RESEARCH ARTICLE*

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The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests

Peter Schall[1] (iD) | Martin M. Gossner[2,3] | Steffi Heinrichs[1] | Markus Fischer[4] |
Steffen Boch[4] | Daniel Prati[4] | Kirsten Jung[5] | Vanessa Baumgartner[6] |
Stefan Blaser[4] | Stefan Böhm[5] | François Buscot[7,8] | Rolf Daniel[9] |
Kezia Goldmann[7] | Kristin Kaiser[9] | Tiemo Kahl[10,11] | Markus Lange[12,13] |
Jörg Müller[14] | Jörg Overmann[6] | Swen C. Renner[15,16] (iD) | Ernst-Detlef Schulze[13] |
Johannes Sikorski[6] | Marco Tschapka[5,17] | Manfred Türke[8,12,18] (iD) |
Wolfgang W. Weisser[2] | Bernd Wemheuer[9] | Tesfaye Wubet[7,8] | Christian Ammer[1]

[1]Department of Silviculture and Forest Ecology of the Temperate Zones, University of Göttingen, Göttingen, Germany

[2]Terrestrial Ecology Research Group, Department of Ecology and Ecosystem Management, School of Life Sciences Weihenstephan, Technical University of Munich, Freising, Germany

[3]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[4]Institute of Plant Sciences, University of Bern, Bern, Switzerland

[5]Institute of Evolutionary Ecology and Conservation Genomics, University of Ulm, Ulm, Germany

[6]Leibniz-Institute DSMZ – German Collection of Microorganism and Cell Cultures, Braunschweig, Germany

[7]Department of Soil Ecology, UFZ-Helmholtz Centre for Environmental Research, Halle-Saale, Germany

[8]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[9]Department of Genomic and Applied Microbiology, University of Göttingen, Göttingen, Germany

[10]Silviculture, University of Freiburg, Freiburg, Germany

[11]Biosphere Reserve Vessertal-Thuringian Forest, Schmiedefeld am Rennsteig, Germany

[12]Institute of Ecology, Friedrich-Schiller-University, Jena, Germany

[13]Max-Planck Institute for Biogeochemistry, Jena, Germany

[14]Department of Biodiversity Research/Systematic Botany, University of Potsdam, Potsdam, Germany

[15]Institute of Zoology, University of Natural Resources and Life Sciences, Vienna, Austria

[16]Smithsonian Conservation Biology Institute, National Zoo, Front Royal, VA, USA

[17]Smithsonian Tropical Research Institute, Balboa, Panama

[18]Institute of Biology, Leipzig University, Leipzig, Germany

Correspondence
Peter Schall
Email: peter.schall@forst.uni-goettingen.de and
Martin M. Gossner
Email: martin.gossner@wsl.ch

Abstract

1. For managed temperate forests, conservationists and policymakers favour fine-grained uneven-aged (UEA) management over more traditional coarse-grained even-aged (EA) management, based on the assumption that within-stand habitat heterogeneity enhances biodiversity. There is, however, little empirical evidence to support this assumption. We investigated for the first time how differently grained forest management systems affect the biodiversity of multiple above- and below-ground taxa across spatial scales.

2. We sampled 15 taxa of animals, plants, fungi and bacteria within the largest contiguous beech forest landscape of Germany and classified them into functional groups. Selected forest stands have been managed for more than a century at different spatial grains. The EA (coarse-grained management) and UEA (fine-grained) forests are comparable in spatial arrangement, climate and soil conditions. These were compared to forests of a nearby national park that have been unmanaged for at least 20 years. We used diversity accumulation curves to compare γ-diversity for Hill numbers ^0D (species richness), ^1D (Shannon diversity) and ^2D (Simpson diversity) between the management systems. Beta diversity was quantified as multiple-site dissimilarity.

3. Gamma diversity was higher in EA than in UEA forests for at least one of the three Hill numbers for six taxa (up to 77%), while eight showed no difference. Only bacteria showed the opposite pattern. Higher γ-diversity in EA forests was also found for forest specialists and saproxylic beetles.

4. Between-stand β-diversity was higher in EA than in UEA forests for one-third (all species) and half (forest specialists) of all taxa, driven by environmental heterogeneity between age-classes, while α-diversity showed no directional response across taxa or for forest specialists.

5. *Synthesis and applications.* Comparing EA and uneven-aged forest management in Central European beech forests, our results show that a mosaic of different age-classes is more important for regional biodiversity than high within-stand heterogeneity. We suggest reconsidering the current trend of replacing even-aged management in temperate forests. Instead, the variability of stages and stand structures should be increased to promote landscape-scale biodiversity.

1 | INTRODUCTION

Globally, new forest management and conservation approaches are under discussion to better integrate economic and biodiversity conservation objectives and to replace the classical even-aged (EA) management systems (Messier et al., 2015). In countries of the temperate zone, two approaches for reducing biodiversity loss in managed forests are currently being discussed: (1) to reject complete biomass removals by leaving retention trees (Lindenmayer et al., 2012) and (2) to manage at a rather fine spatial grain by single tree or group selection cuttings leading to uneven-aged (UEA) forests (Puettmann et al., 2015). Both alternatives attempt to ensure habitat continuity (Fritz, Gustafsson, & Larsson, 2008; Grove, 2002). In clear-cut systems, it is suggested that some trees be retained to carry-over structural elements into the next rotation (Gustafsson, Kouki, & Sverdrup-Thygeson, 2010; Lindenmayer et al., 2012). In shelterwood systems, in which a cohort of EA trees is replaced by a new evenly aged cohort through repeated cuttings over decades, additional fine-grained management is proposed to further enhance the physical structure of the environment within single stands (i.e. habitat heterogeneity; Pommerening & Murphy, 2004; Figure 1a,b). In Germany, shelterwood cutting has, since the late 1980s, gradually been replaced by target diameter cuttings (Finkeldey & Ziehe, 2004). Repeated target diameter cuttings focus on harvesting single trees instead of tree cohorts and form the initial step in development of UEA stands (Otto, 1992).

