. Is it a question of quantity or quality? Forest Ecology and Management 291:377–385.

Arx G von, Graf Pannatier E, Thimonier A, Rebetez M (2013) Microclimate in forests with varying leaf area index and soil moisture: potential implications for seedling establishment in a changing climate. J Ecol 101:1201–1213. Available online at: https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/1365-2745.12121.

Baber K, Otto O, Kahl T, Gossner MM, Wirth C, Gminder A, Bässler C (2016) Disentangling the effects of forest-stand type and dead-wood origin of the early successional stage on the diversity of wood-inhabiting fungi. Forest Ecology and Management 377:161–169.

Baldrian P (2017) Forest microbiome. diversity, complexity and dynamics. FEMS Microbiology Reviews 41:109–130.

Bässler C, Ernst R, Cadotte M, Heibl C, Müller J (2014) Near-to-nature logging influences fungal community assembly processes in a temperate forest. Journal of Applied Ecology 51:939–948.

Bässler C, Müller J, Dziock F, Brandl R (2010) Effects of resource availability and climate on the diversity of wood-decaying fungi. Journal of Ecology 98:822–832.

Biedermann P, Müller J, Gregoire J-C, Gruppe, A., Hagge J, Hammerbacher A, Hofstetter RW, Kandasamy D, Kolarik M, Kostovcik M, Krokene P, Salle A, Six DL, Turini T, Vanderpool D, Wingfield MJ, Bässler C (2019) Bark Beetle Population Dynamics in the Anthropocene. Challenges and Solutions. Trends in Ecology & Evolution, in press.

Crockatt ME, Bebber DP (2015) Edge effects on moisture reduce wood decomposition rate in a temperate forest. Global Change Biology 21:698–707.

Davis KT, Dobrowski SZ, Holden ZA, Higuera PE, Abatzoglou JT (2019) Microclimatic buffering in forests of the future: the role of local water balance. Ecography 42:1–11. Available online at: https://onlinelibrary.wiley.com/doi/full/10.1111/ecog.03836.

Dormann CF, Fründ J, Blüthgen N, Gruber B (2009) Indices, Graphs and Null Models: Analyzing Bipartite EcologicalNetworks. The Open Ecology Journal 2.

Edman M, Kruys N, Jonsson BG (2004) Local dispersal sources strongly affect colonization patterns of wood-decaying fungi on spruce logs. Ecological Applications 14:893–901.

Eichenberg D, Pietsch K, Meister C, Ding W, Yu M, Wirth C (2017) The effect of microclimate on wood decay is indirectly altered by tree species diversity in a litterbag study. J Plant Ecol 10:170–178. Available online at: https://academic.oup.com/jpe/article/10/1/170/2966854?login=true.

Fukami T, Dickie IA, Wilkie JP, Paulus BC, Park D, Roberts A, Buchanan PK, Allen RB (2010) Assembly history dictates ecosystem functioning. evidence from wood decomposer communities. Ecology Letters 13:675–684.

Gora EM, Lucas JM, Yanoviak SP (2019) Microbial Composition and Wood Decomposition Rates Vary with Microclimate From the Ground to the Canopy in a Tropical Forest. Ecosystems 22:1206–1219. Available online at: https://link.springer.com/article/10.1007/s10021-019-00359-9.

Grove S (2002) Saproxylic Insect Ecology and the Sustainable Management of Forests. Annual Review of Ecology, Evolution and Systematics 33:1–23.

Hagge J, Bässler C, Gruppe, Axel, Hoppe B, Kellner H, Krah F-S, Müller J, Seibold S, Stengel E, Thorn S (2019) Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. Proceedings. Biological sciences 286:20191744.

Heilmann-Clausen J, Christensen M (2004) Does size matter? - On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management 201:105–117.

Hill MO (1973) Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54:427–432.

Hoppe B, Krger K, Kahl T, Arnstadt T, Buscot F, Bauhus J, Wubet T (2015) A pyrosequencing insight into sprawling bacterial diversity and community dynamics in decaying deadwood logs of Fagus sylvatica and Picea abies. Sci Rep 5:9456. Available online at: https://www.nature.com/articles/srep09456.

Hsieh TC, Ma KH, Chao A (2016) iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Methods Ecol Evol 7:1451–1456. Available online at: https://besjournals.onlinelibrary.wiley.com/doi/full/10.1111/2041-210X.12613.

Kahl T, Arnstadt T, Baber K, Bassler C, Bauhus J, Borken W, Buscot F, Floren A, Heibl C, Hessenmoller D, Hofrichter M, Hoppe B, Kellner H, Kruger D, Linsenmair KE, Matzner E, Otto P, Purahong W, Seilwinder C, Schulze ED, Wende B, Weisser WW, Gossner MM (2017) Wood decay rates of 13 temperate tree species in relation to wood properties, enzyme activities and organismic diversities. Forest Ecology and Management 391:86–95.

Keeton WS (2006) Managing for late-successional/old-growth characteristics in northern hardwood-conifer forests. Forest Ecology and Management 235:129–142. Available online at: https://www.sciencedirect.com/science/article/pii/S0378112706005214.

Krah F-S, Hess J, Hennicke F, Kar R, Bässler C (2021) Transcriptional response of mushrooms to artificial sun exposure. Ecology and Evolution 11:10538–10546. Available online at: https://onlinelibrary.wiley.com/doi/full/10.1002/ece3.7862.

Krah F-S, Seibold S, Brandl R, Baldrian P, Müller J, Bässler C (2018) Independent effects of host and environment on the diversity of wood-inhabiting fungi. Journal of Ecology DOI: 10.1111/1365-2745.12939.

Leonhardt S, Hoppe B, Stengel E, Noll L, Moll J, Bässler C, Dahl A, Buscot F, Hofrichter M, Kellner H (2019) Molecular fungal community and its decomposition activity in sapwood and heartwood of 13 temperate European tree species. PLOS ONE 14:e0212120. Available online at: https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0212120.

Lustenhouwer N, Maynard DS, Bradford MA, Lindner DL, Oberle B, Zanne AE, Crowther TW (2020) A trait-based understanding of wood decomposition by fungi. PNAS 117:11551–11558. Available online at: https://www.pnas.org/content/117/21/11551.short.

Moll J, Heintz-Buschart A, Bässler C, Hofrichter M, Kellner H, Buscot F, Hoppe B (2021) Amplicon Sequencing-Based Bipartite Network Analysis Confirms a High Degree of Specialization and Modularity for Fungi and Prokaryotes in Deadwood. mSphere 6. Available online at: https://pubmed.ncbi.nlm.nih.gov/33441408/.

Moll J, Kellner H, Leonhardt S, Stengel E, Dahl A, Bässler C, Buscot F, Hofrichter M, Hoppe B (2018) Bacteria inhabiting deadwood of 13 tree species are heterogeneously distributed between sapwood and heartwood. Environmental Microbiology 20:3744–3756. Available online at: https://sfamjournals.onlinelibrary.wiley.com/doi/full/10.1111/1462-2920.14376.

Müller J, Ulyshen M, Seibold S, Cadotte M, Chao A, Bässler C, Vogel S, Hagge J, Weiß I, Baldrian P, Tláskal V, Thorn S (2020) Primary determinants of communities in deadwood vary among taxa but are regionally consistent. Oikos 129:1579–1588. Available online at: https://onlinelibrary.wiley.com/doi/full/10.1111/oik.07335.

Pasanen H, Junninen K, Boberg J, Tatsumi S, Stenlid J, Kouki J (2018) Life ater tree death. Does restored dead wood host different fungal communities to natural woody substrates? Forest Ecology and Management 409:863–871.

Pasanen H, Juutilainen K, Siitonen J (2019) Responses of polypore fungi following disturbance-emulating harvesting treatments and deadwood creation in boreal Norway spruce dominated forests. Scand. J. Forest Res. 34:557–568.

Peura M, Gonzalez RS, Müller J, Heurich M, Vierling LA, Monkkonen M, Bassler C (2016) Mapping a 'cryptic kingdom'. Performance of lidar derived environmental variables in modelling the occurrence of forest fungi. Remote Sensing of Environment 186:428–438.

Purahong W, Hoppe B, Kahl T, Schloter M, Schulze E-D, Bauhus J, Buscot F, Krüger D (2014) Changes within a single land-use category alter microbial diversity and community structure: molecular evidence from wood-inhabiting fungi in forest ecosystems. Journal of Environmental Management 139:109–119. Available online at: https://www.sciencedirect.com/science/article/pii/S0301479714001224.

Purahong W, Wubet T, Krüger D, Buscot F (2017) Molecular evidence strongly supports deadwood-inhabiting fungi exhibiting unexpected tree species preferences in temperate forests. ISME J 12:289–295. Available online at: https://www.nature.com/articles/ismej2017177.

Seibold S, Müller J, Baldrian P, Cadotte MW, Štursová M, Biedermann PH, Krah F-S, Bässler C (2019) Fungi associated with beetles dispersing from dead wood – Let's take the beetle bus! Fungal Ecol. 39:100–108. Available online at: http://www.sciencedirect.com/science/article/pii/S1754504818300825.

Seibold S, Rammer W, Hothorn T, Seidl R, Ulyshen MD, Lorz J, Cadotte MW, Lindenmayer DB, Adhikari YP, Aragón R, Bae S, Baldrian P, Barimani Varandi H, Barlow J, Bässler C, Beauchêne J, Berenguer E, Bergamin RS, Birkemoe T, Boros G, Brandl R, Brustel H, Burton PJ, Cakpo-Tossou YT, Castro J, Cateau E, Cobb TP, Farwig N, Fernández RD, Firn J, Gan KS, González G, Gossner MM, Habel JC, Hébert C, Heibl C, Heikkala O, Hemp A, Hemp C, Hjältén J, Hotes S, Kouki J, Lachat T, Liu J, Liu Y, Luo Y-H, Macandog DM, Martina PE, Mukul SA, Nachin B, Nisbet K, O'Halloran J, Oxbrough A, Pandey JN, Pavlíček T, Pawson SM, Rakotondranary JS, Ramanamanjato J-B, Rossi L, Schmidl J, Schulze M, Seaton S, Stone MJ, Stork NE, Suran B, Sverdrup-Thygeson A, Thorn S, Thyagarajan G, Wardlaw TJ, Weisser WW, Yoon S, Zhang N, Müller J (2021) The contribution of insects to global forest deadwood decomposition. Nature 597:77–81. Available online at: https://www.nature.com/articles/s41586-021-03740-8.

Stokland JN, Siitonen J, Jonsson BG (2012) Biodiversity in dead wood. Cambridge University Press, 509pp.

Thom D, Sommerfeld A, Sebald J, Hagge J, Müller J, Seidl R (2020) Effects of disturbance patterns and deadwood on the microclimate in European beech forests. Agricultural and Forest Meteorology 291:108066. Available online at: http://www.sciencedirect.com/science/article/pii/S0168192320301684.

Tlaskal V, Zrustova P, Vrska T, Baldrian P (2017) Bacteria associated with decomposing dead wood in a natural temperate forest. Fems Microbiology Ecology 93.

Vogel S, Alvarez B, Bassler C, Muller J, Thorn S (2017) The Red-belted Bracket (Fomitopsis pinicola) colonizes spruce trees early after bark beetle attack and persists. Fungal Ecol. 27:182–188.

4 Relevance of sex, gender and/or diversity

The participating institutions are committed to the goal of actively supporting career perspectives of female scientists, diversity, and internationalization in academia (see *2.5 Measures to advance research careers in the General Introduction*). The applicants will make their graduate students aware of the support and workshops provided in their institutions and by this research unit (*3.2.4 Gender Equality Measures in Research Networks Module*).

Project Description – Project Proposals

Prof. Dr. Goddert von Oheimb, Dresden (PI)
Dr. Andreas Fichtner, Lüneburg (Co-PI)

SP8: Understorey plant assemblages and primary production

Project Description

1 Starting Point

1.1 State of the art and preliminary work

Understorey plant communities are a major component of temperate forest plant diversity by hosting more than 80% of vascular plants on average (Gilliam 2007), regulating various direct (e.g. pollination, seed dispersal, decomposition) and indirect (e.g. habitat provision for a large number of species) plant-animal interactions and considerably contributing to the volatilome (Gilliam 2007; Landuyt et al. 2019). Likewise, they play an essential role for multiple ecosystem functions such as primary productivity or nutrient cycling, and have a strong impact on tree recruitment processes (Landuyt et al. 2019). Further important notable forest-dwelling taxa are wood-dependent bryophytes and lichens, which strongly rely on the availability of suitable substrates such as old living trees or dead wood (Friedel et al. 2006; Ódor et al. 2006; Fritz et al. 2009; Dittrich et al. 2014; Kaufmann et al. 2018). They also represent a vital component of forest biodiversity (Kriebitzsch et al. 2013) and are related to important ecosystem processes such as microclimate regulation, decomposition or habitat provisioning.

Past research in temperate deciduous forests has demonstrated that these taxa strongly respond to changes in habitat conditions across spatial and temporal scales (Hermy and Verheyen 2007; von Oheimb and Härdtle 2009; Bernhardt-Römermann et al. 2015; Dittrich et al. 2016; Perring et al. 2018; Fichtner et al. 2020a; Zellweger et al. 2020). There is numerous evidence that changes in resource availability (in particular light), microclimate, and substrate supply (e.g. deadwood amount) lead to shifts in community composition and diversity of understorey plants and wood-related cryptogams at the local (α-diversity) scale (e.g. Aude and Poulsen 2000; Härdtle et al. 2003; Decocq et al. 2004; von Oheimb et al. 2007; De Frenne et al. 2013; Dormann et al. 2020). Thus, modifications of the biotic and abiotic environment by enhancing structural complexity at the patch (Enhancement of Structural Complexity (ESC) treatments) and district (i.e. landscape) level (Enhancement of Structural Beta Complexity (ESBC) treatments) are expected to have important functional consequences for species assemblages and related ecosystem processes of a forest (Landuyt et al. 2019). For example, Schall et al. (2020) have shown that the complexity of different forest management systems within a ‘virtual’ (i.e. modelled) forest landscape across Germany strongly promotes regional vascular plant diversity (γ-diversity) due to a higher spatial heterogeneity in habitat conditions among stands. Burrascano et al. (2018), however, found no evidence that structural heterogeneity between patches enhances taxonomic β-diversity of understorey vascular plants by comparing managed and unmanaged forest stands in Italy. Consequently, the direction and magnitude of ESBC effects on taxonomic and functional β-diversity of understorey plant communities and wood-dependent cryptogams in ‘real’ (i.e. experimentally manipulated) forest landscapes still remains unclear, and how such compositional and functional changes translate into both above- and belowground productivity of forest understories at the landscape level has never been addressed so far. Thus, a critical next step is to understand how the taxonomic and functional composition of these taxa is shaped by environmental filters across spatial scales to predict at which spatial scale (i.e. local patches or landscapes) the enhancement of structural complexity has the greatest potential to preserve vascular plant, bryophyte, and lichen diversity and to maintain the related ecosystem processes.

Light availability at the forest floor and microclimatic buffering are often related to stand structural complexity (Kovács et al. 2017) and act as key environmental filters in shaping the taxonomic and functional composition of understorey plant communities (de Frenne et al. 2015; Blondeel et al. 2020a). The community responses to changes in environmental conditions, however, may vary with different components of biodiversity (i.e. taxonomic, phylogenetic or functional diversity). For example, taxonomic diversity increased, but functional diversity decreased with increasing light availability, and the opposite pattern was found for microclimatic buffering (de Pauw et al. 2021). Species may also respond differently to altered environmental conditions, causing a shift in functional strategies of component species (Laughlin et al. 2011; Katabuchi et al. 2017). Thus, functional traits often provide deeper insights into community assembly processes, and trait-based approaches are expected to be better predictors of community responses to changes in environmental conditions (Díaz and Cabido 2001). More recently, trait-environment relationships of European deciduous forests understories have come into focus. While macroclimate and soil properties mainly affect the functional composition (community trait means) of the understorey at larger spatial scales (Chelli et al. 2019; Cubino et al. 2021), light availability and microclimate were found to be more important at the local scale (Vanneste et al. 2019; Maes et al. 2020; Chelli et al. 2021). In addition, local heterogeneity in topography and woody species diversity were identified as important environmental drivers for community trait variation (Vanneste et al. 2019). However, the relative importance of environmental means (e.g. changes in environmental conditions induced by ESC treatments at the patch level) and environmental heterogeneity at larger spatial scales (e.g. changes in environmental conditions induced by ESBC treatments at the district and landscape level, respectively) have remained unclear. Nevertheless, these studies greatly contributed to our understanding of aboveground traits associated to the leaf economic and plant size spectra of forest understorey vegetation, but we currently lack information on how environmental factors affect root trait variation within understorey plant communities, both at the α-diversity and β-diversity scale.

