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Implications of forest structure on carbon dioxide fluxes

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Abstract: Implications of forest structure on carbon dioxide fluxes

Forests provide numerous crucial ecosystem services to society that are sensitive to climate and to extreme climate events such as droughts. One of the services of interest is the ability to sequester the greenhouse gas carbon dioxide (CO_2). Species mixture and structural heterogeneity has been suggested to reduce the effect of climate variability on forests. It is important to understand how increasing diversity and heterogeneity will help dampen the effect of climate events on CO_2 uptake. Currently, knowledge about the ability of different forests to resist or recover from the effect of climate events is limited. To mitigate this knowledge gap, this thesis examines the implications of forest structure on CO_2 fluxes. Chapter 1 provides the general background of the topic. Chapter 2 examines the implications of structural diversity for seasonal and annual CO_2 fluxes in two temperate deciduous forests for a period of 11 years. The two forest sites have similar mean stand age and near-identical climate conditions but different stand structure. The main question asked was how management and related structural diversity may affect CO_2 fluxes. We show that the annual net ecosystem productivity (NEP) was on average 13 % higher in the managed, even-aged, and homogenous forest, than in the unmanaged, uneven-aged, and structurally diverse forest. The homogenous forest was observed to have, however, stronger sensitivities of seasonal NEP and gross primary productivity (GPP) to environmental variables. Chapter 3 relies on data from 21 Fluxnet sites to explore the effect of nine structural parameters on the temporal stability of light-saturated photosynthetic capacity (GPP_{1000}) and on its resistance to changes in water availability during droughts. The study addresses two questions, (a) Do structurally diverse forests have lower variation in annual GPP_{1000}? (b) Are structurally diverse forests more resistant to drought events? The results show that unmanaged forests and forests managed as high forests, which have higher basal areas and tend to be older and more diverse in size than coppice forests, had more stable annual GPP_{1000}. The differences between individual sites in anomalies in GPP_{1000} in response to droughts were mostly explained by growing season air temperature. Forest structure could have influenced the response to droughts, but in our case the structure effect could not be separated from environmental effects. Chapter 4 presents a new model of soil water and related fluxes in forests, Forest Soil Water Model - FSWM, developed in the R environment. The model is suitable for predicting soil water in a wide range of forest soils. FSWM incorporates the Gash model for interception, the Ritchie model for soil evaporation and the Richards equation for soil water movement. FSWM's performance was evaluated against soil water measurements at 12 sites. The model performance was good for deciduous broadleaf forests, moderate for mixed forests and evergreen needle leaf forests. FSWM offers flexibility in simulating soil horizons with different depths and it is helpful when comparing modelled with observed values at different soil depths. With these characteristics, FSWM is a flexible and freely available tool for ecosystem and hydrological research. Additionally, two co-author papers are included in the appendix. The first paper assessed the net ecosystem CO_2 exchange (NEE), total evapotranspiration and net primary production of two neighbouring beech (Fagus sylvatica L.) forests in central Germany differing in site management. We found the interannual variability was higher in the managed, even-aged stand, and the unmanaged forest was a weaker sink of CO_2 during a dry year. The second paper investigated the factors influencing the interannual variability (IAV) of photosynthetic capacity at light saturation, a key ecosystem functional property determining gross primary productivity. The study found that the older and species rich forest had reduced IAV of GPP$_{1000}$. In general, the results of this thesis support the idea that unmanaged forests, mostly older and diverse, have lower interannual variability in NEP, GPP and GPP$_{1000}$ as the result of their adaptation to the habitat by selecting appropriate species, developing structure to make best use of the light, water, and nutrient resources. During droughts, the effect of the forest structure was not clear. More research covering a large range of different sites is still required to get definitive results involving more structural attributes and sites from different climates.