While there is much evidence that biodiversity generally benefits from the retention tree approach when compared with clear-cutting (Fedrowitz et al., 2014; Lindenmayer et al., 2012; Vanderwel, Malcolm, & Mills, 2007; Figure 1b), evidence for positive effects on biodiversity of the fine-grained approach in comparison with traditional shelterwood EA management is weak. Nevertheless, all over temperate Europe, fine-grained (so called "close-to-nature") systems are advocated over the traditional coarse-grained shelterwood system, as it is assumed that they mimic the prevailing natural disturbance regime (Pro Silva 2012). European beech (*Fagus sylvatica*) forests, which would naturally dominate across Central Europe (Bohn & Neuhäusl, 2004), are characterised by small-scale gap dynamics, as observed in primeval beech forest remnants of eastern Central Europe (Hobi, Commarmot,
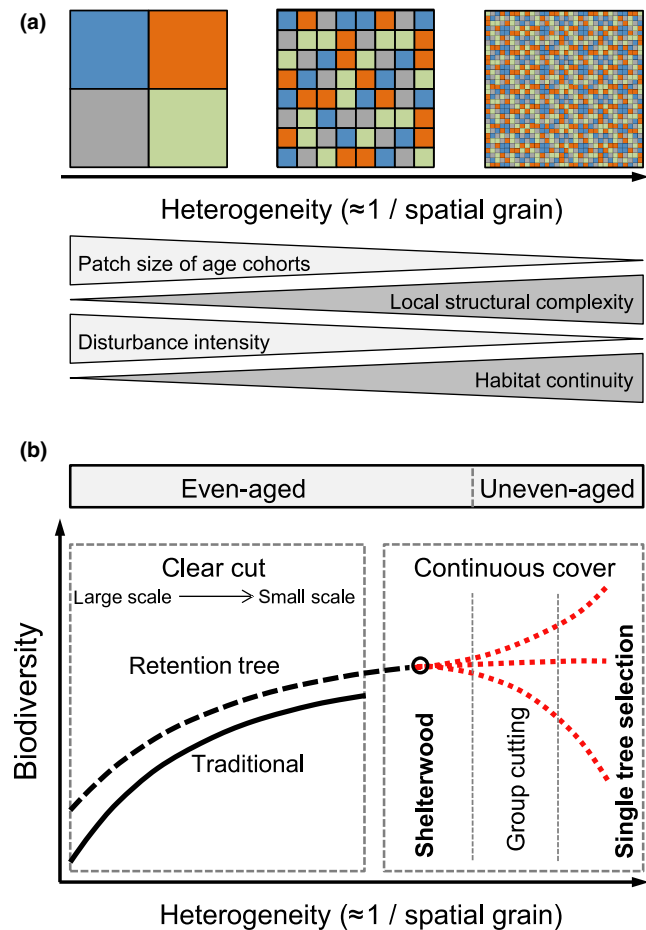
FIGURE 1 Conceptual framework of possible effects of spatial grain on biodiversity resulting from different forest management systems. (a) Forest management systems basically differ in the patch size of cohorts of even-aged trees resulting in different structural complexity on the confined area of a forest stand. Man-made (or natural) disturbance is the driver of spatial grain and also affects local habitat continuity. (b) Spatial grain of forest management systems ranging from large-scale clear-cut to single tree selection. In clear-cut systems, biodiversity benefits from retaining trees and a smaller patch size by enhanced habitat continuity and habitat connectivity (black line). In European beech forests, age-class forests traditionally resulted from shelterwood cuttings over about 30 years. The red dashed line indicates the potential biodiversity effect of forest management systems which further increase spatial heterogeneity, e.g. by group and single tree selection resulting in uneven-aged forests. The forest management systems considered in this study are printed in bold typeface

& Bugmann, 2015). However, also in other parts of the world, management approaches are requested that emulate small-scale gap dynamics (Coates & Burton, 1997; Ott & Juday, 2002).

Even though fine-grained management has been shown to reduce the diversity of particular taxonomic groups compared with unmanaged forests (Bässler et al., 2014; Birkhofer et al., 2012; Paillet et al., 2010), it is generally thought to facilitate *local biodiversity* (α-diversity observed at distinct sampling units) more than coarse-grained management (Pro Silva, 2012). Single tree removals increase variation in tree diameter, height and age at small scales which in turn increases

within-stand heterogeneity of biotic and abiotic resources, such as the distribution of foliage and microclimatic conditions (Brunet, Fritz, & Richnau, 2010; Carey, Lippke, & Sessions, 1999). This is assumed to promote a high diversity of microhabitats and niches by simultaneously limiting intraspecific competition (heterogeneity–diversity hypothesis; MacArthur & MacArthur, 1961; Wilson, 2000). However, the generality of the positive relationship between heterogeneity and diversity has been challenged; there may be a tradeoff between area and heterogeneity at the local spatial scale (Allouche, Kalyuzhny, Moreno-Rueda, Pizarro, & Kadmon, 2012; Stein, Gerstner, & Kreft, 2014). The "area-heterogeneity-tradeoff hypothesis" suggests that resource heterogeneity and resource availability are negatively related. Decreasing resource availability (i.e. the effective habitat area) may reduce the size of local populations and increase the likelihood of local extinctions.

At larger spatial scales, the heterogeneity–diversity relationship may still apply (Stein et al., 2014). In a managed forested landscape (assuming all forest stands are of equal size), heterogeneity is driven by forest stands that differ in age or tree species composition, each providing specific resources favouring different species assemblages. Thus, a more diverse forest landscape should promote *regional biodiversity* (γ-diversity). For EA forests, however, the effectiveness of regional-scale heterogeneity for promoting biodiversity is subject to at least two different filters: species must be able (1) to endure unfavourable environmental conditions created by the final harvest and (2) to colonise suitable habitats that develop over time. In particular, forest specialists with low dispersal capacity might be unable to overcome these filters.

In contrast to existing studies (e.g. Brunet et al., 2010; Paillet et al., 2010), the present work for the first time quantifies effects of forest management on biodiversity not only by comparing pairs of differently managed (mostly mature) stands but also by comparing whole management systems of different spatial grains; i.e. coarse-grained EA and fine-grained UEA systems, using extensive empirical biodiversity data.