Changes in environmental conditions can also invoke trait variation within a species (Bolnick et al. 2011; Fajardo and Siefert 2018; Carlucci et al. 2015). However, intraspecific trait variability (ITV) has rarely been addressed in trait-environment relationships of understorey forest plant species so far, and information is limited to ITV of two aboveground traits (specific leaf area and plant height; Blondeel et al. 2020b; Chelli et al. 2021; Govaert et al. 2021). First results of forest herb species suggest that the relative importance of ITV in explaining community trait responses strongly depends on species identity (Blondeel et al. 2020b; Chelli et al. 2021) and that changes in community trait distribution is rather driven by changes in species abundance and not in ITV (Govaert et al. 2021). Thus, we still have an incomplete understanding on the role of ITV in shaping trait combinations of understorey plant communities across environmental gradients and spatial scales. Exploring the relative importance of functional traits associated with the whole-plant economic spectrum (Weigelt et al. 2021) by incorporating both belowground traits and ITV in trait-environment relationships analyses can therefore provide new insights for our understanding of functional biodiversity patterns and functional changes in forest understories across spatial scales. This whole-plant perspective may also enhance our knowledge on community assembly mechanisms driving understorey functioning (e.g. biomass productivity) in forests.

Given that light is one of the major limiting resources for primary production of the understorey, increasing light availability at the forest floor will promote aboveground understorey biomass (Axmanová et al. 2013; Landuyt et al. 2020) – its relative contribution to belowground biomass, however, is largely unknown. Similarly, more productive understories often host more plant species (Axmanová et al. 2012), but the role of herb layer species diversity in driving aboveground biomass of forest understories remains controversial (Zhang et al. 2017; Wasof et al. 2018). Specifically from a β-perspective, we currently do not know if the effect of increasing light levels related to a higher structural heterogeneity between patches (ESBC treatment) on both above- and belowground understorey productivity is mediated by taxonomic and/or functional diversity of the understorey.

Preliminary work

G von Oheimb and A Fichtner have long standing interest in phytodiversity patterns and dynamics of forest ecosystems and have wide experience in designing and carrying out observational and experimental short- and long-term studies in a broad range of different forest types (e.g. Brunet & von Oheimb 1998; Härdtle et al. 2003; von Oheimb and Brunet 2007; Fichtner et al. 2012). Research has involved studies on patterns of species richness and population dynamics of understorey species and wood-dependent bryophytes and lichens related to natural disturbances, forest management and global change drivers (in particular land-use change, climate change, pollution, alien species; e.g. Friedel et al. 2006; von Oheimb et al. 2007; von Oheimb and Härdtle 2009; Dziedek et al. 2016; Fichtner et al. 2018a, 2020a; Petzold et al. 2018; Baumann et al. 2021; Dittrich et al. 2021). An important focus of their research also is on functional biodiversity. As a member of BEF-China (DFG research unit FOR 891) G von Oheimb contributed to the establishment of a large-scale forest BEF experiment (Bruelheide et al. 2014). Both PIs are currently involved in the IRTG TreeDi (DFG GRK 2324). Main research activities in BEF-China/ TreeDi are biodiversity effects on community assembly processes and on several ecosystem functions, in particular primary productivity, nutrient cycling, herbivory and microbial activity in soil, including multitaxa effects on multifunctionality (e.g. von Oheimb et al. 2011; Lang et al. 2012, 2014; Trogisch et al. 2017; Huang et al. 2018; Schuldt et al. 2018, 2019; Kunz et al. 2019).

The PIs intensively studied the impact of the functional composition of species on community processes, primary productivity and drought responses (Fichtner et al. 2017, 2018b, 2020b; Bongers et al. 2020). For example, Fichtner et al. (2017) reported from the BEF-China experiment that for species with an acquisitive resource-use strategy (i.e. mainly deciduous tree species) positive diversity effects on individual tree productivity were brought about by reduced competitive effects from neighbour trees in species-mixtures, whereas conservative species (i.e. mainly evergreen species) benefitted from facilitation (Fig. 1). Furthermore, in the early stages of the BEF-China experiment, most of the variation in tree growth among richness treatments were explained by community-weighted means (CWMs) of trait values (Kröber et al. 2015). However, comparing the effects of CWMs and functional diversity (FD) over time in this experiment, Bongers et al. (in press) found that FD steadily increased and after seven years the effects of FD values on productivity became larger than effects of CWM. The authors explained this effect by intensified tree-tree interactions when trees get bigger, which supports previous results from the BEF-China experiment (Huang et al. 2018; Kunz et al. 2019).

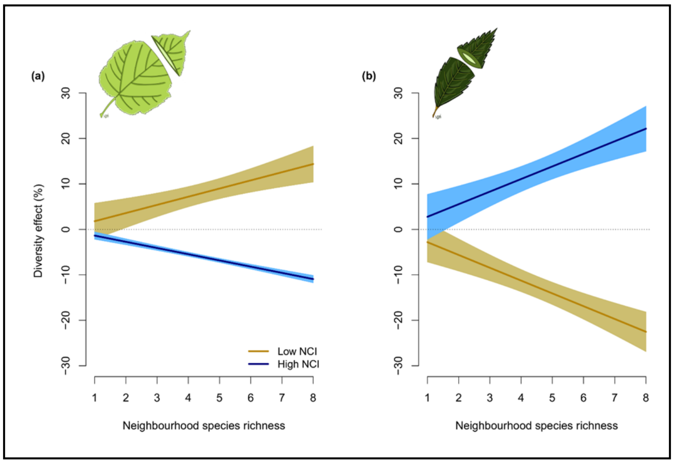


Fig. 1: Trait-dependent variation in diversity effects with neighbourhood competition and tree species richness. Diversity effects indicate the change (%) in individual tree productivity (relative growth rate of wood volume of a focal tree growing with heterospecific compared to growing with conspecific neighbours) in response to neighbourhood species richness at low and high value of neighbourhood competition index (NCI; computed as the 10 and 90% quantile of NCI for (a) acquisitive and (b) conservative species). Figure from Fichtner et al. (2017).

In the different research areas mentioned above the PIs deployed a whole-plant perspective including belowground processes for a long period of time, e.g. in global change ecology (Friedrich et al. 2011; Meyer-Grünefeldt et al. 2015; Dziedek et al. 2016), land-use change and management legacies (Mausolf et al. 2018), and functional biodiversity research (Bu et al. 2017; Guillemot et al. 2020; Madsen et al. 2021).

In the intensive study sites we sampled “before” and “first year after” data of the understorey vegetation in 2018 and 2019. The second re-survey was done in 2021. In five circular subplots of 50 m^2 each per patch we recorded the understorey vegetation (i.e., bryophyte layer, herb and shrub layer). One subplot was in the centre of the patch, the other four subplots were spread in the four subcardinal directions at a distance of 12.5 m from the centre. In each subplot we recorded all vascular plant species of the shrub and herb layer as well as all terricolous bryophytes and lichens, and quantified the cover of each species in 5% intervals with a refinement at cover values <10% and <1% (Dittrich et al. 2013). We found that the treatments caused only slight change in species composition within the sampling period 2018 to 2021, while β-diversity strongly differed for the ESBC-treated patches compared to the controls (Fig. 2).

The same sampling method has also been applied to the extensive sites with each eight subplots per patch. However, as patch values are based on a mean of the relevant subplots, data of both intensive and extensive sites can be used for the β-diversity analyses. For the extensive sites, understorey vegetation data are available for 2016-2019, and sampling will be re-initiated in 2022. The data from all permanent plot surveys are available to the PhD student right from the beginning and can be used for the first manuscript.

In the intensive sites, wood-dependent bryophyte and lichen species were sampled on the lower trunk section (0 to 2 m) on those trees where the trunk remained after the treatment (i.e., living trees, snags and habitat trees). On trees where only the stump remained after the treatment the lower trunk section 0 to 0.5 m was surveyed. Like in the understorey vegetation, species abundance was estimated using the scale of Dittrich et al. (2013; see above). In the tree crown sections, only species presence was recorded. Surveys on tree trunks were done before the intervention in 2018, and the tree crowns could be accessed shortly after the intervention in spring 2019. The sample trees are the same as included in fungal community sampling in SP7. The sampling of wood-dependent bryophytes and lichens in the intensive sites was stratified in order to incorporate always one tree of each of the three most relevant tree species (*Fagus sylvatica, Fraxinus excelsior, Quercus petraea*) per patch. Among these species, we randomly selected one tree per species per patch of those trees which were supposed to be cut or to be manipulated (habitat trees). In the patches AW and DW we additionally sampled one tree per species of the remaining stand in six selected patches. We recorded data on wood-dependent bryophyte and lichen communities on a total of 346 trees. A re-survey is planned for October 2021.

In the extensive sites, we sampled epiphyte data in the years 2016, 2018 and 2019. In these patches, one untreated sample tree, one representative of any type of manipulated objects (i.e. lying and standing deadwood) and a left-over stump were included, i.e., 184 objects (23 per district) were surveyed. As these patches are largely dominated by *Fagus sylvatica*, only individuals of this species were sampled.

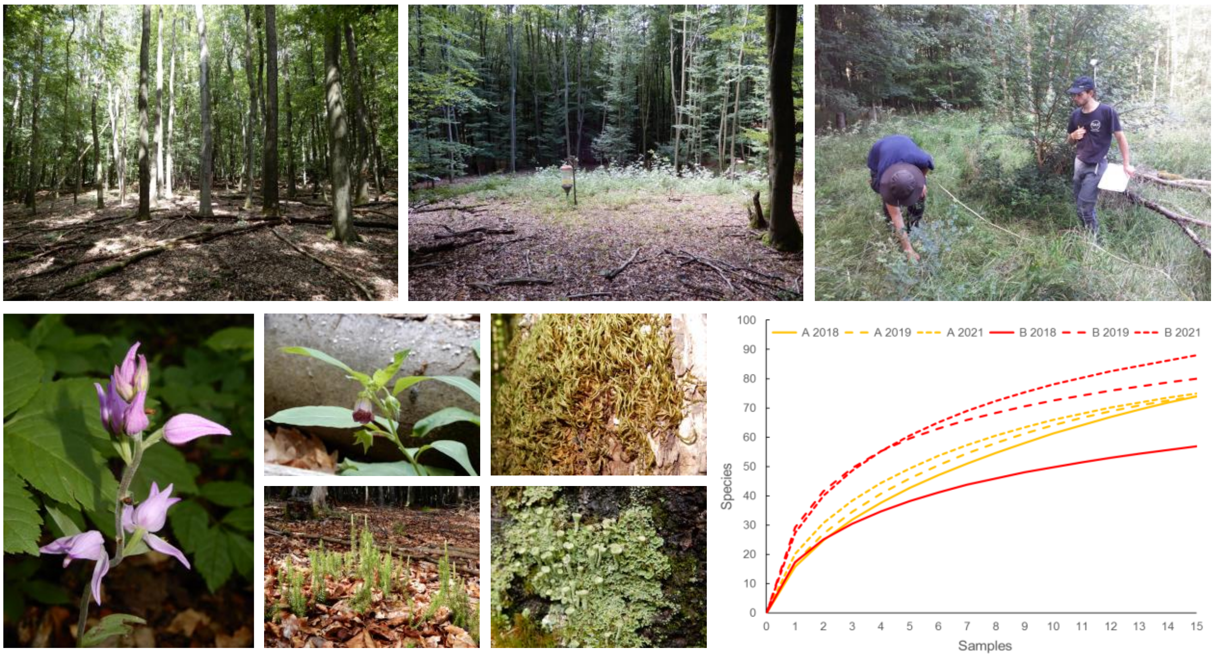


Fig. 2: Upper row: Example of control patch (left) and ESBC treatment patch (centre) in the Saarland site, vegetation sampling in Sailershausen, June 2021 (right). Bottom row: Example species from the study sites: *Cephalanthera rubra*, *Atropa belladonna*, *Lycopodium annotinum*, *Leucodon sciuroides*, *Cladonia pyxidata* (photos: S Dittrich). Bottom right: sample rarefaction of herb layer data in the districts A (control) and B (ESBC treatments), university forest Sailershausen.

1.2 Project-related publications

1. Baumann M, Dittrich S, Körner M, Krause S, **von Oheimb G** (2021) Temporal changes in the ground vegetation in spruce forests in the Erzgebirge (Ore Mountains) – bryophytes are better indicators of the impact of liming and of sulphur and nitrogen deposition than the herb layer. Applied Vegetation Science 24: e12598.
2. Brunet J, **von Oheimb G** (1998) Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology 86:429-438.
3. Bu WS, Liu XJ, Schmid B, Li Y, Härdtle W, **von Oheimb G**, Liang Y, Sun Z, Huang Y, Bruelheide H, Ma K (2017) Inter- and intraspecific variation in specific root length drives aboveground biodiversity effects in young experimental forest stands. Journal of Plant Ecology 10:158-169.
4. **Fichtner A**, Härdtle W, Li Y, Bruelheide H, Kunz M, **von Oheimb G** (2017) From competition to facilitation: How tree species respond to neighbourhood diversity. Ecology Letters 20:892-900.
5. **Fichtner A**, Härdtle W, Matthies D, Arnold V, Erfmeier A, Hemke T, Jansen D, Lütt S, Schmidt M, Sturm K, **von Oheimb G**, Ohse B (2020a) Safeguarding the rare woodland species *Gagea spathacea*: Understanding habitat requirements is not sufficient. Plant Species Biology 35:120-129.

6. Madsen CP, Kunz M, **von Oheimb G**, Hall J, Sinacore KA, Turner BJ, Potvin C (2021) Influence of neighbourhoods on the extent and compactness of tropical tree crowns and root systems. Trees – Structure and Functions 35:1673-1686.
7. Mausolf K, Härdtle W, Jansen K, Delory BM, Hertel D, Leuschner C, Temperton VM, **von Oheimb G**, **Fichtner A** (2018) Legacy effects of land-use modulate tree growth responses to climate extremes. Oecologia 187:825-837.
8. **von Oheimb G,** Härdtle W (2009) Selection harvest in temperate deciduous forests: impact on herb layer richness and composition. Biodiversity and Conservation 18:271-287.
9. Schuldt A, Ebeling A, Kunz M, Staab M, Guimarães-Steinicke C, Bachmann D, Buchmann N, Durka W, **Fichtner A**, Fornoff F, Härdtle W, Hertzog L, Klein AM, Roscher C, Schaller J, **von Oheimb G**, Weigelt A, Weisser W, Wirth C, Zhang J, Bruelheide H, Eisenhauer N (2019) Multiple plant diversity components drive consumer communities across ecosystems. Nature Communications 10:1460.

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

10. Bongers FJ, Schmid B, Bruelheide H, Bongers F, Li S, **von Oheimb G**, Li Y, Cheng A, Ma K, Liu X. Functional diversity effects on productivity increase with age in a forest biodiversity experiment. Nature Ecology & Evolution (accepted 6th September 2021)

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.2.3 Patents

Not applicable

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

Four years

2.2 Objectives

The main objective of this subproject is to investigate to which extent a higher spatial heterogeneity of temperate forests via ESBC treatments increases the β-diversity of non-tree vascular plants, terricolous bryophytes, and lichens in the understorey vegetation, and how this feedbacks to their above- and belowground functioning (biomass productivity). We also intent to analyse the effects of ESBC treatments on diversity pattern and community assembly processes of wood-dependent bryophytes and lichens. Based on the data of the preliminary surveys of these taxa (*see 1.1*) it became obvious, however, that community dynamics are slow, and we therefore plan to do in-depth investigations in the second phase. In preparation of phase 2, we devote one WP (WP3) to the re-survey of these taxa in order to extend our time series.