Key words:
Carbon dioxide, droughts, photosynthetic capacity, forest structure, interannual variability, soil water model

Zusammenfassung: Bedeutung der Waldstruktur für Kohlendioxid-Flüsse

Wälder bieten der Gesellschaft zahlreiche wichtige Ökosystemdienstleistungen (ESS, ecosystem services), die empfindlich gegenüber dem Klima und extremen Klimaereignissen wie bspw. Dürren sind. Eine für diese Arbeit relevante ESS ist die Fähigkeit, das Treibhausgas Kohlendioxid (CO_2) zu speichern. Es wird vermutet, dass Artendurchmischung und strukturelle Heterogenität, den Effekt von Klimaschwankungen auf Wälder reduzieren können. Es ist wichtig zu verstehen, wie zunehmende Diversität und Heterogenität dazu beitragen können, die Effekte von Klimaereignissen auf die CO_2-Aufnahme zu dämpfen. Gegenwärtig ist die Fähigkeit verschiedener Wälder, den Klimaauswirkungen zu widerstehen oder sich von diesen zu erholen noch unbekannt. Diese Arbeit untersucht deshalb die Bedeutung von der Waldstruktur für die CO_2-Flüsse, um diese Wissenslücke zu füllen. Kapitel 1 enthält den allgemeinen Hintergrund zur Thematik. Kapitel 2 untersucht die Rolle von struktureller Diversität für die saisonalen und jährlichen CO_2-Flüsse in zwei gemäßigten Laubwäldern für einen Zeitraum von elf Jahren. Die beiden Waldgebiete haben ein ähnliches Bestandsalter und nahezu gleiche Klimabedingungen, jedoch ist die Bestandstruktur unterschiedlich. Die Hauptfrage war, wie sich das Management und damit verbundene strukturelle Diversität auf die CO_2-Flüsse auswirken kann. Wir zeigen, dass die jährliche Nettoökosystemproduktivität (NEP, net ecosystem productivity) im gemanagten, gleichaltrigen und homogenen Wald im Durchschnitt um 13 % höher war als im unbewirtschafteten, ungleichaltrigen und strukturell vielfältigen Wald. Das homogene Waldgebiet zeigte jedoch eine stärkere Empfindlichkeit der saisonalen NEP und der Bruttoprimärproduktivität (GPP, gross primary productivity) gegenüber Umwelteinflüssen. Kapitel 3 stützt sich auf Daten von 21 Fluxnet-Standorten, um den Effekt von neun strukturellen Parametern auf die zeitliche Stabilität der lichtgesättigten photosynthetischen Kapazität (GPP_{1000}) und auf ihre Widerstandfähigkeit gegenüber Veränderungen der Wasserverfügbarkeit während Dürren zu untersuchen. Die Studie befasst sich mit zwei Fragen: (a) Haben strukturell vielfältige Wälder eine geringere Variation der jährlichen GPP_{1000}? Und (b) Sind strukturell vielfältige Wälder resistenter gegenüber Dürreereignissen? Die Ergebnisse zeigen, dass unbewirtschaftete Wälder und als Hochwald bewirtschaftete Wälder, die höhere Grundflächen haben und tendenziell älter und vielfältiger in der Größe sind, stabilere jährliche GPP_{1000} haben. Die Unterschiede zwischen den einzelnen Standorten hinsichtlich der Anomalien der GPP_{1000} während Dürreperioden wurden hauptsächlich durch die Lufttemperatur in der Vegetationszeit erklärt. Kapitel 4 präsentiert ein neues Modell des Bodenwassers und dem damit verbundenen Flüssen in Wäldern – Forest Soil Water Model (FSWM), welches mithilfe von R entwickelt wurde. Das Modell eignet sich für das Simulieren von Bodenwasser in einem weiten Spektrum von Waldböden. FSWM beinhaltet das Gash-Modell für Interzeption, das Ritchie-Modell für Bodenverdunstung und die Richard-Gleichung für Bodenwasserbewegung. Die Leistungfähigkeit von FSWM wurde anhand von Bodenwassermessungen an 12 Standorten geprüft. Die Modellleistung war gut für Laubwälder, mäßig für Misch- und immergrüne Nadelwälder. FSWM bietet Flexibilität beim Simulieren von Bodenhorizonten mit verschiedenen Tiefen und ist nützlich, wenn modellierte und beobachtete Werte von verschiedenen Bodentiefen miteinander verglichen werden. Mit diesen Eigenschaften ist FSWM ein flexibles und frei verfügbares Werkzeug für Ökosystemund hydrologische Forschung. Es sind zusätzlich zwei Co-Autorenbeiträge im Anhang enthalten. Der erste Aufsatz bewertete den Nettoökosystemaustausch (NEE, net ecosystem exchange) von CO_2, die Gesamtevapotranspiration und die Nettoprimärproduktion (NPP, net primary production) für zwei benachbarte Buchenwälder (Fagus syvatica L.) in Mitteldeutschland, die sich im Standortmanagement unterschieden. Wir fanden heraus, dass die zwischenjährliche Variabilität im bewirtschafteten, gleichaltrigen Bestand höher, und die Funktion als CO_2-Senke im unbewirtschafteten Wald während eines Trockenjahres niedriger war. Die Waldstruktur hätte die Reaktion auf Dürren beeinflussen können, aber in unserem Fall konnte der Struktureffekt nicht von den Umwelteinflüssen getrennt werden. Der zweite Aufsatz untersuchte Faktoren, die die zwischenjährliche Variabilität (IAV, interannual variability) der photosynthetischen Kapazität bei Lichtsättigung beeinflussen, einer wichtigen funktionalen Eigenschaft des Ökosystems, die die GPP bestimmt. Die Studie ergab, dass der ältere und artenreiche Wald die IAV der photosynthetischen Kapazität bei Lichtsättigung reduzierte. Im Allgemeinen unterstützen die Ergebnisse dieser Arbeit die Idee, dass unbewirtschaftete Wälder, vor allem ältere und artenreiche, eine geringere IAV in NEP, GPP und GPP_{1000} aufweisen. Grund hierfür ist ihre Anpassung an das jeweilige Habitat durch die Selektion geeigneter Arten, wodurch eine Waldstruktur entsteht, die Licht, Wasser und Nährstoffressourcen effizienter nutzen kann. Der Effekt der Waldstruktur war während Dürreperioden nicht eindeutig. Um eindeutige Ergebnisse zu bekommen, sind weitere Untersuchungen notwendig, die ein breites Spektrum von verschiedenen Standorten aus verschiedenen Klimazonen und mehr strukturelle Attribute abdecken.