These forest management systems may affect biodiversity in three different ways. First, if heterogeneity drives biodiversity at both local and regional scales, the effect of forest management on biodiversity should vary with the spatial grain. UEA forests resulting from fine-grained management should show higher stand scale α-diversity, while γ- and between-stand β-diversity should be higher in EA forests. The size and direction of the forest management effect would then be scale-dependent (Chase & Knight, 2013). Second, if biodiversity is driven only by heterogeneity at the local scale, between-stand β-diversity should be equal in UEA and EA forests and a higher stand scale α-diversity due to higher within-stand β-diversity in UEA should result in a higher γ-diversity compared to EA. Third, if heterogeneity drives biodiversity only at larger scales, stand scale α-diversity in EA and UEA should be equal, and higher between-stand β-diversity in EA should promote γ-diversity in this management system. A higher between-stand β-diversity, however, may reduce the evenness of organismic communities in EA through rare species that inhabit only specific developmental phases. As a consequence, γ-diversity is expected to show divergent responses between EA and UEA for Hill numbers of

different orders. That is, even if species richness ^0D may be increased in EA by rare species, UEA may show a higher diversity when species frequencies are accounted for (e.g. Shannon diversity ^1D or Simpson diversity ^2D). Which mechanisms control biodiversity in temperate European forest landscapes is still an open and challenging question.

We specifically asked: Does biodiversity respond to the type of forest management, and if so, at which spatial scale and at which order of diversity?

2 | MATERIALS AND METHODS

2.1 | Study sites and forest management

The study was conducted within the framework of the Biodiversity Exploratories project (Fischer et al., 2010; www.biodiversity-exploratories.de). The studied forests are located in central Germany, Thuringia, along the forested hill chains of Hainich, Westerwald, and Dün (51°02′45″N to 51°22′12″N, 10°12′28″E to 10°32′03″E). They are part of one of the largest ancient deciduous forest regions in Germany and span a triangular area of 400 km². The geological surface is Triassic limestone, locally covered by periglacial loess. The natural vegetation is a mesophytic deciduous forest dominated by *F. sylvatica* on nutrient-rich soils, with only minor contributions of other tree species (*Fraxinus excelsior*, *Acer pseudoplatanus*, *Carpinus betulus*, *Tilia* sp., *Ulmus* sp.) in mid and late successional stages (Bohn & Neuhäusl, 2004). The forests have been managed for far more than a century under continuous cover forestry at different grains, as EA and UEA forest management systems (Wäldchen, Schulze, Schöning, Schrumpf, & Sierra, 2013). Experimental plots (100 m × 100 m in size) of different beech forest management systems were located within stands of a larger area of the same type and were separated by at least 3 km.

The EA forests (N = 17 plots) have been traditionally managed for about two centuries as stands of about 4–8 ha in size with a rotation period of 120–140 years following natural regeneration from shelterwood trees. Proportional to their share on rotation period, we selected plots from the following developmental phases: thicket (about 20 years old; three plots), pole wood (20–40 years; three plots), immature timber (40–80 years; four plots), mature timber (80–120 years; four plots), and thicket with shelterwood trees (120–140 years; three plots). Large tree (dbh >65 cm) occurrence was 4.5 ± 6.3 trees per ha and dead wood volume was 27.8 ± 12.1 m³/ha (Table S1, Figure S1). This traditional EA system of beech management has become increasingly uncommon over the last decades and is being replaced by finer grained regeneration systems that rely on the final harvest of single trees (so called target diameter harvest), groups of trees, and, infrequently, creation of larger gaps (canopy openings up to 1,000 m²). In fact, current certified forest management best practice guidelines strongly discourage the shelterwood system, claiming that it is "not natural", "too large in scale", "too high in disturbance intensity" and "homogenising within-stand variability" (FSC Working Group Germany 2012). The traditional shelterwood system in European beech forests starts around age 120–140 by removing around 15% of the growing stock (preparatory felling to improve surface soil conditions which

facilitate seed germination). In a mast year, another 30% of the growing stock is removed after seed fall. The remaining trees should be evenly distributed providing a largely uniform canopy shelter. After the regeneration is established, the remaining trees are harvested irregularly over 10–30 years in subsequent cuttings, which reduce the growing stock in 2–4 further steps (Burschel & Huss, 2003). Young growth, thickets and pole woods are kept quite dense to foster self-pruning. With the late pole stage, after a branchless bole of around 6 m is achieved, the silvicultural management begins. Thinning from above is applied favouring vigorous trees by removing competitors. Comparable measures are carried out up to a stand age of around 100 years one to two times per decade. Between 25 and 90 m³/ha are removed per decade, depending on stand age and site quality. Because the EA system comprises many different stages with different stem densities, stand volumes, etc., the mean values for these attributes show a much higher variation among stands than those of the UEA stands (Table S1).

In the present study, UEA forests (N = 13 plots) are managed by single tree harvests and thinning interventions. The single tree selection system of broadleaved temperate forests in the Hainich-Dün region is exceptional both in length and spatial extent (Schütz, 2001), dating back 140 years in Hainich and 250 in Dün and covering a total of 5,000 ha (Wäldchen et al., 2013). In these forests, dead wood is less than in EA systems (17.7 ± 8.2 m³/ha) and large trees (dbh >65 cm) are more frequent (17.9 ±9.8 trees per ha), with an age of 180–230 years based on tree ring counts (Mund, 2004). UEA management in the Hainich area aims to maintain a growing stock of approximately 300–350 m³/ha. Interventions take place every 5 years and are focused mainly on overstory trees which have reached a diameter at breast height of more than 50 cm. These trees account for 75% of the harvest; although they represent only 5%–10% of the total stem number (>7 cm dbh), they are 45%–50% of the growing stock. Trees between 25 and 50 cm dbh (representing 20%–30% of stem number and 40%–45% of the growing stock) account for only 20% of the harvested timber. The amount of harvested small trees is even lower (5%, 7 cm to 25 cm dbh). These trees account for 60%–70% of the stems and 10%–15% of the growing stock (Fritzlar & Biehl, 2006). Around 50 m³ per ha (10%–15% of the growing stock) are removed per intervention.

We included unmanaged (UNM, N = 13 plots) forests of the nearby Hainich National Park as a baseline ecosystem. These forests are located primarily within the UNESCO World Heritage Site "Primeval Beech Forests of the Carpathians and the Ancient Beech Forests of Germany". In the 19th century, they were managed as coppice with standards for firewood and timber production; they then underwent a transformation process to high forests for several decades. Time since abandonment of management is 20 years (five plots) to 70 years (eight plots). The amount of dead wood is 21.6 ± 13.5 m³ per ha and large trees (dbh >65 cm) have a frequency of 20.2 ± 9.2 trees per ha.