In particular, this subproject will test the following specific hypotheses:

Hypothesis 1*: The increase in spatial heterogeneity caused by ESBC treatments will enhance the taxonomic β-diversity of non-tree vascular plants, terricolous bryophytes, and lichens found in the forest understorey*. In addition, we expect the increase in spatial heterogeneity caused by ESBC treatments to enhance the functional β-diversity of forest herbs. With regard to functional diversity, this hypothesis will be tested using two complementary approaches: (1) measuring functional β-diversity using leaf and plant size-related traits (**WP1.1**), and (2) taking a whole-plant perspective when measuring functional β-diversity by also considering root traits (**WP1.2**). This two-step approach is justified by the fact that we expect the increase in light availability and heterogeneity in the forest understorey due to ESC treatments to affect more strongly leaf and plant size-related traits. In addition, measuring root traits will require more time than measuring leaf and plant size traits, making this two-step approach an adequate strategy for testing H1.

Hypothesis 2*: The increase in taxonomic and functional β-diversity positively affects the aboveground and belowground productivity of understorey plant communities at the district level.* To test this hypothesis we will harvest both aboveground and belowground plant biomass (**WP2**).

Data exchange and collaboration within the consortium

For the whole RU and syntheses in SP Z we provide data for vascular plants, terricolous bryophytes and lichens for all 234 patches for all years. Additionally, we will measure and compile traits of non-tree vascular plants to be added to the trait database (see also SP 9). Our subproject will measure *understorey primary aboveground and belowground productivity* as an important ecosystem function, contributing to the multifunctionality analysis. In preparation of phase 2, we will re-survey wood-dependent bryophytes and lichens at least two times in order to extend our time series data. We therefore provide data for the whole RU and syntheses in SP Z also for these taxa.

We will closely collaborate (Fig. 3) with SP 1 and SP 3, because we rely on structural measures of the overstorey to explain diversity patterns and productivity. We will provide important data for tree recruitment to SP 1 and for the analyses of aboveground arthropod and small mammal taxa and their ecosystem functions (SP 6, SP 9). We want to link data on understorey vegetation to soil biodiversity and functioning (SP 4, SP 7), decomposer diversity, decomposition rates and nutrient fluxes (SP 5) and volatilome analyses (SP 2). With our sampling of wood-dependent bryophytes and lichens we will jointly analyse the assembly processes on dead wood with SP 7. For analyses of multifunctionality and statistical analyses, we will closely collaborate with SP Z.

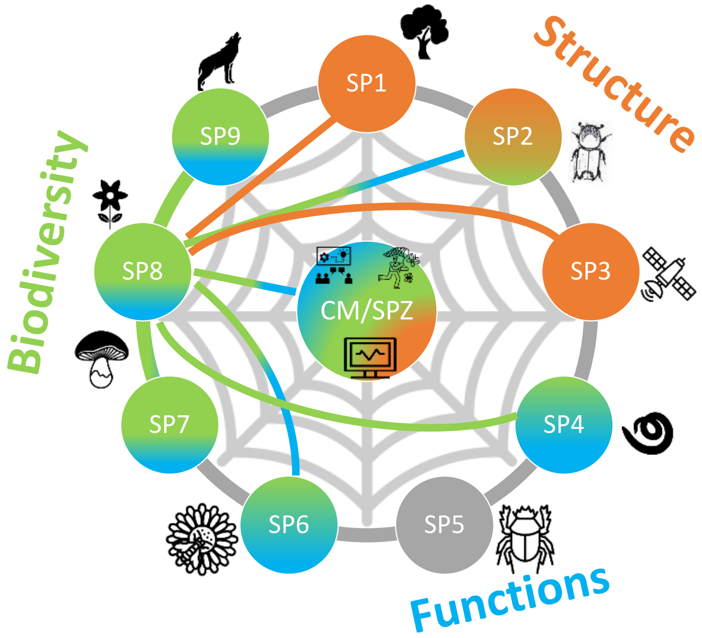


Fig. 3: Close cooperation of SP 8 with other subprojects, the colour of arrows indicate the type of data exchanged; green: species data, blue: functions, brown: structure.

2.3 Work programme including proposed research methods

WP1.1: Taxonomic and aboveground functional β-diversity of understorey plant communities

In this work package, **we aim to investigate if the increased spatial heterogeneity caused by ESBC treatments led to an increase in taxonomic and <u>aboveground</u> functional β-diversity of the understorey vegetation at the district level**. To achieve this, WP1.1 consists of two tasks: continuation of the vegetation sampling for the taxonomic diversity analysis and measurement of functional traits for the functional diversity analysis.

In all patches of the 11 sites, we will continue to record the understorey vegetation in the ESBC-treated districts on an annual basis using the methods described above (preliminary work, *1.1*). In the course of the first phase of the RU we will then have a time series of up to seven years (intensive sites, including one survey before the treatments) and up to nine years (extensive sites, data only from after the treatments) for these districts. After establishment of the 11 control districts, we will expand the vegetation sampling accordingly. At each subplot (see section preliminary work), photosynthetically active radiation (PAR) will be measured annually at 1.3 m above ground using light sensors and hemispherical photos. Data on chemical soil properties, air temperature and relative humidity will be used from SP Z.

At each of the 11 sites, functional β-diversity will be measured in control and ESBC-treated districts. To do this, our strategy will rely on the following principle: measuring a small number of key functional traits that are associated with major axes of variation in plant form and function on 5 to 10 individuals per species and per patch across all experimental sites. This strategy has two main advantages. First, measuring only a small set of well-documented functional traits will allow us to measure trait values on a large number of species within and across sites, which is essential to accurately describe changes in the functional composition of understorey plant communities due to ESBC treatments. It will also benefit the scientific community by enriching trait databases with trait values measured on forest herbs across Germany (Iversen et al. 2017; Kattge et al. 2020; Guerrero-Ramírez et al. 2021). Second, measuring traits on several individuals per species and per patch will allow us to explicitly consider intraspecific trait variability in our functional diversity assessment, which is an important innovation of our subproject.

Considering the large number of species found in the understorey of our forest patches (~250 vascular plant species expected in the herb layer across the 11 districts with ESBC treatments), we will measure trait values on species that altogether represent at least 90% of the ground cover (Chelli et al. 2021). This means that trait values will not be measured on rare species, whose low abundance in the forest understorey makes them unlikely to contribute strongly to differences in functional diversity between forest patches. Furthermore, following Vanneste et al. (2019) and Maes et al. (2020), we will not measure traits on trees, large shrubs and non-seed plants such as ferns, thus focusing our functional diversity assessment on herbaceous species and dwarf shrubs. There are two main reasons for this: (1) focusing on species that remain structurally part of the understorey throughout their life cycles, and (2) avoiding bias in the calculation of trait statistics and functional diversity metrics (excluding trees, large shrubs and non-seed plants, the current data set comprises ~200 plant species, the majority of these being very rare). On each selected species, we will measure two leaf traits [leaf nitrogen concentration (N_{leaf}) and leaf mass per area (LMA)] and one whole-plant trait (plant height). These aboveground traits have been chosen because they are associated with two important axes of variation in plant form and function: (1) a conservation gradient ranging from acquisitive (high N_{leaf} and low LMA) to conservative species (low N_{leaf} and high LMA), and (2) a plant size gradient ranging from short to tall plants (Wright et al. 2004; Díaz et al. 2016; Weigelt et al. 2021). All traits will be measured by the doctoral researcher and a technician, supported by student helpers, using standardized methods (Pérez-Harguindeguy et al. 2013). Samples for these trait measurements will be collected at the intensive sites in June/July 2022, and in the extensive sites in June/July 2023. Plant height will be measured directly in the field. Depending on the plant species and their abundance in the forest understorey, between 2 to 4 young, undamaged, and healthy leaves will be collected from 5 to 10 individuals for leaf trait measurements. Leaf area will be determined using a leaf area meter (LI-COR, LI-3100) or by image analysis. After scanning, leaf samples will be dried in an oven and weighed. For each plant individual, LMA will be calculated as the ratio between leaf dry weight and leaf area. The C/N content of dried leaf samples will then be determined using an elemental analyser.

Data analysis: Leaf and plant size-related trait values will be used to measure functional diversity metrics at α- and β-scales. At the patch level (α-scale), functional diversity metrics (e.g., functional richness) will be calculated using probabilistic methods to capture intraspecific variability in trait values (Wong and Carmona 2021). At the district level (γ-scale), we will rely on an attribute-diversity approach to quantify and partition functional γ-diversity into α and β components (Chao et al. 2019). Importantly, this attribute-diversity approach has the potential to be extended to situations where trait values are available at the individual level (Chao et al. 2019), which will be important in the context of this subproject.

Output: Data on understorey vegetation and aboveground functional traits of vascular plants for all patches. Manuscript I on the effects of increased spatial heterogeneity caused by ESBC treatments on taxonomic and aboveground functional β-diversity of the understorey vegetation.

WP1.2: Whole-plant functional β-diversity of understorey plant communities

In this work package, **we aim to investigate if the increased spatial heterogeneity caused by ESBC treatments led to an increase in whole-plant functional β-diversity of the understorey vegetation at the γ-level**.

In comparison with WP1.1, our work in WP1.2 will aim to refine our functional diversity assessment of forest herbs by adopting a whole-plant perspective and including not only leaf and plant size traits, but also root traits. As opposed to leaf trait variation, which is mainly explained by one axis of variation ranging from acquisitive to conservative species (Wright et al. 2004, Díaz et al. 2016), most of the variation in fine root trait strategies in higher plants is explained by two orthogonal gradients constituting the root economics space: a root-fungi collaboration gradient and a fast-slow conservation gradient (Bergmann et al. 2020). Although the root conservation gradient is analogous to the one found in leaves and represents the usual trade-off observed between “fast” and “slow” return on investment (Bergmann et al. 2020; Weigelt et al. 2021), most of the fine root trait variation is in fact explained by a root collaboration gradient, along which species display resource uptake strategies ranging from “do-it-yourself” (DIY) to “outsourcing” (OUT) (Bergmann et al. 2020). DIY species mainly rely on their roots to take up soil resources. They do so by producing long but fine roots (high specific root length, low root diameter) allowing for efficient exploration of the soil environment. OUT plant species, however, tend to rely more on symbiotic associations with e.g. arbuscular mycorrhiza to explore the soil and take up resources. OUT species build shorter but thicker roots that are able to support a higher number of fungal associations (Ma et al. 2018; McCormack and Iversen 2019; Bergmann et al. 2020).

In addition to the two major axes of variation considered in WP1.1, namely a conservation gradient from acquisitive to conservative species and a plant size gradient from short to tall species, the adoption of a whole-plant approach in WP1.2 will provide us with a unique opportunity: explicitly considering the root-fungi collaboration gradient as a third major axis of variation in plant form and function when assessing potential shifts in the functional β-diversity of forest herbs due to ESBC treatments.

To do this, three core root traits delimiting the root economics space will be added to the list of traits measured in WP1.1: specific root length (SRL), average root diameter (D), and root tissue density (RTD). These traits will be measured by the doctoral researcher and a technician, supported by student helpers, on the same plants as the ones collected in WP1.1, using standardized protocols (Freschet et al. 2020). Considering the strong positive correlation between N concentration in leaves and roots (Weigelt et al. 2021), we decided not to measure root N concentration in this subproject in order to keep the number of samples to be analyzed with an elemental analyser realistic. Root systems of individual plants will be carefully extracted from the soil, washed under running water, and stored at 4°C in a 60% (v/v) ethanol solution. Morphological root traits (SRL, D, RTD) will be measured by scanning a representative subsample of fine roots at a high resolution using a flatbed scanner. Scanned and non-scanned roots will be stored separately, dried in an oven, and weighed. Root images will be analysed with RhizoVision Explorer (Seethepalli et al. 2021). Specific root length (total root length divided by root dry weight), root tissue density (root dry weight divided by total root volume), and average root diameter will be computed based on the information provided by RhizoVision Explorer.

Data analysis: Leaf, root, and plant size-related trait values will be used to measure functional diversity metrics at α- and β-scales, using the same methods as in WP1.1.

Output: Data on belowground functional traits of vascular plants for all patches. Manuscript II on the impact of increased spatial heterogeneity caused by ESBC treatments on whole-plant functional β-diversity of the understorey vegetation.

WP2: β-diversity – productivity relationships in understorey plant communities

In this work package, **we aim to investigate if an increase in taxonomic and/or functional β-diversity of forest herbs positively affects the aboveground and belowground productivity of the understorey vegetation**.

In each forest patch, the aboveground productivity of the understorey vegetation (in g/m^2) will be assessed every second year by harvesting plant biomass in three 1-m^2 and randomly positioned quadrats. In each quadrat, trees (<1 m in height), shrubs, herbaceous species, and terricolous bryophytes and lichens will be harvested separately, oven-dried (65°C for 72 h), and weighed.

After harvesting the aboveground biomass, three soil cores (up to 30 cm depth) will be collected in each quadrat. Soil cores will be divided into three different layers (0-10, 10-20, 20-30 cm). After pooling the cores collected in each quadrat by depth, roots will be extracted from the soil and washed. Roots of woody and herbaceous species will then be sorted, oven-dried (65°C for 72 h), and weighed. Root biomass data measured in different soil layers will be used to estimate the belowground productivity of forest patches (in g/cm^3).

Data analysis: The above- and belowground productivity of understorey plant communities at the district level (γ-scale) will be estimated by averaging the shoot and root productivity, respectively, measured across forest patches (α-scale) in this WP. These γ-productivity measures (response variables), as well as taxonomic and functional diversity data collected in WP1.1 and WP1.2 (predictor variables), will be used to investigate the directionality and strength of the β-diversity – γ-productivity relationship in understorey plant communities using statistical modelling (e.g., linear mixed-effect models). The mechanistic links hypothesized in this subproject between ESBC treatments, increased spatial heterogeneity in abiotic conditions, increased taxonomic and/or functional diversity of forest herbs, and increased shoot and root productivity of understorey plant communities at the district scale, will be tested using structural equation modelling.

Output: Data on aboveground and belowground biomass of the understorey vegetation on all patches. Manuscript III on the effect of taxonomic and functional β-diversity of forest herbs on the aboveground and belowground productivity of the understorey vegetation.

WP3: Wood-dependent bryophytes and lichens

As mentioned above, we will focus our main analyses on data from WP1 and WP2. Due to our previous sampling activities we are, however, able to provide data on wood-dependent bryophytes and lichens for the whole RU and syntheses in SPZ. In order to extend our time series and in preparation of phase 2, we will re-survey these taxa at least two times (autumn 2023 and 2025) using the methods as described above (preliminary work, *1.1*).

Output: Patch-species abundance data on wood-dependent bryophytes and lichens. Joint analysis and manuscript preparation with SP 7 on species assembly processes on dead wood.

Statistical analyses

The statistical analyses of SP 8 will be conducted by the doctoral researcher under supervision of G von Oheimb and A Fichtner, and in close collaboration with the RU Team in SP Z including the Mercator Fellows and collaborators and particularly with support by the *statistics and synthesis - Postdoc* in SP Z.

Table 1: Overview of work programme and schedule. The understorey vegetation surveys and PAR measurements will be continued in 2024 and 2015 to provide data for the whole RU and syntheses in SP Z and to extend the time series in preparation of phase 2.