Schlagwörter: Kohlenstoffdioxid, Dürreereignissen, photosynthetischen Kapazität, Waldstruktur, zwischenjährliche Variabilität, Bodenwassermodell

Declaration

I hereby declare that I wrote this PhD thesis under the supervision of Prof. Alexander Knohl, Dr. Mark Rayment and Dr. Fernando Moyano. Any sources of information and used literature have been acknowledged.

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Rijan Tamrakar

Contents

CHAPTER 1

Introduction

1.1 Role of forests in climate mitigation

Forests provide numerous societal services like provisioning (e.g., food, fuelwood, timber, etc.), regulating (e.g., climate regulation, water regulation, pollination, etc.), cultural (e.g., spiritual, recreations, educational, etc.) and supporting (e.g., soil formation, nutrient cycling, primary production) services (ALCAMO et al., 2003). Among these services, climate regulation has been hugely discussed and debated in the context of climate change (CANADELL et al., 2008; LAW et al., 2018). Terrestrial ecosystems absorbed 30 % of anthropogenic carbon dioxide (CO_2) emissions in the last five decades (LE QUÉRÉ et al., 2018) mostly through carbon accumulation in forest biomass and soils (PAN et al., 2011). Temperate forests contributed to 31 % of the global terrestrial carbon sink between 1990 to 2007 (PAN et al., 2011).