Climatic and edaphic gradients and the spatial arrangement of plots are comparable between EA and UEA. Plots of UNM are located at a slightly lower elevation (50 m on average) and in closer proximity to each other (mean distance 2.7 km vs. 13.9 km for EA and UEA; Table S1). This is because unmanaged forests in this region are restricted in their

occurrence to the National Park. For UNM, we found no relationship between distance and compositional dissimilarity (Table S9). This lack of distance decay in species similarity in UNM due to their spatial arrangement may reduce β-diversity and γ-diversity. The α-diversity of mobile taxa, in contrast, may be enhanced. We report results for UNM in Supporting Information, but these should be interpreted with caution.

2.2 | Sampling of taxonomic groups

Methods were optimised for each taxon to get a representative sample of the communities occurring in a particular 1-ha plot. Arthropods, bryophytes and lichens were sampled in 2008 and vascular plants in 2009. Birds and bats were assessed in 2009 and 2010, deadwood fungi in 2010 and 2011 (all three groups on all plots in both years) and ectomycorrhizal fungi (DNA) and bacteria (RNA and DNA) in 2011. Two pitfall traps and four flight-interception traps (two in the understorey and two in the canopy) were used for arthropod sampling. Arthropods were then separated into spiders, harvestmen and pseudoscorpions (henceforth "harvestmen"), beetles, hymenopterans, lacewings and true bugs. Vascular plants, bryophytes, lichens and deadwood fungi were sampled in 20 m × 20 m quadrats located in the centre of each plot. Birds were monitored by the number of observed males, and bats by their flight activities. Assessment of below-ground taxa (ectomycorrhizal fungal DNA, bacterial RNA/DNA) was based on soil samples from a sampling campaign for microbial analysis. All taxa cover a broad spectrum of functional groups, and are also assumed to respond in different ways to forest management, driven by variation in mobility and structural and microclimatic habitat requirements.

Six taxa were separated into forest specialists and non-forest specialists to analyse whether these groups were specifically affected by the grain of forest management. Vascular plants were classified according to Schmidt, Kriebitzsch, and Ewald (2011), birds according to Glutz von Blotzheim and Bauer (1988) and bats, beetles, spiders and true bugs based on expert knowledge (see Acknowledgements). For beetles, the most abundant and diverse group, we additionally considered five subgroups, saproxylic (according to Seibold et al., 2015), rare and threatened species (according to the German Red list of endangered species; Gruttke et al., 2016; J. Schmidl & J. Büche, unpublished data), and large and small species. We did this because of their relevance to nature conservation, because large and small species may respond at different spatial scales to heterogeneity (Mori et al., 2015), and because they may show different patterns within (subplot level: two pitfall traps, four flight-interception traps per plot) and between plots. We classified all species of categories 1, 2 and 3 of the German Red List, which corresponds to CR, EN and VU in the IUCN Red List, as threatened (IUCN 2001). For details on sampling and processing, see Appendix S1.

We quantified the completeness of the sampling by sampling coverage (Chao et al., 2014). Sampling coverage of taxa for pooled forest management systems ranged between 91% (hymenopterans) and 100% (bats) with 10 of the 15 taxa and all forest specialist groups exceeding 95%. For some taxa within forest management systems, however, sampling coverage decreased to 80% (Table S2).

2.3 | Statistical analyses

To compare species γ-diversity between forest management systems for the 15 taxonomic groups, we used the methods framework published by Chao et al. (2014). This "diversity accumulation curve" framework extended methods for rarefaction and extrapolation of species richness (species accumulation curve) (Colwell et al., 2012) in providing estimators and confidence intervals for higher order Hill numbers (Jost, 2006). This facilitates the comparison of multiple assemblages (Figure S2). Hill numbers ^qD quantify diversity in units of equivalent numbers of equally abundant species by increasingly weighting abundance with the order of diversity q. Diversities with orders <1 disproportionately favour rare species, at order 1 species are weighted proportionally to their frequency in the samples, while all orders >1 disproportionately favour common species. This allows us to analyse the effects of forest management systems on the diversity of rare and common species within one framework. We estimated species diversity curves for orders 0, 1 and 2: ^0D species richness, ^1D the exponential of Shannon's entropy, ^2D the inverse of Simpson's concentration, for all species of each taxonomic group (henceforth "taxa"), forest and non-forest specialists, as well as different functional groups among beetles (see chapter "Sampling of taxonomic groups" and Appendix S1).

Diversity of EA and UEA forest management systems was compared for a range of base sample sizes (BSS) to assess the robustness of the findings. As BSS we used minimum reference sample size (i.e. classical rarefaction), maximum reference sample size and an intermediate value (Table S3). We did not extrapolate beyond maximum reference sample size to factor out differences in the quality of species pool estimates between forest management systems and taxa, which can affect the shape of the accumulation curve when extrapolating. This was observed for species-poor taxa due to a relatively more frequent occurrence of singleton species. In Figures 2 and 3, we present results of maximum reference sample size except for bats, harvestmen, lacewings and lichens. For these taxa, we present results for rarefaction, as estimated pool size (Chao's estimator) of a single forest management system exceeded the pool size of the combined forest management systems (bats in EA, harvestmen, lacewings and lichens in UNM). Note that neither the trend nor the significance of the findings was affected by this conservative presentation of results. Significantly different estimates are indicated by pairwise non-overlapping 95% confidence intervals (CI), obtained by bootstrapping based on 200 replications.