	2022									2023												2024												2025												2026		
Technician (duration)	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨												
WP1.1 - Taxonomic and aboveground functional β-diversity of understorey plant communities																																																
Compilation of vegetation survey data from previous years	▨	▨																																														
Understorey vegetation survey	▨		▨	▨	▨								▨		▨	▨	▨								▨		▨	▨	▨								▨		▨	▨	▨							
PAR measurements			▨	▨	▨										▨	▨	▨										▨	▨	▨										▨	▨	▨							
Sampling of aboveground traits			▨	▨											▨	▨																																
Lab measurements of aboveground traits					▨	▨	▨	▨									▨	▨	▨	▨																												
Statistical analyses and writing of manuscript I																					▨	▨	▨	▨	▨	▨																						
WP1.2 - Whole-plant functional β-diversity of understorey plant communities																																																
Root sampling to measure belowground traits			▨	▨											▨	▨																																
Lab measurements of belowground traits									▨	▨	▨	▨	▨	▨							▨	▨	▨	▨	▨	▨																						
Statistical analyses and writing of manuscript II																															▨	▨	▨	▨	▨													
WP2- β-diversity – productivity relationships in understorey plant communities																																																
Field sampling of above- and belowground plant biomass			▨	▨	▨																						▨	▨	▨																			
Lab analyses						▨	▨	▨																						▨	▨	▨	▨	▨	▨	▨												
Statistical analyses and writing of manuscript III																																					▨	▨			▨	▨						
WP3 - Wood-dependent bryophytes and lichens																																																
Survey of wood-dependent bryophytes and lichens																		▨	▨																							▨	▨					
Compilation of WP3 data with data from SP 7																			▨	▨																								▨	▨			
Manuscript writing with SP 7																																													▨	▨	▨	
Report																																																
Writing report																																															▨	▨

3 Bibliography concerning the state of the art, the research objectives, and the work programme

Aude E, Poulsen RS (2000) Influence of management on the species composition of epiphytic cryptogams in Danish *Fagus* forests. Applied Vegetation Science 3:81-88

Axmanová I, Chytrý M, Zelený D, Li CF, Vymazalová M, Danihelka J, … Diekmann M (2012) The species richness productivity relationship in the herb layer of European deciduous forests. Global Ecology and Biogeography 21:657-667

Axmanová I, Chytrý M, Danihelka J, Lustyk P, Kočí M, Kubešová, S, … Gogoleva PA (2013) Plant species richness-productivity relationships in a low-productive boreal region. Plant Ecology 214:207-219

Baumann M, Dittrich S, Körner M, Krause S, von Oheimb G (2021) Temporal changes in the ground vegetation in spruce forests in the Erzgebirge (Ore Mountains) – bryophytes are better indicators of the impact of liming and of sulphur and nitrogen deposition than the herb layer. Applied Vegetation Science 24:e12598

Bergmann J, Weigelt A, van der Plas F, Laughlin DC, Kuyper TW, Guerrero-Ramirez N, … Mommer L (2020) The fungal collaboration gradient dominates the root economics space in plants. Science Advances 6:eaba3756

Bernhardt-Römermann M, Baeten L, Craven D, De Frenne P, Hedl R, Lenoir J, … Verheyen K (2015) Drivers of temporal changes in temperate forest plant diversity vary across spatial scales. Global Change Biology 21:3726-3737

Blondeel H, Perring MP, Depauw L, De Lombaerde E, Landuyt D, De Frenne P, Verheyen K (2020a) Light and warming drive forest understorey community development in different environments. Global Change Biology 26:1681-1696

Blondeel H, Perring MP, De Lombarde E, Depauw L, Landuyt D, Govaert S, … Verheyen K (2020b) Individualistic responses of forest herb traits to environmental change. Plant Biology 22:601-614

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, … Vasseur D (2011) Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26:183-192

Bongers FJ, Schmid B, Sun Z, Li Y, Härdtle W, von Oheimb G, Li Y, Li S, Staab M, Ma K, Liu X (2020) Growth–trait relationships in subtropical forest are stronger at higher diversity. Journal of Ecology 108:256-266

Bongers FJ, Schmid B, Bruelheide H, Bongers F, Li S, von Oheimb G, Li Y, Cheng A, Ma K, Liu X. Functional diversity effects on productivity increase with age in a forest biodiversity experiment. Nature Ecology & Evolution in press

Bruelheide H, Nadrowski K, Assmann T, Bauhus J, Both S, ... Schmid B (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. Methods in Ecology and Evolution 5:74-89

Brunet J, von Oheimb G (1998) Migration of vascular plants to secondary woodlands in southern Sweden. Journal of Ecology 86:429-438

Bu WS, Liu XJ, Schmid B, Li Y, Härdtle W, von Oheimb G, Liang Y, Sun Z, Huang Y, Bruelheide H, Ma K (2017) Inter- and intraspecific variation in specific root length drives aboveground biodiversity effects in young experimental forest stands. Journal of Plant Ecology 10:158-169

Burrascano S, Ripullone F, Bernardo L, Borghetti M, Carli E, Colangelo M, … Blasi C (2018) It’s a long way to the top: Plant species diversity in the transition from managed to old-growth forests. Journal Vegetation Science 29:98-109

Carlucci MB, Debastiani VJ, Pillar VD, Duarte LDS (2015) Between- and within-species trait variability and the assembly of sapling communities in forest patches. Journal of Vegetation Science 26:21-31

Chao A, Chiu C-H, Villéger S, Sun IF, Thorn S, Lin YC, Chiang JM, Sherwin W (2019) An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecological Monographs 89:e01343

Chelli S, Simonetti E, Wellstein C, Campetella G, Carnicelli S, Andreetta A, Giorgini D, Puletti N, Bartha S, Canullo R (2019) Effects of climate, soil, forest structure and land use on the functional composition of the understorey in Italian forests. Journal of Vegetation Science 30:1110-1121

Chelli S, Ottaviani G, Simonetti E, Campetella G, Wellstein C, Bartha S, Cervellini M, Canullo R (2021) Intraspecific variability of specific leaf area fosters the persistence of understorey specialists across a light availability gradient. Plant Biology 23:212-216

Cubino JP, Biurrun I, Bonari G, Braslavskaya T, Font X, Jandt U, … Chytrý M (2021) The leaf economic and plant size spectra of European forest understory vegetation. Ecography 44:1311-1324

De Frenne P, Rodriguez-Sanchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, …Verheyen K (2013) Microclimate moderates plant responses to macroclimate warming. Proceedings of the National Academy of Sciences of the United States of America, 110:18561-18565

De Frenne P, Rodríguez-Sánchez F, De Schrijver A, Coomes DA, Hermy M, Vangansbeke P, Verheyen K (2015) Light accelerates plant responses to warming. Nature Plants 1:15110

De Pauw K, Meeussen C, Govaert S, Sanczuk P, Vanneste T, Bernhardt-Römermann M, … De Frenne P (2021) Taxonomic, phylogenetic and functional diversity of understorey plants respond differently to environmental conditions in European forest edges. Journal of Ecology 109:2629-2648

Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Wattez-Franger A, … Bardat J (2004) Plant diversity in a managed temperate deciduous forest: Understorey response to two silvicultural systems. Journal of Applied Ecology 41:1065-1079

Díaz S, Cabido M (2001) Vive la différence: Plant functional diversity matters to ecosystem processes. Trends in Ecology and Evolution 16:646-655

Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, … Gorné LD (2016) The global spectrum of plant form and function. Nature 529:167-171

Dittrich S, Hauck M, Jacob M, Bade C, Rommerskirchen A, Leuschner C (2013) Response of epiphyte and ground vegetation diversity to natural age dynamics in a Central European mountain spruce forest. Journal of Vegetation Science 24:675–687

Dittrich S, Jacob M, Bade C, Leuschner C, Hauck M (2014) The significance of deadwood for total bryophyte, lichen, and vascular plant diversity in an old-growth spruce forest. Plant Ecology 215:1123-1137

Dittrich S, Leuschner C, Hauck M (2016) Change in the bryophyte diversity and species composition of Central European temperate broad-leaved forests since the late nineteenth century. Biodiversity and Conservation 25:2071-2091

Dittrich S, Thiem E, Albrecht BM, von Oheimb G (2021) Cryptogamic epiphytes and microhabitat diversity on non-native green ash (*Fraxinus pennsylvanica* Marsch., Oleaceae) in urban habitats. iForest 14:393-399

Dormann CF, Bagnara M, Boch S, Hinderling J, Janeiro-Otero A, Schäfer D, Schall P, Hartig F (2020) Plant species richness increases with light availability, but not variability, in temperate forests understorey. BMC Ecology 20:43

Dziedek C, Härdtle W, von Oheimb G, Fichtner A (2016) Nitrogen addition enhances drought sensitivity of young deciduous tree species. Frontiers in Plant Science 7:1100

Fajardo A, Siefert A (2018) Intraspecific trait variation and the leaf economics spectrum across resource gradients and levels of organization. Ecology 99:1024-1030

Fichtner A, Sturm K, Rickert C, Härdtle W, Schrautzer J (2012) Competition response of European beech *Fagus sylvatica* L. varies with tree size and abiotic stress: minimizing anthropogenic disturbances in forests. Journal of Applied Ecology 49:1306-1315

Fichtner A, Härdtle W, Li Y, Bruelheide H, Kunz M, von Oheimb G (2017) From competition to facilitation: How tree species respond to neighbourhood diversity. Ecology Letters 20:892-900

Fichtner A, Härdtle W, Bruelheide H, Kunz M, Li Y, von Oheimb G (2018b) Neighbourhood interactions drive overyielding in mixed-species tree communities. Nature Communications 9:1144

Fichtner A, Matthies D, Armbrust M, Jansen D, Sturm K, Walmsley D, von Oheimb G, Härdtle W (2018a) Nitrogen cycling and storage in *Gagea spathacea* (Liliaceae) – ecological insights for protecting a rare woodland species. Plant Ecology 219:1117-1126

Fichtner A, Härdtle W, Matthies D, Arnold V, Erfmeier A, Hemke T, Jansen D, Lütt S, Schmidt M, Sturm K, von Oheimb G, Ohse B (2020a) Safeguarding the rare woodland species *Gagea spathacea*: Understanding habitat requirements is not sufficient. Plant Species Biology 35:120-129

Fichtner A, Schnabel F, Bruelheide H, Härdtle W, Kunz M, Mausolf K, Schuldt A, von Oheimb G (2020b) Neighbourhood diversity mitigates drought impacts on tree growth. Journal of Ecology 108:865-875

Freschet G, Pagès L, Iversen C, Comas L, Rewald B, Roumet C, … McCormack M (2020) A starting guide to root ecology: strengthening ecological concepts and standardizing root classification, sampling, processing and trait measurements. hal-02918834

Friedel A, von Oheimb G, Dengler J, Härdtle W (2006) Species diversity and species composition of epiphytic bryophytes and lichens – a comparison of managed and unmanaged beech forests in NE Germany. Feddes Repertorium 117:172-185

Friedrich U, von Oheimb G, Dziedek C, Kriebitzsch WU, Selbmann K, Härdtle W (2011) Mechanisms of *Molinia caerulea* encroachment in dry heathland ecosystems with chronic nitrogen inputs: the importance of the pioneer phase. Environmental Pollution 159:3553-3559

Fritz Ö, Niklasson M, Churski M (2009) Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. Applied Vegetation Science 12:93-106

Gilliam FS (2007) The ecological significance of the herbaceous layer in temperate forest ecosystems. BioScience 57:845-858

Govaert S, Vangansbeke P, Blondeel H, Steppe K, Verheyen K, De Frenne P (2021) Rapid thermophilization of understorey plant communities in a 9 year-long temperate forest experiment. Journal of Ecology 109:2434-2447

Guerrero-Ramírez NR, Mommer L, Freschet GT, Iversen CM, McCormack ML, Kattge J, … Weigelt A (2021) Global root traits (GRooT) database. Global Ecology Biogeography 30:25-37

Guillemot J, Kunz M, Schnabel F, Fichtner A, Madsen CP, Gebauer T, Härdtle W, von Oheimb G, Potvin C (2020) Neighbourhood-mediated shifts in tree biomass allocation drive overyielding in tropical species mixtures. New Phytologist 228:1256-1268

Härdtle W, von Oheimb G, Westphal C (2003) The effect of light and soil conditions on the species richness of the ground vegetation of deciduous forests in northern Germany (Schleswig-Holstein). Forest Ecology and Management 182:327-338

Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: A review of past land-use effects on forest plant species composition and diversity. In Nakashizuka T (ed.) Sustainability and diversity of forest ecosystems Springer, Tokyo, Japan, pp 361-371

Huang Y, Chen Y, Castro-Izaguirre N, Baruffol M, Brezzi M, Lang A, Li Y, Härdtle W, von Oheimb G, ... Schmid B (2018) Impacts of species richness on productivity in a large-scale subtropical forest experiment. Science 362: 80-83

Iversen CM, McCormack ML, Powell AS, Blackwood CB, Freschet T, Kattge J, … Violle C (2017) A global fine-root ecology database to address below-ground challenges in plant ecology. New Phytologist 215:15-26

Katabuchi M, Wright SJ, Swenson NG, Feeley KJ, Condit R, Hubbell SP, Davies SJ (2017) Contrasting outcomes of species- and community-level analyses of the temporal consistency of functional composition. Ecology 98:2273-2280

Kattge J, Bönisch G, Díaz S, Lavorel S, Prentice IC, Leadley P, … Wirth C (2020) TRY plant trait database - enhanced coverage and open access. Global Change Biology 26:119-188

Kaufmann S, Hauck M, Leuschner C (2018) Effects of natural forest dynamics on vascular plant, bryophyte, and lichen diversity in primeval *Fagus sylvatica* forests and comparison with production forests. Journal of Ecology 106:2421-2434

Kovács B, Tinya F, Ódor P (2017) Stand structural drivers of microclimate in mature temperate mixed forests. Agricultural and Forest Meteorology 234:11-21

Kriebitzsch WU, Bültmann H, von Oheimb G, Schmidt M, Thiel H, Ewald J (2013) Forest-specific diversity of vascular plants, bryophytes and lichens. In Kraus D, Krumm F (eds) Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, pp 158-169

Kröber W, Li Y, Härdtle W, Ma K, Schmid B, Schmidt K, Scholten T, Seidler G, von Oheimb G, Welk E, Wirth C, Bruelheide H (2015) Early subtropical forest growth is driven by community mean trait values and functional diversity rather than the abiotic environment. Ecology and Evolution 5:3541-3556

Kunz M, Fichtner A, Härdtle W, Raumonen P, Bruelheide H, von Oheimb G (2019) Neighbour species richness and local structural variability modulate aboveground allocation patterns and crown morphology of individual trees. Ecology Letters 22:2130-2140

Landuyt D, De Lombaerde E, Perring MP, Hertzog LR, Ampoorter E, Maes S, de Frenne P, Ma S, Proesmans W, Blondeel H, Sercu BK, Wang B, Wasof S, Verheyen K (2019) The functional role of temperate forest understorey vegetation in a changing world. Global Change Biology 25:3625-3641

Landuyt D, Maes SL, Depauw L, Ampoorter E, Blondeel H, Perring MP, … Verheyen K (2020) Drivers of above-ground understorey biomass and nutrient stocks in temperate deciduous forests. Journal of Ecology 108:982-997

Lang AC, Härdtle W, Baruffol M, Böhnke M, Bruelheide H, Schmid B, von Wehrden H, von Oheimb G (2012) Mechanisms promoting tree species coexistence: Experimental evidence with saplings of subtropical forest ecosystems of China. Journal of Vegetation Science 23:837-846

Lang AC, von Oheimb G, Scherer-Lorenzen M, Bo Y, Trogisch S, Ma K, Härdtle W (2014) Mixed afforestations of young subtropical trees promote nitrogen acquisition and retention. Journal of Applied Ecology 51:224-233

Laughlin DC, Moore MM, Fulé PZ (2011) A century of increasing pine density and associated shifts in understory plant strategies. Ecology 92:556-561

Ma Z, Guo D, Xu X, Lu M, Bardgett RD, Eissenstat, McCormack ML, Hedin LO (2018) Evolutionary history resolves global organization of root functional traits. Nature 555:94-97

Madsen CP, Kunz M, von Oheimb G, Hall J, Sinacore KA, Turner BJ, Potvin C (2021) Influence of neighbourhoods on the extent and compactness of tropical tree crowns and root systems. Trees – Structure and Functions 35:1673-1686

Maes SL, Perring MP, Depauw L, Bernhardt-Römermann M, Blondeel H, Brümelis G, … Verheyen K (2020) Plant functional trait response to environmental drivers across European temperate forest understorey communities. Plant Biology 22:410-424

Mausolf K, Härdtle W, Jansen K, Delory BM, Hertel D, Leuschner C, Temperton VM, von Oheimb G, Fichtner A (2018) Legacy effects of land-use modulate tree growth responses to climate extremes. Oecologia 187:825-837

McCormack ML, Iversen CM (2019) Physical and Functional Constraints on Viable Belowground Acquisition Strategies. Frontiers in Plant Science 10:1215

Meyer-Grünefeldt M, Calvo L, Marcos E, von Oheimb G, Härdtle W (2015) Impacts of drought and nitrogen addition on *Calluna*-heathlands differ with plant life-history stage. Journal of Ecology 103:1141-1152

Ódor P, Heilmann-Clausen J, Christensen M, Aude E, van Dort K, Piltaver W, … Grebenc T (2006) Diversity of dead wood inhabiting fungi and bryophytes in semi-natural beech forests in Europe. Biological Conservation 131:58-71

von Oheimb G, Brunet J (2007) Dalby Söderskog revisited: long-term vegetation changes in a south Swedish deciduous forest. Acta Oecologica 31:229-242

von Oheimb G, Friedel A, Bertsch A, Härdtle W (2007) The effects of windthrow on plant species richness in a Central European beech forest. Plant Ecology 191:47-65

von Oheimb G, Härdtle W (2009) Selection harvest in temperate deciduous forests: impact on herb layer richness and composition. Biodiversity and Conservation 18:271-287

von Oheimb G, Lang AC, Bruelheide H, Forrester DI, Wäsche I. Yu M, Härdtle W (2011) Individual-tree radial growth in a subtropical broad-leaved forest: the role of local neighbourhood competition. Forest Ecology and Management 261:499-507.