In recent years, the frequency of occurrence of meteorological anomalies have increased (IPCC, 2018). In some circumstances, these events have severe impacts on terrestrial ecosystem (BABST et al., 2012; IPCC, 2012; REICHSTEIN et al., 2013). In the case of terrestrial ecosystems, these events can partially offset carbon sinks or even cause net carbon losses releasing CO_2 to the atmosphere (CIAIS et al., 2005; GRANIER et al., 2007; XIAO et al., 2011). Global analysis of extreme events indicated that the anomalies in CO_2 uptake by vegetation was of similar magnitude to the total terrestrial carbon sink (ZSCHEISCHLER et al., 2013). In addition to immediate responses, many studies have shown that such extreme events can also show time-lagged responses such as mortality, fires or pest infestations (CIAIS et al., 2005; KURZ et al., 2008; PAGE et al., 2002; ZENG et al., 2009).

One of the suggested methods to mitigate the impact of extreme climates on forest ecosystems is creating more diverse forest because species-rich forests provide higher levels of ecosystem functions (GAMFELDT et al., 2013; LIANG et al., 2016; ZHANG et al., 2012). For example, mixed spruce/beech forests (GRIESS et al., 2011; PRETZSCH et al., 2010) and oak /beech (PRETZSCH et al., 2013) mostly outyield pure stands of the same species by about 20 %. The influence of species richness on productivity is, however, modulated by climate (JUCKER et al., 2016) and site conditions (POTTER et al., 2014). Furthermore, the temporal stability in productivity of diverse forests are higher (JUCKER et al., 2014; MORIN et al., 2014) than monocultures. The key processes that enhances forest productivity and temporal stability are overyielding (when productivity of a mixture exceeds the average productivity of monocultures of component species - SCHMID et al. 2008), species asynchrony, complementarity (MORIN et al., 2011) and species interaction (JUCKER et al., 2014; MORIN et al., 2014).

In addition to creating more species rich forests, efforts have been made to create forest with complex horizontal and vertical structures that resemble old-growth forests (PUETTMANN et al., 2015) because they are believed to have more ecological resistance and stability (POMMERENING, 2002). Forest management practices, particularly in Europe and North America, are towards uneven-aged and multi-species forests (BAUHUS et al., 2009). The presence of trees with different sizes (in terms height and root depth) leads to differential resource availability e.g. water (BRIENEN et al., 2017; DAWSON, 1996) and light (DHÔTE, 1994). Additionally, competition dynamics among trees are affected by population hierarchy (Zang et al., 2012).

1.2 Forest structure

Species diversity conflates structural and genetic diversity. Many studies have so far studied effect of species diversity on productivity, or drought sensitivity. In this thesis, we split these factors and focus on the structural diversity.

Forest structure can be defined as horizontal and vertical distribution of trees in forest stand. The horizontal structure can be quantified based on dbh, spatial distribtion of trees, or canopy distribution. The vertical structure on the other hand can be assessed by tree height.

In the recent times, the management of forests in an ecologically sustainable manner is widely considered to be desirable (Fares et al., 2015; Rutishauser et al., 2015; Sasaki et al., 2016). Appropriate indicators to characterize the forests are essential to assess the results of such management activities (Lindenmayer et al., 2000). Forest stand structural indices can be used in assessing the impact and success of management, and providing further recommendations for choosing the appropriate management strategies (Müller et al., 2000; Pommerening et al., 2013). Further, the values of stand structural indices can be used to differentiate forest management regimes and intensities (Young et al., 2017). Species richness and species diversity are the two most common approaches to describe diversity in forest structure (Spellerberg et al., 2003). Other approaches include describing forests in terms of (a) its stand structure i.e. varieties of trees (in terms size), logs, and snags and their spatial arrangement (Lindenmayer et al., 2000) and (b) functions (e.g. carbon sequestration, biomass production, see Franklin et al., 2002). Species composition, structural and functional attributes are usually interdependent (Hakkenberg et al., 2016; Pretzsch et al., 2016). For example Pretzsch et al. (2016) found that the forests with two species were more structurally heterogeneous (diverse vertical structure) than the forests with monoculture of same species. For simplification and to include attributes of all three different approaches, McElhinny et al. (2005) introduced the term 'structural attributes' to characterise the forest structure pooling attributes from all three approaches. Forest stand structure is then described by either single stand structural attributes (e.g. canopy cover, number of species) or combination of different stand structural attributes (e.g. structural complexity index, Zenner et al. 2000). McElhinny et al. (2005) and Río et al. (2016) have listed indices of around 50 different stand structure attributes. The stand elements characterised by latter include: stand density, species proportion, species composition, horizontal spatial pattern, species intermingling, vertical pattern, size distribution and age composition. Two studies have in particular, examined the inter-relationships and inter-dependencies between these stand structural indices (Schall et al., 2018; Sterba et al., 2006). Schall et al. (2018) found significant correlation between many pairs and thus suggested to use multiple structural indices for reliable classifications of different forest types along axes of stand structures.