Beta diversity share of γ-diversity was quantified as species turnover (Table S4), which, other than species nestedness and total β (Table S5), is the β-component that effectively contributes to γ-diversity. This facilitates comparisons between forest management systems that are unbiased by richness differences of samples within an assemblage. We quantified β-diversity as a multiple-site turnover component of Jaccard dissimilarity (Baselga, 2012) based on 200 resamplings of nine plots per forest management system. Differences between EA and UEA were tested by comparing resamplings pairwise (i.e. for two-sided $p < .05$ at least 196 of 200 comparisons showed larger values for
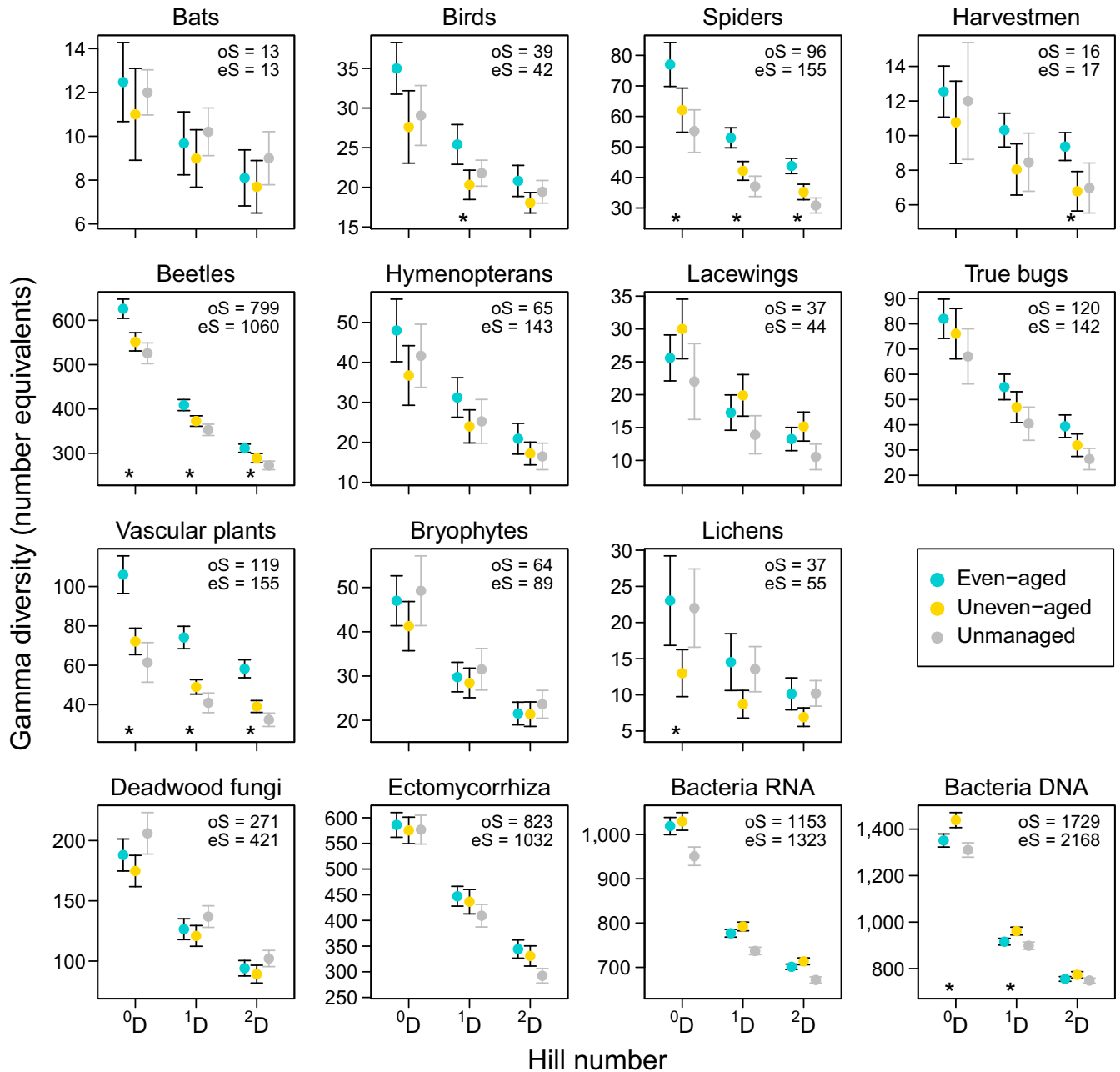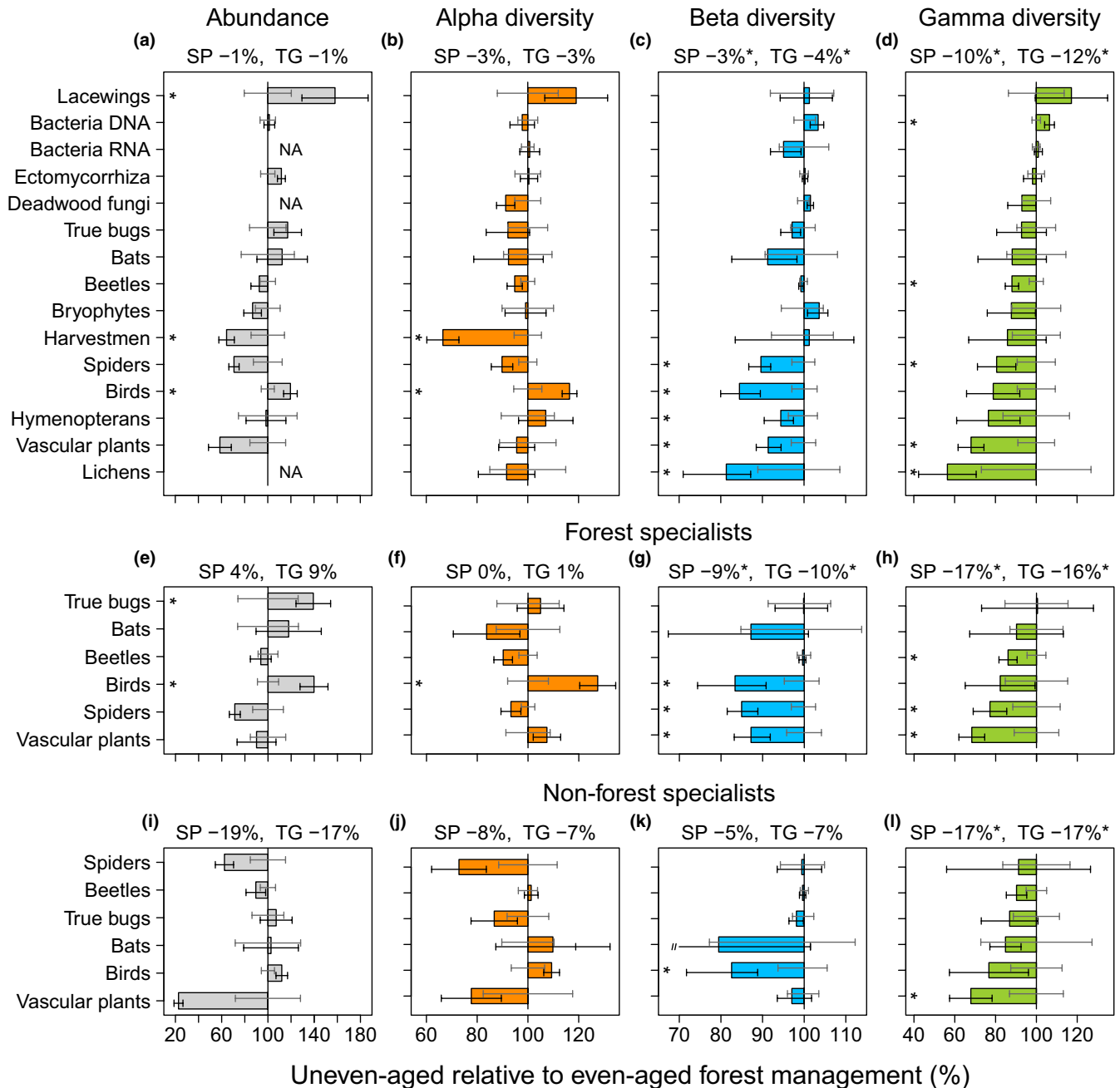
FIGURE 2 Gamma diversity of forest management systems for 15 taxonomic groups in even-aged (EA, $N = 17$), uneven-aged (UEA, $N = 13$) and unmanaged forests ($N = 13$, Table S3). Diversity was quantified for Hill numbers ^0D, ^1D and ^2D, which increasingly weight abundance of species, using sample size-based rarefaction and extrapolation to factor out differences in sample size. Note that unmanaged forests were located in closer proximity to each other than EA and UEA, which limits the direct comparison with managed forests. *$p < .05$ significant difference between EA and UEA. Observed (oS) and estimated species richness (eS, Chao's incidence estimator) of the pooled data indicate the completeness of sampling