Pérez-Harguindeguy N, Díaz S, Garnier E, Lavorel S, Poorter H, Jaureguiberry P, … Cornelissen JHC (2013) New handbook for standardized measurement of plant functional traits worldwide. Australian Journal of Botany 61:167-234

Perring MP, Bernhardt-Römermann M, Baeten L, Midolo G, Blondeel H, Depauw L, … Verheyen K (2018) Global environmental change effects on plant community composition trajectories depend upon management legacies. Global Change Biology 24:1722-1740

Petzold J, Dittrich S, Fichtner A, Härdtle W, von Oheimb G (2018) Effects of forest management intensity on herb layer plant diversity and composition of deciduous forest communities in Northern Germany. Tuexenia 38:79-96

Schall P, Heinrichs S, Ammer C, Ayasse M, Boch S, Buscot F, … Gossner MM (2020) Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems? Journal of Applied Ecology 57:1363-1375

Schuldt A, Assmann T, Brezzi M, Buscot F, Eichenberg D, ... Bruelheide H (2018) Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications 9:2989

Schuldt A, Ebeling A, Kunz M, Staab M, Guimarães-Steinicke C, ... Eisenhauer N (2019) Multiple plant diversity components drive consumer communities across ecosystems. Nature Communications 10:1460

Seethepalli A, Dhakal K, Griffiths M, Guo H, Freschet GT, York LM (2021) RhizoVision Explorer: Open-source software for root image analysis and measurement standardization. bioRxiv 2021.04.11.439359

Trogisch S, Schuldt A, Bauhus J, Blum JA, Both S, ... Bruelheide H (2017) Toward a methodical framework for comprehensively assessing forest multifunctionality. Ecology and Evolution 7:10652-10674

Vanneste T, Valdés A, Verheyen K, Perring M, Bernhardt-Römermann M, Andrieu E, … De Frenne P (2019) Functional trait variation of forest understorey plant communities across Europe. Basic and Applied Ecology 34:1-14

Wasof S, Lenoir J, Hattab T, Jamoneau A, Gallet-Moron E, Ampoorter E, … Decocq G (2018) Dominance of individual plant species is more important than diversity in explaining plant biomass in the forest understorey. Journal of Vegetation Science 29:521-531

Weigelt A, Mommer L, Andraczek K, Iversen CM, Bergmann J, Bruelheide H, … McCormack ML (2021) An integrated framework of plant form and function: the belowground perspective. New Phytologist 232:42-59

Wong MKL, Carmona CP (2021) Including intraspecific trait variability to avoid distortion of functional diversity and ecological inference: Lessons from natural assemblages. Methods in Ecology and Evolution 12:946-957

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, … Villar R (2004) The worldwide leaf economics spectrum. Nature 428:821-827

Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, … Coomes D (2020) Forest microclimate dynamics drive plant responses to warming. Science 368:772-775

Zhang Y, Chen HYH, Taylor AR (2017) Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees. Functional Ecology 31:419-426

4 Relevance of sex, gender and/or diversity

The participating institutions are committed to the goal of actively supporting career perspectives of female scientists; diversity and internationalization in academia (see *2.5 Measures to advance research careers* in the General Introduction). The applicants will make their graduate students aware of the support and workshops provided in their institutions and by this research unit (*3.2.4 Gender Equality Measures in Research Networks Module*).

Project Description – Project Proposals

Prof. Dr. Jörg Müller, Würzburg (PI)
Assoc. Prof. Dr. Simon Thorn, Würzburg (PI)
Prof. Dr. Wolfgang Weisser, München (Co-PI)

SP9: Multifunctionality and the biodiversity of higher trophic levels

---

Project Description

1 Starting Point

1.1 State of the art and preliminary work

Interactions between trophic levels are fundamental for community assembly in ecosystems. Nevertheless, many existing ecological studies are restricted to interactions within a single trophic level. This restriction has its roots in Tansley (1935), who defined a "horizontal community" as organisms with similar habits and within one trophic level, assuming that interactions within this trophic level are most crucial for the assembly of local communities. In contrast, food web ecology specifically considers interactions between different trophic levels, but is still mainly restricted to particular interactions (e.g. plant-pollinator interactions) or to particular species. In addition, studies often focus either on “brown” (dead organic matter as energy source) or “green” food webs (living plants) rather than considering these two food webs simultaneously (Benbow et al. 2019). Therefore, Thompson et al. (2012) proposed a framework linking concepts of community ecology and ecosystem ecology via food web theory, to improve studies on the relationship between biodiversity and ecosystem functions (BEF, see also Hines et al. 2015). The lack of studies considering interactions between trophic levels is also apparent in BEF research. Some early studies considered several trophic levels (Naeem et al. 1994) and there are also more recent studies considering several trophic levels (Scherber et al. 2010; Tilman et al. 2014). However, a literature review about the number of trophic levels considered in BEF studies (Seibold et al. 2018) shows that only 14% of the studies adopted a multitrophic perspective, of which the vast majority are reviews or meta-analyses (e.g. Lefcheck et al. 2015) of studies which themselves are restricted to single, specific trophic levels. This is despite the fact that studies such as Soliveres et al. (2016) have shown that multitrophic richness had a stronger positive influence on ecosystem functions in grassland than any single richness, although even the higher trophic levels, i.e. 2^{nd} order consumers and predators (Fig. 1), were not taken into account. However, higher trophic levels have the potential to strongly affect community assembly and ecosystem processes. A meta-analysis has shown that both vertebrates and insects have strong top-down effects on phytophagous insects by influencing their survival (Vidal and Murphy 2018). This is in line with findings on the effect of bat exclusions on arthropod densities in tree crowns (Kalka et al. 2008). Thus, repeated calls for more multitrophic community analyses and linkages with food web concepts also in biodiversity ecosystem function research are not surprising (Hines et al. 2019; Hines et al. 2015; Seibold et al. 2018; Thompson et al. 2012).

Another dimension that has enriched BEF research is the consideration not only of taxonomic diversity but also of functional or phylogenetic diversity. Tilman et al. (1997) showed in grassland experiments that vegetation’s functional composition and functional diversity are the principal factors explaining ecosystem functions. Similarly, Schuldt et al. (2018) showed functional-trait diversity to be superior to tree species richness explaining individual functions and multifunctionality. Because many traits have a phylogenetic signal, Srivastava et al. (2012) advocated for an incorporation of phylogenetic diversity in BEF studies. This is particularly promising for describing the ecological difference in those groups with high number of species, but limited availability of trait information, as in many insects or microbes (Cadotte et al. 2013).

BEF research frameworks range from small-grain highly controlled BEF studies, to small grain observational studies to large grain uncontrolled studies (Manning et al. 2019). In all of them, a number of practical obstacles can prevent a consideration of some and particular higher trophic levels. These include a sufficient grain size for higher trophic levels as birds particularly in small grain studies. A second challenge is the standardized recording of highly mobile or difficult-to-record species groups such as bats or birds. A third challenge are hyperdiverse species groups with incomplete identification keys, such as dipterans and hymenopterans, which include many functionally important species, e.g. parasitoids or pollinators, or even more challenging, the detection of fungi and bacteria in soil, wood, and air. In these areas, however, various methods have become available in recent years that allow the processing of large numbers of samples in manageable periods of time (see below), allowing for comprehensive analyses in ecological studies (e.g. Penone et al. 2019).

In SP9, we will use the experimental setting of the RU with extensive background information on environmental conditions, data on various ecosystem processes and data on other species groups, to study specifically the role of diversity of higher trophic levels and ecosystem functioning. We will focus specifically on well-selected representatives of higher trophic levels (see Fig. 1), use modern species identification techniques to close the knowledge gap for forests, and allow addressing the hypotheses of the research unit.

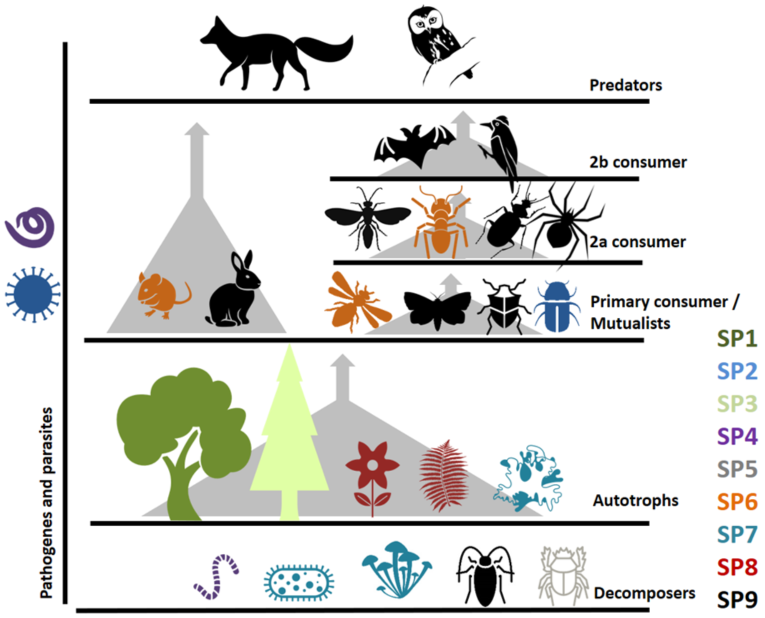


Fig. 1: Taxa within green and brown food webs included in this research unit. Icons symbolize the taxa of different trophic levels collected within the research unit, black icons indicate all taxa collected by SP9, and other colors indicate the contribution of other subprojects. Note the focus of the black icons in higher trophic levels.

In forests, biodiversity of different trophic levels promotes ecosystem functions (Mori et al. 2018; Ratcliffe et al. 2017). This is thought to be the result of three major mechanisms (see also Coordination Project). First, “biodiversity begets biodiversity” across trophic levels, e.g. diverse plant communities promote diversity of consumers, and these increase the diversity of predators (see red arrow in Fig. 2). Here, multifunctionality is finally determined by biodiversity effects on functions directly related to the respective trophic level (coloured arrows in Fig. 2) or by indirect effects (red arrows in Fig. 2), when e.g. functions of a higher/lower trophic level are affected by the diversity of lower/higher trophic levels (Schuldt et al. 2018). In SP9, we will focus on the propagating of biodiversity effects through the higher trophic levels and the direct effects in determining single functions and multifunctionality (Fig. 2).

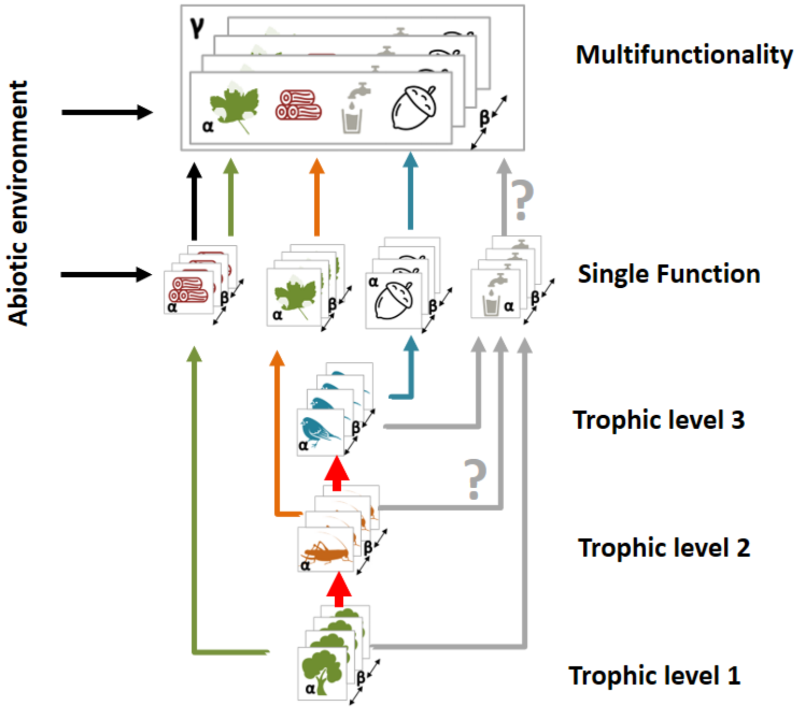


Fig. 2: Effect of α- and β-diversity of different trophic levels on α- and β-multifunctionality via directly related functions of the respective trophic level, e.g. when herbivore diversity affects herbivory resistance of plants (coloured arrows), via propagation across the food web (red arrows), and via indireclty related functions (gray arrows). In addition, variation in the environment can result in diversity independent effects on multifunctionality (black arrows).

Second, the role of ecological dissimilarity between species might determine the multifunctionality more than dissimilarity in taxonomic identity (Srivastava et al. 2012). In this case, functional and/or phylogenetic diversity measures can be more powerful in explaining ecosystem functions in forests than taxonomic diversity (Schuldt et al. 2018). Therefore, in SP 9, we will not only analyse the taxonomic diversity, but also functional and phylogenetic diversities of higher trophic level.

Third, the β-diversity of species rather than α-diversity may affect γ-diversity and γ-multifunctionality of the landscape scale. Here, the higher diversity in heterogeneous landscapes is often determined by the between patch diversity, as manipulated in our ESBC treated districts in comparison to control districts. The role of β-diversity on the multifunctionality of a landscape is unknown so far, and specifically for higher trophic levels. Moreover, if taxonomic or functional β-diversity of higher trophic levels are more relevant for ecosystem functioning is unknown. There have been several methodological developments in recent times, which allow quantifying taxonomic, functional and phylogenetic diversity measures on the β-diversity scale (Chao et al. 2017, 2019), promising for partitioning the different contributions of diversity, α and β, but also of taxonomic and functional/phylogenetic diversities of higher trophic levels on ecosystem functions. In SP9, we will study β-diversity of species of higher trophic levels in our sites with ESBC treatments and the control sites and link this to multifunctionality of these sites at the β- and γ-scale.

Preliminary work

The PIs have extensive experience in measuring biodiversity of higher trophic levels with different techniques, such as autonomous sound recorders, metabarcoding or camera trapping. Furthermore, they have built up an excellent network of taxonomists in charge of the identification of hyperdiverse taxa. W Weisser has contributed methods to quantify ecosystem functions (Meyer et al. 2015) also across large, forested landscapes (Soliveres et al. 2016).