Table 1.1 lists studies looking into relationship between different structural indices and forest functions. Most of the studies have assessed the relationship of forest structure indices like stem number, basal area, diameter at breast height (DBH), etc. and productivity (for e.g. Ali et al. 2016; Dănescu et al. 2016; Schall et al. 2018), few others have focused

Table 1.1: List of studies investigating the relationship between different structural indices and forest functions.

Structural index	Forest functions	Reference
Stand density, stand composition	Drought response of radial growth	Bello et al. (2019b)
Stem number, basal area, canopy projection area, stand volume, species proportion by the share of conifers, species richness, the exponential Shannon diversity, Pielou's index of segregation, etc.	Timber volume, timber volume growth rate	Schall et al. (2018)
Stand structural complexity index from effective number of vertical layers	Microclimate	Ehbrecht et al. (2017)
Stand age, tree species diversity	Temporal stability of ecosystem-level photosynthetic capacity	Musavi et al. (2017)
Coefficient of variation, Gini coefficient, Shannon index, and Shannon evenness of DBH and height distribution, closeness to a J-shaped distribution and skewness of DBH distribution, Shannon index and Shannon evenness of species	Basal area increment	Dănescu et al. (2016)
Shannon-Wiener index of species, DBH and height distribution, stand age	Aboveground carbon (C) storage	Ali et al. (2016)
Stand structural complexity index, silvicultural management intensity, naturalness	Diversity of mosses and higher plants, fungi, birds	Gossner et al. (2014)
Stand composition and tree size	Sensitivity of tree ring growth to droughts	Merlin et al. (2015)
Canopy rugosity	Aboveground net primary productivity, light use efficiency, nitrogen use efficiency	Hardiman et al. (2013)
Canopy rugosity	Net primary productivity	Hardiman et al. (2011)
Stand density index, the average height of dominant and codominant trees (site index)	Periodic annual increment	Long et al. (2010)
Shannon–Wiener index for basal area, DBH and height, integrated Shannon-Wiener index for species and DBH, and species and height, Gini coefficient of DBH and height	Periodic annual increment, periodic annual survivor growth, periodic annual mortality, periodic annual recruitment	Lei et al. (2009)
Shannon's index based on species and basal area	Basal area growth, recruitment, and mortality	Liang et al. (2007)
Age, dominant height at base age of 100 year (site quality), species mixture, relative density index, DBH	Individual tree basal area increment	Hein et al. (2006)
Canopy complexity, species richness, foliage height diversity	Productivity, insect diversity	Ishii et al. (2004)
Tree top height, crown closure, vertical stand structure, conifer proportion	Wind damage	Dobbertin (2002)
Age, Basal area, DBH, crown cover, fertility, species richness, Shannon diversity index, reciprocal of Simpson diversity index, Pielou index of evenness, Hill's index of diversity	Diversity of ground vegetation	Pitkänen (1997)

on drought sensitivity of radial growth (for e.g. Bello et al. 2019b; Merlin et al. 2015) and some animal diversity (e.g. Dobbertin 2002; Gossner et al. 2014). Results on productivity were mostly positive, i.e. higher values of structural diversity meant higher forest productivity. Different studies used different structural indices. Ali et al. (2016) reported the strongest correlation of stand age followed by indices based on DBH and height, and the effect of species diversity was least on aboveground carbon storage. Similarly, Hardiman et al. (2011) concluded that the increase in canopy structural complexity provide a mechanism for the potential maintenance of productivity in ageing forests. Hein et al. (2006) however did not find forest structure as a predictor of productivity but the site quality.