one forest management system) (Baselga & Orme, 2012). Within- and between-plot β-diversity was assessed by multiplicative biodiversity partitioning. We used Mantel correlation to analyse the drivers of β-diversity within forest management systems. The drivers investigated were distance between plots (spatial distance), mean air temperature (general thermal climate) and daily temperature range, a measure which efficiently quantifies the alteration of forest microclimate by canopy opening through thinnings and harvests (Chen et al., 1999)

and has been found to be an important driver for forest biodiversity (Müller et al., 2015).

Alpha diversity was quantified as observed and estimated asymptotic species richness (Chao1-estimator). The latter follows the same approach as described above for γ-diversity, but is based on species abundances on the plot level (Chao, 1984). With this we tested for differences between EA and UEA using ANOVA (Table S6, Figures S7–S11).

FIGURE 3 Abundance (a, e, i) and α- (b, f, j), β- (c, g, k) and γ- (d, h, l) diversity of even-aged and uneven-aged forest management systems for 15 taxonomic groups. We distinguished all species of a taxon (a–d) and groups of forest (e–h) and of non-forest specialist species (i–l). Diversity of the uneven-aged (UEA, $N = 13$) was standardised to the even-aged forest management system (EA, $N = 17$) accounting for differences in sample size (Tables S3, S4, S6, S7). The overall response is given for taxonomic groups (TG) and species (SP, log weighting of species number). Error bars (UEA: black, EA: grey) indicate 95% CI for γ, 90% quantile for β-diversity and SE for α-diversity and abundance. *$p < .05$ significant difference between even-aged and uneven-aged forests. Gamma diversity was analysed using sample size-based rarefaction and extrapolation. Beta diversity was measured as multiple-site beta turnover component of Jaccard dissimilarity and quantified using 200 resamplings of nine plots per forest management system. Alpha diversity was analysed using t-test and abundance using Kruskal–Wallis test

If management systems support different species assemblages, this would result in habitat specialists or exclusive species. Based on 500 resamplings of nine plots per forest management system, we quantified the fraction of exclusive species per system, relating exclusive species to species richness per resampling (Table S8). Differences between EA and UEA were assessed by pairwise comparison (i.e. for

two-sided $p < .05$ at least 488 of 500 resamplings showed larger values for one forest management system). Note that the percentage of exclusive species characterises resamplings ($N = 9$) and may decrease with increasing sampling completeness (Colwell & Coddington, 1994).

For analysing γ-diversity the iNEXT function in the package "iNEXT" version 2.0 (Chao et al., 2014), for β-diversity the function

beta.sample in the package "betapart" version 1.3 (Baselga & Orme, 2012), for Mantel test the function mantel in the package "ecodist" and for multiplicative partitioning and estimating asymptotic species richness the functions multipart and estimateR in the package "vegan" were used in R version 3.1.2 (R Core Team, 2014).

3 | RESULTS

Regional γ-diversity was higher in EA compared to UEA (up to 77.1% for lichens ^0D) for 6 of the 15 taxa for at least one of the three Hill numbers ^0D, ^1D and ^2D, while eight groups showed no difference (Figure 2). On average, ^0D was 17.2%, ^1D 16.9% and ^2D 15.0% higher in EA. Bacterial DNA was the only taxon with higher γ-diversity in UEA. Spiders, beetles and vascular plants showed consistently higher diversities in EA across diversities ^0D, ^1D and ^2D and this was confirmed for forest specialists (Figure S3, Table S3). Across taxa, forest specialists were 20.7% ^0D, 20.2% ^1D and 18.0% ^2D more diverse in EA than in UEA. The same response was found for beetle subgroups, i.e. saproxylic species across trap types and small species in pitfall traps (Figures S4–S6). Rare, threatened and large beetles showed no response to forest management.

The higher γ-diversity in EA compared to UEA across taxa and also in forest specialists was driven by between-stand β-diversity (Figure 3c,g; Table S4) and not by local α-diversity (Figure 3b,f; Table S6) or species abundances (Figure 3a,e; Table S7). A few taxa showed higher abundances and α-diversity in EA (harvestmen) or UEA (birds), but with no indication of α-diversity being driven by species abundances (Figures S7 and S8; responses of observed and estimated richness were unidirectional). Only in saproxylic beetles sampled in pitfall traps, the higher α-diversity in EA compared to UEA was driven by higher abundance (Figures S9–S11).