J Müller and S Thorn have successfully tested insect trapping via Malaisetraps in forests (Kortmann et al. 2021b; Uhler et al. 2021), canopy fogging (Müller et al. 2018) and light trapping (Roth et al. 2021) to cover all three spatial dimensions of forests. Moreover, they have intensively tested rearing of standardized deadwood objects with subsequent metabarcoding and blasting against Central European libraries to identify species and important functional groups within arthropod communities (Hagge et al. 2019; Vogel et al. 2021). These initial studies have shown how many functionally important, but cryptic species, e.g. parasitoids, are present in samples from all three sampling methods and that the results derived from these can be well related to altered forest structures as now experimentally manipulated in the Research Unit (RU) (Kortmann et al. 2021b; Müller et al. 2018; Vogel et al. 2021). Moreover, particularly light trapping, which can be applied simultaneously on more than 60 plots per night, as well as Malaise traps, are highly suitable standardised methods in forests of different vegetation densities (Kortmann et al. 2021a; Müller et al. 2012).

We further tested autonomous bat recorders to measure bat activity and species richness as well as functional and phylogenetic diversity in response to forest structures in different strata of forests (Müller et al. 2013; 2012). Here, a combination of light trapping and bat recorders in suitable nights is an effective way to collect data from three diverse taxa representing three important trophic levels (moths as primary consumer, parasitoids as consumer 2a, and bats as consumer 2b, see Fig. 1). To measure the function predation pressure, we tested new kind of dummies of adult insects in temperate forests in addition to the established caterpillar dummies (see Fig. 7f in the Coordination project). We further have used autonomous sound recorders in the Müller lab in different projects to monitor biodiversity by bioacoustics approaches. Comparing bird species counts by an excellent ornithologist in the field, with identification from audio data with the same time window in 60 plots, we found overall 10 additional species with the bioacoustic method just because of better standardisation of time windows (Fig. 3). This is in line with a recent publication on winter birds in boreal forests (Shaw et al. 2021), demonstrating the usefulness of acoustic approaches for comprehensive biodiversity monitoring.

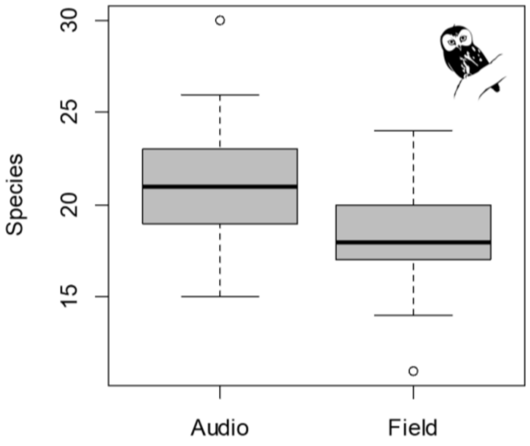


Fig. 3: Comparison of species number identified per 50x50 patch on 60 plots in our intensive patches in the University Forest. Identification is based on 5x10 min point counts per plot by a professional ornithologist (Field) and identification of species from audio data with the same total amount of time (5 days with 10 min) and standardized in all plots.

Based on the autonomous highly standardized monitoring of birds, bats, and medium sized mammals, we have demonstrated that local assemblages of these groups highly depend on the local forest environmental conditions (Moning and Müller 2008; Müller et al. 2012; Stiegler et al. 2020). This is important to mention, because e.g. bats or mammals, have much larger home ranges (Dietz et al. 2007), but their interactions with other trophic levels as e.g. lepidopteran and dipteran prey, occur at a local scale. Here, the patch size of 50x50 m and the district size of about 10-20 ha proposed in our research unit has been tested to be a meaningful spatial scale for studying all trophic levels in forests, including higher trophic ones.

Communities of parasitoids can be identified by metabarcoding from different collection methods as a cryptic but species-rich group at the patch level. However, for caterpillars collected from tree canopies effectively by fogging (Leroy et al. 2021) we recently explored a new cost-effective meta-barcoding approach together with the lab of the Centre for Biodiversity Genomics, University of Guelph. Here the Sequel II (pacbio) allows long reads and is suitable to identify parasitoids and their hyperparasitoids on the level of single larvae. For the first time, this enables estimating parasitation rates as an ecosystem function at the scale of a single patch and with many replicates.

For the intensive plots in Sailershausen we already collected data for insects with light traps, flight interception traps and pitfall traps, for bats with batcorders, and for birds with sound recorders. Furthermore, we sampled caterpillars by canopy fogging and identified the parasitoid load for 60 plots. These data will be immediately available to the PhD student for first publications. Further, we already published phylogenies and trait databases for major taxa, including birds, moths, bats and saproxylic beetles, which are available to the PhD student (Franke et al. 2020; Hagge et al. 2021; Heidrich et al. 2021; Riedinger et al. 2013; Thorn et al. 2016).

Finally, the PIs have developed analytical frameworks in ecology together with statisticians for analysing data from repeated measurements, with dependence in space, for α- and β-diversity, and taxonomic and functional diversity (Chao et al. 2019a; Chao et al. 2019b; Hofner et al. 2011; Kaldhusdal et al. 2015; Kneib et al. 2008). Some of them act as Mercator Fellows or collaborators in the RU.

1.2 Project-related publications

1.2.1 Articles published by outlets with scientific quality assurance, book publications, and works accepted for publication but not yet published.

1. Georgiev K, Chao A, Castro J, Chen Y-H, Choi C-Y, Fontaine J, Hutto R, Lee E-J, **Müller J**, Rost J, Żmihorski M, **Thorn S** (2020) Salvage logging changes the taxonomic, phylogenetic and functional successional trajectories of forest bird communities. Journal of Applied Ecology 57:1103-1112
2. Heidrich L, Bae S, Levick S, Seibold S, **Weisser W**, Krzystek P, Magdon P, Nauss T, Schall P, Serebryanyk A, Wollauer S, Ammer C, Bassler C, Doerfler I, Fischer M, Gossner MM, Heurich M, Hothorn T, Jung K, Kreft H, Schulze ED, Simons N, **Thorn S, Muller J** (2020) Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests. Nature Ecology & Evolution 4:1431-1431.
3. Kortmann M, Roth N, Buse J, Hilszczański J, Jaworski T, Morinière J, Seidl R, **Thorn S, Müller JC** (2021) Arthropod dark taxa provide new insights into diversity responses to bark beetle infestations. Ecological Applications in press.
4. **Müller J**, Mehr M, Bässler C, Fenton MB, Hothorn T, Pretzsch H, Klemmt H-J, Brandl R (2012) Aggregative response in bats: prey abundance versus habitat. Oecologia 169:673-684
5. **Müller J**, Brandl R, Brändle M, Förster B, De Araujo BC, Gossner MM, Ladas A, Wagner M, Maraun M, Schall P, Schmidt S, Heurich M, **Thorn S**, Seibold S (2018) LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127:814-824.
6. Seibold S, Bassler C, Baldrian P, Reinhard L, **Thorn S**, Ulyshen MD, Weiss I, **Müller J** (2016) Dead-wood addition promotes non-saproxylic epigeal arthropods but effects are mediated by canopy openness. Biological Conservation 204:181-188.

7. Simons NK, Felipe-Lucia MR, Schall P, Ammer C, Bauhus J, Blüthgen N, Boch S, Buscot F, Fischer M, Goldmann K, Gossner MM, Hänsel F, Jung K, Manning P, Nauss T, Oelmann Y, Pena R, Polle A, Renner SC, Schloter M, Schöning I, Schulze E-D, Solly EF, Sorkau E, Stempfhuber B, Wubet T, **Müller J**, Seibold S, **Weisser WW** (2021) National Forest Inventories capture the multifunctionality of managed forests in Germany. Forest Ecosystems 8:5.
8. **Thorn S**, Bassler C, Bernhardt-Romermann M, Cadotte M, Heibl C, Schafer H, Seibold S, **Müller J** (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters 19:163-170.
9. **Thorn S**, Chao A, Bernhardt-Römermann M, Chen YH, Georgiev KB, Heibl C, **Müller J**, Schäfer H, Bässler C (2020) Rare species, functional groups, and evolutionary lineages drive successional trajectories in disturbed forests. Ecology 101:e02949
10. Uhler J, Redlich S, Zhang J, Hothorn T, Tobisch C, Ewald J, **Thorn S**, Seibold S, Mitesser O, Morinière J, Bozicevic V, Benjamin CS, Englmeier J, Fricke U, Ganuza C, Haensel M, Riebl R, Botero SR, Rummler T, Uphus L, Schmidt S, Steffan-Dewenter I, **Müller J** (2021) Relationship of insect biomass and richness with land use along a climate gradient. Nature Communications in press. DOI: 10.1038/s41467-021-26181-3

1.2.2 Other publications, both peer-reviewed and non-peer-reviewed

Not applicable

1.2.3 Patents

Not applicable

1.2.3.1 Pending

Not applicable

1.2.3.2 Issued

Not applicable

2 Objectives and work programme

2.1 Anticipated total duration of the project

Four years

2.2 Objectives

The focus of our subproject is the recording of selected taxonomical groups of higher trophic levels (Fig. 1) and of selected functions, to contribute to the testing of the main hypotheses of the RU. Here, the data obtained in this SP will allow the RU to quantify the effects of multidiversity including all trophic levels on γ-multifunctionality at the landscape scale. In our own analyses in SP9, we will focus on direct and indirect effects of diversity and of abiotic environmental conditions at higher trophic levels on ecosystem functions. At the α-scale, we will use the ESC treatments and at the β- and γ-scale will use the ESBC treatments and the control districts of the RU. Moreover, we will focus on the taxonomic and functional parts of biodiversity of the higher trophic level in determining ecosystem functioning.

In order to quantify these types of diversity in a standardized and effective manner at an appropriate scale, we will use methods that allow simultaneous recording of the relevant data. To manage the workload across the different methods and expertise, we will restrict the surveys to the most effective time windows, in terms of individuals or activities, and combine them with expert efforts to identify cryptic species and with results from metabarcoding, as recommended for multitrophic studies (Seibold et al. 2018). For the quantification of multi-functionality, we will look at important functions available in the RU: *primary productivity*, *below and above ground secondary productivity*, *pollination*, *seed dispersal*, *invertebrate herbivory resistance,* and *predation* (see **Data exchange and collaboration** below).

Specifically, we aim on testing three major hypotheses with the focus on higher trophic levels:

Hypothesis 1: *Increasing diversity of taxa at higher trophic levels by* ***E****nhancement of* ***S****tructural* ***C****omplexity (α-scale) not only determines multifunctionality at their respective trophic level but also by propagating through different trophic levels* (Fig. 2).

Here we expect a number of indirect effects on ecosystem functions that have not been known so far, since most studies lack precisely the higher trophic levels.

Hypothesis 2: *The variation in multifunctionality by* ***ESC*** *treatment is better explained by functional/phylogenetic than by taxonomic diversities in higher trophic levels.*

As the contribution of species to ecosystem functions is strongly determined by their traits and is often redundant among species, we expect functional diversities as more important drivers for multifunctionality than taxonomic diversities, ignoring the species' identity.

Hypothesis 3: *The increase in γ-multifunctionality in* ***ESBC*** *districts compared to control districts is explained by β- and γ-diversities of higher trophic levels.*

Here we expect new insights into the role of diversities of higher trophic levels on multifunctionality of landscapes, by our complete cover of the different trophic levels in an experiment with a spatially explicit manipulation of between patch heterogeneity.

Data exchange and collaboration within the consortium

For the whole RU and syntheses in SPZ we provide data for different functional-taxonomic groups and different trophic levels for all 234 patches, particularly the higher trophic levels, at least for one year. These groups are predatory birds, predatory mammals, insectivorous breeding birds, insectivorous bats, predatory spiders, predatory beetles, parasitoid Hymenoptera, parasitoid Diptera, phytophagous beetles, phytophagous moths and phytophagous true bugs (Fig. 1). Additionally, we will measure and compile traits to complement already existing trait databases for all taxa and we will compile phylogenies for all higher-level taxa. To contribute to multifunctionality our subproject will measure *secondary above ground productivity*, *invertebrate herbivory resistance*, *predation* and *parasitism* as important functions provided by higher trophic levels (Schuldt et al. 2018). Furthermore, we will apply continuous measurement from the second year on in six selected sites with 108 patches for time series data in preparation of phase 2. For this, we will select a subset of taxa and methods. We will closely collaborate (Fig. 4) with SPZ, SP1 and, SP3, providing important environmental and structural data and data on primary productivity, with SP4 complementing our own data on secondary productivity, with SP2 and SP5 exchanging species data, with SP6 providing data on ecosystem functions (pollination, seed dispersal and predation) as well as data on small mammals, and with SP8 providing data on herb layer diversity. For analyses of multifunctionality and statistical analyses, we will closely collaborate with SPZ.

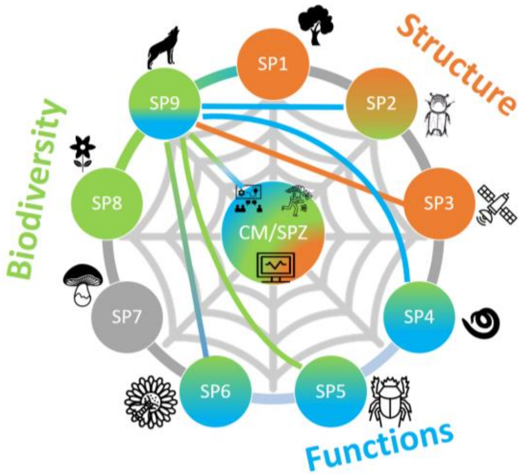


Fig. 4: Close cooperation of SP9 with other subprojects in the RU, the colour of arrows indicate the type of data exchanged; green: species data, blue: functions, brown: structure. The gray spider web indicates that all are interwoven in RU. The grey spider web shows that all projects in the research group are interwoven.

2.3 Work program including proposed research methods

S Thorn, with long lasting expertise in the field of ornithology and in mammal identification, will coordinate all tasks listed in WP1, WP2 and WP5. He will supervise the PhD student in setting up the sound recorders, the nest boxes and the camera traps, as well as in bird sound and mammal picture identification supported by free lancers. J Müller will coordinate all tasks listed in WP3, WP4 and WP6. He will supervise the PhD student in planning the field campaigns and in processing the data. Julian Bittermann (Müller lab), financed by the University Würzburg, will identify moths. W Weisser will bring his experience in experimental design and biodiversity surveys to co-supervise the student for WP1-WP3, and his experience in ecological analysis and biodiversity-functioning research to co-supervise the student for WP4-WP6.

Table 1: Sampling of SP9 in the RU

Year	Area	Number of patches sampled
2022	Intensive patches University Forest	90
2022	Bavarian Forest	90
2023	Lübeck, Saarland, Hunsrück	45
2023	Permanent sampling Bavarian Forest, University Forest	54
2024	Permanent sites in all 6 climate regions	108
2025	Permanent sites in all 6 climate regions	108
	Patches sampled in total	**495**

To collect data for immediate analyses within the RU with one-year data for each patch as well as to start temporal data collection also for the second phase of our RU we will sample all plots once in the first two years according to the general sampling scheme presented in SPZ. In the second year, we will sample the more distant regions, and will also start our continuous measurement on 108 patches in one block of each climate region (see Table 1).

WP1: Breeding birds

This work package consists of three tasks, namely sampling of breeding success with nest boxes, sampling of breeding bird data with sound recorders, measuring predation rates, identification of birds and data storage.

1. Sampling of breeding success with nest boxes

This task includes the setup of two nest boxes of the type „Cavity 1B“ by Schwegler (see www.schwegler-natur.de) at a height of 1.5 m above ground within each 50x50m patch. This allows a survey of breeding success, counting the fledglings and weighing the chicks in a standardized way. In the University Forest all plots are already equipped. Therefore, only 144 patches in the remaining areas need to be equipped. From an earlier project, the Müller lab has a total of over 300 nest boxes. The surveys of the nest boxes will be supported by student theses.

2. Sampling of breeding bird data with sound recorders

Simultaneously with the setup of the nest boxes, the PhD student will set up one autonomous recording unit (Bioacoustic Audio Recorder, Frontier Labs, Salisbury, Australia) in the centre of each patch to detect communities of vocalizing bird species continuously from March to August. The recorders will be mounted at the height of 2.5 m with support of student helpers, in the Bavarian Forest with support of Jens Schlüter, financed by the Bavarian Forest National Park.

3. Measuring predation rates

In cooperation with SP6 we will measure *predation rates by birds*. Here, we will use standardized plastic caterpillars and beetles as a rapid assessment of insect and bird attacks (Meyer et al. 2015). These will be exposed in May at each patch together with the sound recorders.

4. Bird identification and data storage

Sampling of the sound is set to 2-minutes recordings every 15 minutes. From this data we will select all together 5 days with low wind speed, medium or higher temperatures, and no rain: one in March, one in April, two in May and one in the first half of June to cover the breeding season. For each day, we will select five 2-minute time intervals before dawn, during dawn, and after dawn. These data will be analysed by the PhD student with support of bird sound experts (freelancers) to species level using sound amplifying software. Furthermore, we will utilize upcoming AI technologies for autonomous species identification for all data (Kahl et al 2021) and we will analyse established sound indices (Ross et al 2021) using routines developed for high performance computing. All data will be transferred to a database for further analyses by the PhD student.

<u>Output:</u> Patch-species activity data for breeding birds on all patches; *predation pressure* and *breeding success* on all patches.

WP2: Mammals

This work package consists of two tasks, field sampling of mammal data, and identification and data storage.

1. Field sampling

To collect data on medium sized mammals we will setup a wildlife camera trap in the centre of each patch in March together with the sound recorder. The camera works with an infrared flash set to rapid-fire mode, which triggers every second when an animal is detected. Cameras will be used from March to August. The view of the camera will be oriented to cover a range of near ground mammals from mice to red deer. To cover all patches in one year we will buy 180 camera traps. To assess the bat assemblages, we will run autonomous bat call recorders of the type ‘Batcorder 3.0’ (ecoObs, Nuremberg, Germany) for one night in June and July each to quantify activity and species diversity of bats in the patches simultaneously with light trapping (see WP 1). Batcorders will be set up in all patches of each block (1 district with ESCB treatment and 1 control district, with 18 or 30 patches in intensive or extensive sites, respectively), simultaneously. The batcorder is tied to a tree or pole located near the patch centre at the height of 1.5 m. Batcorders are set with a maximum critical frequency of 16 kHz. The sampling will be conducted by the PhD student with student helpers and support by the technicians Jens Schlüter and Linda Seifert.

2. Identification and data storage

Pictures from wildlife cameras will be uploaded using the open source web-based application TRAPPER (Bubnicki et al. 2016). Species identification will be conducted with support of student helpers of the Bavarian Forest National Park. Furthermore, we will utilize upcoming AI technologies for autonomous species identification. All processing will be conducted under the supervision of the PhD student. Data stored on SD cards will be transferred to a database. Bat recordings will be automatically analysed and assigned to a species or species group using bcAdmin4, batIdent1.5 and bcAnalyze3 (ecoObs, Nuremberg, Germany) (Müller et al. 2012). Activity indices of each species or group are generated in 1-min intervals using bcAdmin4. The analyses will be conducted by the PhD student.

Output: Patch-species activity data for medium sized mammals on all patches; Patch-species activity data for bats on all patches.

WP3: Arthropods

This work package consists of two tasks, field sampling of arthropods and identification of various groups.

1. Field sampling

This task includes the sampling of moth assemblages for one night in June and July each representing the peak of moth activity (Roth et al. 2021). Each trap consists of one fluorescent tube (12 V, 15 W; up to 40 m attraction range; (Truxa and Fiedler 2012)) powered by a lead storage battery (12 V, 12 Ah) and equipped with a light sensor to enable automated activation and switch-off controlled by daylight intensity. Moths attracted to the light trap through a plastic funnel into a bucket containing a chloroform-soaked wick. Sampling campaigns are restricted to temperatures at night above 9°C, low precipitation and low wind speed and moon below 85%. Traps are emptied during the next day and insects stored in a freezer (-20°C). Moreover, we will install two flight interception traps in each patch mainly for beetles and true bugs, two pitfall traps for beetles and spiders, one Malaise trap mainly for Diptera and Hymenoptera. All traps will be installed end of April. Malaise traps will be emptied twice per month, the other traps once per month, in May, June and July covering the peak of insect activity in our forest ecosystems. Sample liquid in pitfall and window traps will be 3% copper sulfate, but 70% ethanol in Malaise traps for subsequent barcoding. The insect biomass from the light traps and malaise traps are weighed to estimate the *secondary above ground productivity*. This work will be conducted under the supervision of the PhD student with support by local freelancers, to reduce travel costs. Additionally, the PhD student will conduct one single tree fogging per patch in end of May (as requested by the reviewer). Crown-dwelling arthropods are sampled by pyrethrum knockdown with a SwingFog SN50 machine (Swingtec GmbH, Isny, Germany). In each patch, two mature trees of different species from dominant trees will be selected. Insects will be collected by two tarpaulin sheets (3 × 5 m) under each of the two trees.

2. Identification

Samples will be sorted with support of a technician and of student helpers under the supervision of the PhD student. Identification of beetles, true bugs and spiders will be conducted by external experts. For cryptic species such as parasitoids and dipterans we plan to lump together all samples from one patch and year, which should be analysed by metabarcoding (canopy fogging, by catch of light traps, malaisetraps). These will be pooled first and then sieved to be separated into small and large individuals. Both fractions are then ground separately and samples of both are sequenced together. This will be done to restrict the cost as much as possible, but simultaneously cover a wide range of species collected at each patch. Subsequently the sequences will be blasted against a Central European library to obtain species names or genus information, which allow assigning the OTUs to a BIN species. Moths will be identified by professional taxonomist, Julian Bittermann, financed by the University Würzburg. The data will be transferred to a database and summarized by the PhD student.

<u>Output:</u> Patch-species abundance data for a) moths, b) true bugs, c) phytophagous beetles, d) saproxylic beetles, e) predatory beetles, f) spiders; Patch-species incidence data for g) pollinating Diptera, h) parasitoid Hymenoptera; i) patchspecific parasitation rates of caterpillars.

WP4: Direct and indirect effects of α-diversity on multifunctionality

To test hypothesis 1, “*Increasing diversity of taxa at higher trophic levels by **ESC** (α-scale) not only determines multifunctionality at their respective trophic level but also by propagating through different trophic levels*”, we will combine data on ants, pollinators and small mammals from SP5 with our diversity data from the 1st trophic, 2nd trophic, and predator level (WP1-WP3). Furthermore, we will select some major forest ecosystem functions (*primary productivity*, *below and above ground secondary productivity*, *pollination*, *seed dispersal*, *invertebrate herbivory resistance* and *predation)* collected by our own or provided by the RU for calculation of multifunctionality based on concepts of SPZ. Finally, we will utilise information on environmental conditions as canopy cover or soil conditions from SPZ, SP1 and SP3. To span the range from rare to dominant species we will analyse α-diversity at a specific sample-coverage threshold along the Hill numbers (Chao and Jost 2012). We will fit confirmatory path analyses with mixed effect models to test for direct and indirect effects of diversity as well as effects of environmental conditions on multifunctionality at the α-scale under consideration of replicated measurements in our sites. The supervision of analyses and the related manuscript will be conducted by the PhD student under supervision of J Müller and W Weisser and in close collaboration with the RU Team in SPZ including the Mercator Fellows and collaborators and particularly with support by the *Statistics and synthesis - Postdoc* in SPZ. We will actively participate in the framework development in SPZ and use these approaches for analyses in SP9.

Output: Manuscript I on direct and indirect effects of α-diversity on multifunctionality, for a journals such as Ecology.

WP5: Functional versus taxonomic diversity effects of higher trophic levels on multifunctionality

To test hypothesis 2, "*The variation in multifunctionality by ESC treatment is better explained by functional/phylogenetic than by taxonomic diversities in higher trophic levels*", we will use the same multifunctionality information as in WP4 and diversity data from WP1-WP3. However, we will now analyse the functional-phylogenetic diversity for the higher trophic levels, rather than the taxonomic level. Here, we will built and update phylogenies and trait data bases for moths, phytophagous beetles, saproxylic beetles, parasitoid wasps, predatory beetles, spiders, bats and birds and combine these information to describe the ecological dissimilarity between species (Cadotte et al. 2013). Based on these data we will analyse the functional-phylogenetic diversity as standardized effect size of mean pairwise distances based on Null models. We than will repeat the analyses of WP4 with functional diversity. The supervision of analyses and the related manuscript will be conducted by the PhD student under supervision of S Thorn and J Müller in close collaboration with the Mercator Fellow M Cadotte.

Output: Manuscript II on functional versus taxonomic diversity effects of higher trophic levels on multifunctionality for a journal as Oikos.

WP6: Diversity of higher trophic levels and multifunctionality at β- and γ-scale

To test hypothesis 3, "*The increase in γ-multifunctionality in ESBC districts compared to control districts is explained by β- and γ-diversities of higher trophic levels*", we will use multifunctionality data from WP4 for each of the 22 sites. We than will analyse for the data sets created in WP4 and WP5 the taxonomic and the functional/phylogenetic β-diversities. Multifunctionality based on major functions will be calculated in accordance with the concepts developed in SPZ. With these data we will then fit linear mixed models with all group wise β-diversities (taxonomic and functional) to explain multifunctionality of a district. The supervision of analyses and the related manuscript will be conducted by the PhD student under supervision of W Weisser, J Müller and S Thorn and in close collaboration with the Mercator Fellow Fons van der Plas and SPZ.

Output: Manuscript III on diversity of higher trophic levels and multifunctionality at β- and γ-scale for a journal as Nature Communications.

Table 2: Time table of the work program by month.

	2022									2023												2024											2025												2026		
WP1 - Breeding birds																																															
Sampling of breeding success with nest boxes	▨	▨	▨										▨	▨	▨									▨	▨	▨									▨	▨	▨										
Sampling of breeding bird data with sound recorders	▨	▨	▨										▨	▨	▨									▨	▨	▨									▨	▨	▨										
Measuring predation rates		▨												▨											▨											▨											
Bird identification and data storage				▨	▨	▨										▨	▨	▨									▨	▨	▨									▨	▨	▨							
WP2 - Mammals																																															
Field sampling	▨	▨	▨	▨	▨							▨	▨	▨	▨	▨	▨							▨	▨	▨	▨								▨	▨	▨	▨									
Identification and storage					▨	▨	▨	▨	▨							▨	▨	▨	▨	▨	▨					▨	▨	▨									▨	▨	▨								
WP3 - Arthropods																																															
Field sampling	▨	▨	▨										▨	▨	▨										▨	▨	▨									▨	▨	▨									
Identification				▨	▨	▨	▨	▨							▨	▨	▨	▨	▨								▨	▨	▨	▨								▨	▨	▨	▨	▨				
WP4 - Direct and indirect effects of α-diversity on multifunctionality																																															
Compilation of WP1-3 with data from other SPs																	▨	▨	▨	▨	▨	▨	▨																							
Hypothesis testing analyses																						▨	▨	▨	▨																					
Writing manuscript I																									▨	▨	▨	▨	▨	▨	▨	▨														
WP5 - Functional versus taxonomic diversity effects of higher trophic levels on multifunctionality																																															
Building functional-phylogenetic dissimilarities																										▨	▨	▨	▨																	
Hypothesis testing analyses																													▨	▨	▨	▨	▨	▨	▨											
Writing manuscript II																																		▨	▨	▨	▨	▨	▨	▨							
WP6 - Diversity of higher trophic levels and multifunctionality at β- and γ-scale																																															
Analyses of β-diversities																													▨	▨	▨	▨	▨	▨	▨											
Hypothesis testing analyses																															▨	▨	▨	▨	▨	▨	▨									
Writing manuscript III																																						▨	▨	▨	▨	▨	▨	▨	▨	▨	▨	▨

3 Bibliography concerning the state of the art, the research objectives, and the work programme

Benbow ME, Barton PS, Ulyshen MD, Beasley JC, DeVault TL, Strickland MS, Tomberlin JK, Jordan HR, Pechal JL (2019) Necrobiome framework for bridging decomposition ecology of autotrophically and heterotrophically derived organic matter. Ecological Monographs 89:e01331.

Bubnicki JW, Churski M, Kuijper DPJ (2016) TRAPPER: an open source web-based application to manage camera trapping projects. Methods in Ecology and Evolution 7:1209-1216.

Cadotte M, Cecile HA, Walker SC (2013) The ecology of differences: assessing community assembly with trait and evolutionary distances. Ecology Letters 16:1234-1244

Chao A, Chiu C-H, Villeger S, Sun I-F, Thorn S, Lin Y-C, Chiang J-M, Sherwin WB (2019a) An attribute-diversity approach to functional diversity, functional beta diversity, and related (dis)similarity measures. Ecological Monographs 89:e01343

Chao A, Colwell RK, Gotelli NJ, Thorn S (2019b) Proportional mixture of two rarefaction/extrapolation curves to forecast biodiversity changes under landscape transformation. Ecology Letters 22:1913-1922. doi: 10.1111/ele.13322

Chao A, Jost L (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completness rather than size. Ecology 93:2533-2547

Dietz C, von Helversen O, Nill D (eds) (2007) Handbuch der Fledermäuse Europas und Nordwestafrikas. Kosmos, Stuttgart

Franke S, Brandl R, Heibl C, Mattivi A, Muller J, Pinkert S, Thorn S (2020) Predicting regional hotspots of phylogenetic diversity across multiple species groups. Diversity and Distributions 26:1305-1314.

Grab H, Branstetter MG, Amon N, Urban-Mead KR, Park MG, Gibbs J, Blitzer EJ, Poveda K, Loeb G, Danforth BN (2019) Agriculturally dominated landscapes reduce bee phylogenetic diversity and pollination services. Science 363:282-284.

Hagge J, Bässler C, Gruppe A, Hoppe B, Kellner H, Krah F-S, Müller J, Seibold S, Stengel E, Thorn S (2019) Bark coverage shifts assembly processes of microbial decomposer communities in dead wood. Proc R Soc Lond B Biol Sci 286:20191744.

Hagge J, Müller J, Birkemoe T, Buse J, Christensen RHB, Gossner MM, Gruppe A, Heibl C, Jarzabek-Müller A, Seibold S, Siitonen J, Soutinho JG, Thygeson AS, Thorn S, Drag L (2021) What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. Journal of Animal Ecology 90:1934-1947

Heidrich L, Pinkert S, Roth N, Brandl R, Bässler C, Hacker HH, Busse A, Müller J, Friess N (2021) Noctuid and geometrid moth assemblages show contrasting elevational gradients in body size and color lightness. Ecography 44:1169-1179

Hines J, Ebeling A, Barnes AD, Brose U, Scherber C, Scheu S, Tscharntke T, Weisser WW, Giling DP, Klein AM, Eisenhauer N (2019) Mapping change in biodiversity and ecosystem function research: food webs foster integration of experiments and science policy. In: Eisenhauer N, Bohan DA, Dumbrell AJ (eds) Mechanisms Underlying the Relationship between Biodiversity and Ecosystem Function, vol 61, pp 297-322

Hines J, van der Putten WH, Gerlinde B, Dey D, Wagg C, Voigt W, Mulder C, Weisser WW, Engel J, Melian C, Scheu S, Birkhofer K, Ebeling A, Scherber C, Eisenhauer N (2015) Chapter Four - Towards an Integration of Biodiversity–Ecosystem Functioning and Food Web Theory to Evaluate Relationships between Multiple Ecosystem Services. Advances in Ecological Research 53:161-199

Hofner B, Müller J, Hothorn T (2011) Monotonicity-Constrained Species Distribution Models. Ecology 92:1895-1901

Kahl S, Wood CM, Eibl M, Klinck H (2021) BirdNET: A deep learning solution for avian diversity monitoring. Ecological Informatics 61:101236.