Across forest management systems and taxonomic groups γ-diversity was driven by β-diversity and β-diversity in turn, was driven by its turnover component. Within taxonomic groups, the turnover component share of β-diversity (and hence, as residual, the nestedness component) showed no differences between forest management systems (Figure S12). Between-stand β-diversity showed a unidirectional response to forest management (Figure S12). It was lower in UEA compared to EA on average by 4.3%, being significant in birds (−15.5%), spiders (−10.4%), hymenopterans (6.6%), vascular plants (−8.6%) and lichens (−18.7%) (Figure 3c, Table S4). The response of forest specialists was even stronger (−10% on average) and was found to be significant in three (birds, spiders and vascular plants) out of the six taxa (Figure 3e). The importance of β-diversity for regional diversity is exemplified by birds. In this taxon, high between-stand β-diversity led to higher regional γ-diversity in EA despite lower local α-diversity compared to UEA (Figure S13).

The minor role of within-plot heterogeneity for biodiversity was confirmed by expanding diversity partitioning (^0D, ^1D and ^2D) to the subplot level. For beetles sampled by flight-interception traps (N = 4, Figure S14, Table S12) and pitfall traps (N = 2, Figure S14, Table S13), the within-plot multiplicative ^0D β-diversity was similar between EA

and UEA (1.44 and 1.43 for pitfall traps; 2.89 and 2.90 for flight-interception traps). Additionally, large and small beetles responded similarly (Figure S14), suggesting that the observed low within-plot species turnover is independent of species mobility.

Besides differences in the level of between-stand β-diversity in UEA and EA, β-diversity was also driven by different factors. Matrix correlations revealed that β-diversity in UEA was promoted by geographic distance between stands (vascular plants, beetles and spiders; Table S9) and mean air temperature (beetles and lacewings; Table S10). In contrast, β-diversity of birds, spiders and beetles in EA was promoted by differences between forest developmental phases which resulted in different environmental conditions, as exemplified by forest microclimate (Table S11).

The proportion of exclusive species was lower in UEA compared to EA for birds, spiders, harvestmen and vascular plants. The same pattern was found for forest specialists among spiders and vascular plants (Figure 4).

4 | DISCUSSION

Our results show that the type of forest management affects biodiversity at the regional, but not at the local scale. EA management increased regional biodiversity consistently across taxonomic groups. Only birds benefited from habitat heterogeneity at both spatial scales, showing higher local α-diversity in UEA and higher regional γ-diversity in EA. Neglecting γ-diversity and only focussing on α-diversity (e.g. MacArthur & MacArthur, 1961), thus may result in misleading conclusions and forest management recommendations.

Overall, our results show that there is no consistency in the heterogeneity–diversity relationship across spatial scales for European beech forests, as shown for other ecosystems (Allouche et al., 2012; Chocron, Flather, & Kadmon, 2015; Stein et al., 2014). Across taxa, heterogeneity of a forest landscape provided by different developmental phases of the EA management system promoted biodiversity even when species frequencies are accounted for. Among forest stands, species turnover was thereby shown to be an important component of regional γ-diversity. The higher species turnover in EA, however, did not decrease evenness of organismic communities relative to UEA. Biodiversity of EA was thus driven by both, rare and abundant species. Intermingling of developmental phases by single tree selection leads to high within-stand structural heterogeneity, which is represented by high variation in differently aged and sized neighbouring trees. At the landscape scale, however, such pattern is rather uniform (Hobi et al., 2015) and results in a homogenisation of stand structures and a decrease in regional biodiversity (Beese & Bryant, 1999; Decocq et al., 2004; Werner & Raffa, 2000). In our study, the uniformity of the UEA system was reflected by the low variability in structural attributes and microclimate variables across the respective study plots (Table S1). In contrast, variation in these attributes was high for EA.

Barnes et al. (2016) showed that, besides geographical distance, environmental distance (i.e. differences in microclimate) drives species
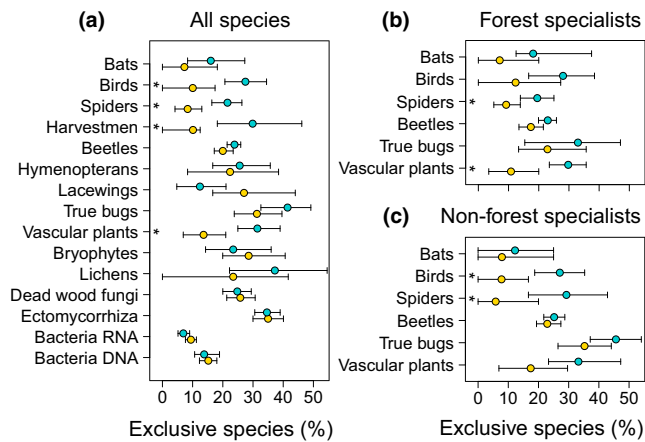
FIGURE 4 Exclusive species in even-aged (EA, N = 17, cyan) and uneven-aged (UEA, N = 13, yellow) forest management systems of different taxonomic groups. We distinguished all species of each taxon (a) and groups of forest specialists (b) and of non-forest specialists (c). The analysis is based on 500 resamplings of nine plots per forest management system. Percentages relate exclusive species to total species per forest management system of resamplings. Error bars indicate the 90% quantile of resamplings. *$p < .05$ significant difference between EA and UEA

turnover among forest stands. In our study, Mantel correlations revealed that microclimatic differences (daily temperature range) explained species turnover of beetles, spiders and birds in the EA. Here the daily temperature amplitude during the growing season was elevated and more variable between stands than in UEA and UNM. This may be explained by more variable canopy height and canopy cover of the different developmental phases. The highest amplitudes were observed in thickets (daily range: 10 ± 1.1°C, daily maximum: 19.0 ± 0.9°C), while the mature timber phase resembled the microclimate of UEA and UNM (Table S1). Our results are in line with recent findings which underscore the contribution of microclimate to biodiversity, in addition to meso-climate (Müller et al., 2015). At the local scale (stand scale α-diversity), a more favourable thermal environment, i.e. higher temperature due to insolation through a partially or completely removed forest canopy (as a result of natural disturbance or management), was found to promote the diversity of producer, consumer, predator and pollinator species compared with adjacent undisturbed forest patches (Müller, Bussler, Gossner, Rettelbach, & Duelli, 2008; Seibold et al., 2014; Winter et al., 2015). For pollinators and arthropod herbivores, this effect is likely caused by bottom-up trophic interactions, driven by increased diversity and abundance of plants (Campbell & Donato, 2014). This has also been shown to be an important mechanism in other ecosystems such as subtropical/tropical mountain forests (Schuldt et al., 2015) and even grasslands (Gossner et al., 2016). Plants benefit from higher light and temperature, in addition to other microclimatic attributes such as canopy throughfall. Even if stand scale α-diversity did not respond to canopy openness, differences in species community composition of open and closed forest patches would promote among stand β- and in turn regional γ-diversity (Chase & Knight, 2013). However, our design does not allow for conclusions on the spatial scale of "optimal" graining.