Kaldhusdal A, Brandl R, Müller J, Möst L, Hothorn T (2015) Spatio-Phylogenetic Multi-Species Distribution Models. Methods in Ecology and Evolution 6:187-197

Kalka MB, Smith AR, Kalko EKV (2008) Bats limit arthropods and herbivory in a tropical forest. Science 320:71

Kneib T, Müller J, Hothorn T (2008) Spatial smoothing techniques for the assessment of habitat suitability. Environmental and Ecological Statistics 15:343-364

Kortmann M, Müller JC, Baier R, Bässler C, Buse J, Cholewińska O, Förschler MI, Georgiev KB, Hilszczański J, Jaroszewicz B, Jaworski T, Kaufmann S, Kuijper D, Lorz J, Lotz A, Łubek A, Mayerhofer S, Meyer M, Meyer S, Morinière J, Popa F, Reith H, Roth N, Seibold S, Seidl R, Stengel E, Wolski GJ, Thorn S (2021a) Ecology versus society: impacts of bark beetle infestations on biodiversity and restorativeness in protected areas of Central Europe. Biological Conservation 254:108931

Kortmann M, Roth N, Buse J, Hilszczański J, Jaworski T, Morinière J, Seidl R, Thorn S, Müller JC (2021b) Arthropod dark taxa provide new insights into diversity responses to bark beetle infestations. Ecological Applications accepted

Lefcheck JS, Byrnes JEK, Isbell F, Gamfeldt L, Griffin JN, Eisenhauer N, Hensel MJS, Hector A, Cardinale BJ, Duffy JE (2015) Biodiversity enhances ecosystem multifunctionality across trophic levels and habitats. Nature Communications 6:6936.

Leroy BML, Lemme H, Braumiller P, Hilmers T, Jacobs M, Hochrein S, Kienlein S, Müller J, Pretzsch H, Stimm K, Seibold S, Jaworek J, Hahn WA, Weisser WW (2021) Relative impacts of gypsy moth outbreaks and insecticide treatments on forest resources and ecosystems – an experimental approach. Ecological Solutions and Evidence 2:e12045

Manning P, Loos J, Barnes AD, Batary P, Bianchi F, Buchmann N, De Deyn GB, Ebeling A, Eisenhauer N, Fischer M, Frund J, Grass I, Isselstein J, Jochum M, Klein AM, Klingenberg EOF, Landis DA, Leps J, Lindborg R, Meyer ST, Temperton VM, Westphal C, Tscharntke T (2019) Transferring biodiversity-ecosystem function research to the management of 'real-world' ecosystems. In: Eisenhauer N, Bohan DA, Dumbrell AJ (eds) Mechanisms Underlying the Relationship between Biodiversity and Ecosystem Function, vol 61, pp 323-356

Meyer ST, Koch C, Weisser WW (2015) Towards a standardized Rapid Ecosystem Function Assessment (REFA). Trends in Ecology & Evolution 30:390-397.

Moning C, Müller J (2008) Environmental key factors and their thresholds for the avifauna of temperate montane forests. Forest Ecology and Management 256:1198–1208

Mori AS, Isbell F, Seidl R (2018) b-Diversity, Community Assembly, and Ecosystem Functioning. Trends Ecol Evol 33:549-564

Müller J, Brandl R, Brändle M, Förster B, De Araujo BC, Gossner MM, Ladas A, Wagner M, Maraun M, Schall P, Schmidt S, Heurich M, Thorn S, Seibold S (2018) LiDAR-derived canopy structure supports the more-individuals hypothesis for arthropod diversity in temperate forests. Oikos 127:814-824.

Müller J, Brandl R, Buchner J, Pretzsch H, Seifert S, Strätz C, Veith M, Fenton MB (2013) From ground to above canopy — bat activity in mature forests is driven by vegetation density and height. Forest Ecology and Management 306:179-184

Müller J, Mehr M, Bässler C, Fenton MB, Hothorn T, Pretzsch H, Klemmt H-J, Brandl R (2012) Aggregative response in bats: prey abundance versus habitat. Oecologia 169:673-684

Naeem S, Thompson LJ, Lawler SP, Lawton JH, Woodfin RM (1994) Declining biodiversity can alter the performance of ecosystems. Nature 368:734-737

Penone C, Allan E, Soliveres S, Felipe-Lucia M, Gossner M, Seibold S, Simons N, Schall P, van der Plas F, Manning P, Manzanedo R, Boch S, Prati D, Ammer C, Bauhus J, Buscot F, Ehbrecht M, Goldmann K, Jung K, Müller J, Müller J, Pena R, Polle A, Renner S, Ruess L, Schöning I, Schrumpf M, Solly E, Tschapka M, Weisser W, Wubet T, Fischer M (2019) Specialisation and diversity of multiple trophic groups are promoted by different forest features. Ecology Letters 22:170–180

Ratcliffe S, Wirth C, Jucker T, van der Plas F, Scherer-Lorenzen M, Verheyen K, Allan E, Benavides R, Bruelheide H, Ohse B, Paquette A, Ampoorter E, Bastias CC, Bauhus J, Bonal D, Bouriaud O, Bussotti F, Carnol M, Castagneyrol B, Checko E, Dawud SM, De Wandeler H, Domisch T, Finer L, Fischer M, Fotelli M, Gessler A, Granier A, Grossiord C, Guyot V, Haase J, Hattenschwiler S, Jactel H, Jaroszewicz B, Joly FX, Kambach S, Kolb S, Koricheva J, Liebersgesell M, Milligan H, Muller S, Muys B, Nguyen D, Nock C, Pollastrini M, Purschke O, Radoglou K, Raulund-Rasmussen K, Roger F, Ruiz-Benito P, Seidl R, Selvi F, Seiferling I, Stenlid J, Valladares F, Vesterdal L, Baeten L (2017) Biodiversity and ecosystem functioning relations in European forests depend on environmental context. Ecology Letters 20:1414-1426.

Riedinger V, Müller J, Stadler J, Brandl R (2013) Phylogenetic diversity of bats decreases in urban environments. Basic and Applied Ecology 14:74-80

Ross S, Friedman NR, Yoshimura M, Yoshida T, Donohue I, Economo EP (2021) Utility of acoustic indices for ecological monitoring in complex sonic environments. Ecological Indicators 121:107114.

Roth N, Hacker H, Heidrich L, Friess N, Garcia-Barros E, Habel J, Thorn S, Müller J (2021) Host specificity and species colouration mediate the regional decline of nocturnal moths in central European forests. Ecography 44:1131-1258

Scherber C, Eisenhauer N, Weisser WW, Schmid B, Voigt W, Fischer M, Schulze ED, Roscher C, Weigelt A, Allan E, Bessler H, Bonkowski M, Buchmann N, Buscot F, Clement LW, Ebeling A, Engels C, Halle S, Kertscher I, Klein AM, Koller R, Konig S, Kowalski E, Kummer V, Kuu A, Lange M, Lauterbach D, Middelhoff C, Migunova VD, Milcu A, Muller R, Partsch S, Petermann JS, Renker C, Rottstock T, Sabais A, Scheu S, Schumacher J, Temperton VM, Tscharntke T (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. Nature 468:553-556.

Schuldt A, Assmann T, Brezzi M, Buscot F, Eichenberg D, Gutknecht J, Hardtle W, He JS, Klein AM, Kuhn P, Liu XJ, Ma KP, Niklaus PA, Pietsch KA, Purahong W, Scherer-Lorenzen M, Schmid B, Scholten T, Staab M, Tang ZY, Trogisch S, von Oheimb G, Wirth C, Wubet T, Zhu CD, Bruelheide H (2018) Biodiversity across trophic levels drives multifunctionality in highly diverse forests. Nature Communications 9:10.

Seibold S, Cadotte MW, MacIvor JS, Thorn S, Müller J (2018) The necessity of multi-tropic approaches in community ecology Trends in Ecology and Evolution 33:754-764

Shaw T, Hedes R, Sandstrom A, Ruete A, Hiron M, Hedblom M, Eggers S, Mikusinski G (2021) Hybrid bioacoustic and ecoacoustic analyses provide new links between bird assemblages and habitat quality in a winter boreal forest. Environmental and Sustainability Indicators online first.

Soliveres S, van der Plas F, Manning P, Prati D, Gossner MM, Renner SC, Alt F, Arndt H, Baumgartner V, Binkenstein J, Birkhofer K, Blaser S, Bluthgen N, Boch S, Bohm S, Borschig C, Buscot F, Diekotter T, Heinze J, Holzel N, Jung K, Klaus VH, Kleinebecker T, Klemmer S, Krauss J, Lange M, Morris EK, Muller J, Oelmann Y, Overmann J, Pasalic E, Rillig MC, Schaefer HM, Schloter M, Schmitt B, Schoning I, Schrumpf M, Sikorski J, Socher SA, Solly EF, Sonnemann I, Sorkau E, Steckel J, Steffan-Dewenter I, Stempfhuber B, Tschapka M, Turke M, Venter PC, Weiner CN, Weisser WW, Werner M, Westphal C, Wilcke W, Wolters V, Wubet T, Wurst S, Fischer M, Allan E (2016) Biodiversity at multiple trophic levels is needed for ecosystem multifunctionality. Nature 536:456–459.

Srivastava DS, Cadotte MW, MacDonald AAM, Marushia RG, Mirotchnick N (2012) Phylogenetic diversity and the functioning of ecosystems. Ecology Letters 15:637-648.

Stiegler J, von Hoermann C, Müller J, Benbow M, Heurich M (2020) Carcass provisioning for scavenger conservation in a temperate forest ecosystem. Ecosphere 11:e03063

Tansley AG (1935) The use and abuse of vegetational concepts and terms. Ecology 16:284-307

Thompson RM, Brose U, Dunne JA, Hall RO, Hladyz S, Kitching RL, Martinez ND, Rantala H, Romanuk TN, Stouffer DB, Tylianakis JM (2012) Food webs: reconciling the structure and function of biodiversity. Trends in Ecology & Evolution 27:689-697.

Thorn S, Bassler C, Bernhardt-Romermann M, Cadotte M, Heibl C, Schafer H, Seibold S, Muller J (2016) Changes in the dominant assembly mechanism drive species loss caused by declining resources. Ecology Letters 19:163-170.

Tilman D, Isbell F, Cowles JM (2014) Biodiversity and Ecosystem Functioning. In: Futuyma DJ (ed) Annual Review of Ecology, Evolution, and Systematics, Vol 45, vol 45, pp 471-493

Tilman D, Knops J, Weldin D, Reich P, Ritchie M, Sieman E (1997) The influence of functional diversity and composition on ecosystem processes. Science 277:1300-1302

Truxa C, Fiedler K (2012) Attraction to light - from how far do moths (Lepidoptera) return to weak artificial sources of light? European Journal of Entomology 109:77-84

Uhler J, Redlich S, Zhang J, Hothorn T, Tobisch C, Ewald J, Thorn S, Seibold S, Mitesser O, Morinière J, Bozicevic V, Benjamin CS, Englmeier J, Fricke U, Ganuza C, Haensel M, Riebl R, Botero SR, Rummler T, Uphus L, Schmidt S, Steffan-Dewenter I, Müller J (2021) Relationship of insect biomass and richness with land use along a climate gradient. Nature Communications in press, DOI: 10.1038/s41467-021-26181-3

Vidal MC, Murphy SM (2018) Bottom-up vs. top-down effects on terrestrial insect herbivores: a meta-analysis. Ecology Letters 21:138-150.

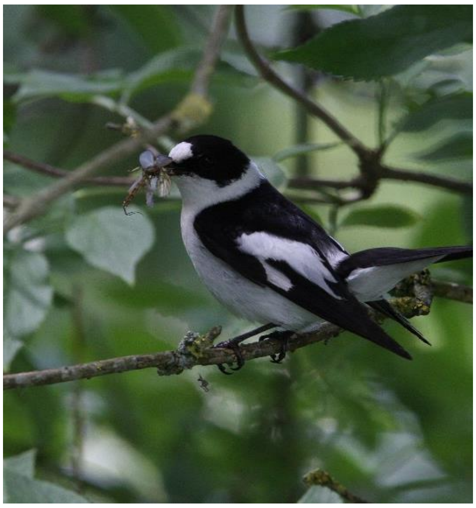
Vogel S, Prinzing A, Bußler H, Müller J, Schmidt S, Thorn S (2021) Abundance, not diversity, of beetle communities determine abundance and diversity of parasitoids in deadwood. Ecology and Evolution 11:6881-6888

4 Relevance of sex, gender and/or diversity

The participating institutions are committed to the goal of actively supporting career perspectives of female scientists; diversity and internationalization in academia (see *2.5 Measures to advance research careers* in the Coordination Project). The applicants will make their graduate students aware of the support and workshops provided in their institutions and by this research unit (*3.2.4 Gender Equality Measures in Research Networks Module*).



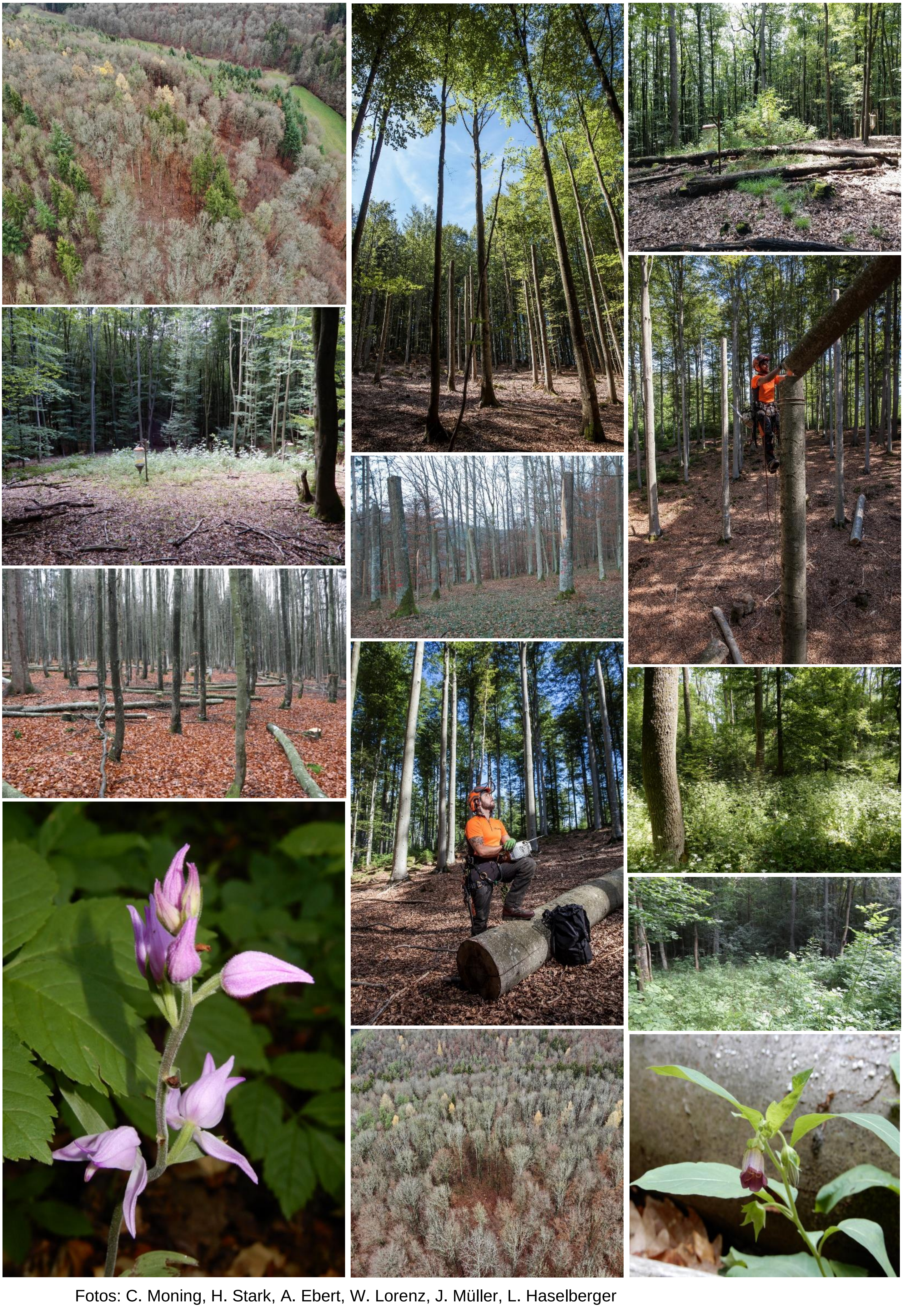








Fotos: C. Moning, H. Stark, A. Ebert, W. Lorenz, J. Müller, L. Haselberger