Differentiation among the species groups of forest and non-forest specialists further showed that EA management not only promotes generalists or disturbance indicators as previously reported for plants (Boch et al., 2013) or ground-dwelling beetles (Lange et al., 2014). Early developmental phases of the EA systems likely also promote species of early-successional forest stages that have been shown to be important for biodiversity (Jonsell, Weslien, & Ehnström, 1998; Kouki, Löfman, Martikainen, Rouvinen, & Uotila, 2001; Swanson et al., 2010), but are missing in the UEA. This is supported by a higher fraction of exclusive species that we found in EA compared to UEA. In addition, EA was also characterised by a higher volume of dead wood and variation in dead wood fractions (Figure S1). These differences are not due to different management intensities. Density-related natural mortality (in pole woods) and the final harvest (in thickets and thickets with shelterwood) especially contributed to dead wood enrichment in EA, mechanisms which are damped in UEA. Thus, EA seems to provide even more suitable habitats for deadwood-dependent forest specialists under current management practices. The dead wood amount in UEA may be increased by leaving more harvest residuals. However, Müller et al. (2015) showed that for saproxylic beetles, the environmental conditions where dead wood is located seems to be as important as the mere amount. In their study, species richness was much higher on logs exposed to sunny conditions than in the shade. Higher amounts of dead wood in UEA forests may not lead directly to higher saproxylic beetle diversity compared to the EA forests, which provides higher light availability and air temperatures in specific stages. In any case, our results further support the claims that reduced habitat connectivity (Janssen et al., 2016), extinction due to unsuitable habitats (Grove, 2002) or lack of niches (Brunet et al., 2010) are very unlikely to operate as important filters for biodiversity in the EA system in comparison to UEA.

The lack of a positive response of local biodiversity to within-stand heterogeneity, on the other hand, indicates that in European beech forests high habitat heterogeneity within forest stands (i.e. UEA) is not a strong driver of local biodiversity. However, no indication was found that local biodiversity and abundance was reduced by an area-heterogeneity-tradeoff in UEA (Allouche et al., 2012).

The diversity of UNM forests was mostly not different from managed forests (α-diversity: Figures S7–S11, γ-diversity: Figures 2, S3–S6). Reasons may include their age—still young—as indicated by closed canopy, lack of decay phase and low dead wood volume. This applies as well to most unmanaged forests in central Europe which had been managed over centuries prior to set-aside.

Our result that the almost unidirectional positive response of organismic regional diversity to EA management is driven by heterogeneity between forest stands is also highly relevant for other forest types. Similar to our study, Sebek et al. (2015) demonstrated a positive effect of clearings within a closed canopy oak forest on saproxylic beetle diversity due to post-logging residues and stumps. In North American hardwood forests, bird species of open habitats benefited from shelterwood cutting in closed forests, while closed forest species did not decrease markedly, thereby increasing regional diversity (Vanderwel et al., 2007). This suggests that opening up the canopy

and creating gaps rather than, e.g. target diameter harvest, results in increased biodiversity of closed canopy hardwood forests across the temperate zone.

Globally, forest management is shifting from EA management systems, e.g. clear-cuts with complete tree removal at large scales or shelterwoods, towards silvicultural approaches which include retention trees or cuttings carried out at smaller scales and at lower intensities (Lindenmayer et al., 2012; Puettmann et al., 2015). In southern Ontario, for example, selection harvesting is recommended for most broadleaf forests (Falk, Burke, Elliott, & Holmes, 2008). Our findings show that biodiversity is sensitive to different types of forest management even when clear-cuts are avoided. Moreover, our study highlights that biodiversity responds positively to forest management, if silviculture creates a variety of environmental conditions at the regional scale. Against the background of the framework presented in Figure 1, we conclude, from prior knowledge and from our results, that both extremes—large-scale clear-cuts and single tree selection cuttings—result in low heterogeneity at the landscape scale compared with systems acting at intermediate spatial grains. Maximising within-stand heterogeneity seems to have no additional positive effect on biodiversity, as also indicated by the significance of larger scale heterogeneity for biodiversity in temperate beech forests (Gossner et al., 2013). At the same time, when focusing on biodiversity, our findings support recent claims that close-to-nature silviculture should vary across time and at larger spatial scales (O'Hara, 2016). Whether our results can be transferred to management system with less-shading species such as pine, systems that operate with much larger stand sizes (≫4–8 ha) and with much shorter rotation periods needs to be clarified by future studies. However, the results of our study are supported by similar conclusions derived from temperate forests in other parts of the world (e.g. Angers, Messier, Beaudet, & Leduc, 2005). These authors, who studied North American broadleaf temperate forests, assumed that "a recurring application of selection cutting might lead to a homogenisation of forest structure and composition, a reduction of key structural features and a reduction in biological diversity at both the stand and landscape scales" (see also Holmes, Pitt, McIlwrick, & Hoepting, 2012; Kern et al., 2017). Our findings underpin this view by data from multiple taxa in another temperate forest ecosystem suggesting a general pattern.

Therefore, we question the current trend towards complete replacement of EA management by selection systems, which we consider to be driven by assumptions rather than by evidence. In this context, focusing on stand scale α-diversity only, as has been done in most management and conservation-oriented studies, may be misleading because it ignores compositional variability between stands. To promote biodiversity and to avoid forest homogenisation over large areas, the silvicultural systems and the intensity level of partial cuttings should be varied among and within stands.

AUTHORS' CONTRIBUTIONS

P.S., M.M.G. and C.A. designed the analysis; P.S. and M.M.G. analysed data; P.S., M.M.G., S.H. and C.A. wrote the draft of the manuscript; M.F., S.Bo., D.P. and K.J. contributed to writing; all other authors provided data and substantially contributed to revision. P.S. and M.M.G. contributed equally to this work.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.4236t (Schall et al., 2017).

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