1.3 Implications of forest structure on droughts

Droughts are defined as a period with prolonged deficiency of rainfall or abnormally dry weather sufficiently long to cause a hydrological imbalance (World Meteorological Organization, 1992). Droughts can be the result of hydrometeorological anomalies (Van Loon, 2015) or alteration of the water cycle by anthropogenic activities (Van Loon et al., 2016). At least 52 exceptional drought events occurred at macro-regional scale between 1951-2016 worldwide (Spinoni et al., 2019). The frequency and severity of drought events are expected to increase in future (Spinoni et al., 2019; Spinoni et al., 2017; Trenberth et al., 2014).

Droughts negatively affect forests around the globe (Allen et al., 2015; Anderegg et al., 2013; Choat et al., 2018; Granier et al., 2007; Reichstein et al., 2013; Reichstein et al., 2007). In trees, water travels from the soil to the leaves, via hydraulic supply network formed by xylem tissue (Tyree et al., 2002). When the water demand for transpiration is higher than the supply in root from the soil, the trees start responding from the molecular to ecosystem level to mitigate the effect of drought (Barbeta et al., 2016). At shorter time-scales, the trees respond by closing their stomata at the leaf-atmosphere interface to down-regulate transpiration (Bréda et al., 2006) and by shedding leaves (Ogaya et al., 2006) to limit water loss. At longer time-scales, trees reduce shoot-growth to increase root-to-shoot ratio; enhance fine root growth; develop deeper roots; amass solutes to reduce the water potential in the root tissue (Brunner et al., 2015); modifying xylem conduits (Pallardy, 2002). Further severe droughts leads to canopy or whole plant death and cause of which is mostly related to failure of hydraulic networks of trees (Anderegg et al., 2012; Davis et al., 2002; Nardini et al., 2013; Venturas et al., 2016). The response strategies, however, varies with biomes (Vicente-Serrano et al., 2013), species (Ogaya et al., 2006), and age of trees/stands (Cavender-Bares et al., 2000).

The response of forests to droughts can be modified by tree species mixing and heterogeneous structure (Pretzsch et al., 2013). However, most of the studies have so far looked at the effect of species diversity on drought sensitivity. Here, we report some recent publication that focus on species diversity (Table 1.2). Our review suggests that the direction and strength of the modification depends on the species mixture (Bello et al. 2019b; Grossiord 2019; Lebourgeois et al. 2013 and biomes (Grossiord et al., 2014c). We define effect as positive when the drought sensitivity is reduced by species diversity and negative when drought sensitivity is enhanced by species diversity. Five studies showed

Table 1.2: List of studies reporting the effect of species diversity on the drought responses of the forest. Species mixture are the names of species reported in the study. The conclusion column categorized study conclusion as negative (drought sensitivity increased with the increase in species diversity), neutral (no clear effect of species mixing on drought sensitivity), positive (drought sensitivity was reduced by increasing species diversity), and both (effect of structure were different from site to site, positive in some sites and negative in others).

Study	Region/Forests	Species mixture	Conclusion
BELLO et al. (2019b)	Orléans forest, France	*Quercus petraea* and *Pinus sylvestris*	Negative
TOÏGO et al. (2015)	Orléans forest, France	*Quercus petraea* and *Pinus sylvestris*	Negative
GROSSIORD et al. (2014b)	South-central Tuscany, Italy	*Quercus cerris* and *Quercus petraea*	Negative
GROSSIORD et al. (2014d)	Boreal forests	*Betula pendula*, *Pinus sylvestris*,and *Picea abies*	Negative
VANHELLEMONT et al. (2019)	Northern Belgium	*Fagus sylvatica*, *Quercus robur*, and *Q. rubra*	Neutral
ZALLONI et al. (2019)	Vesuvio National Park, Italy	*Quercus ilex L.* and *Pinus pinea*	Neutral
DĂNESCU et al. (2018)	South-western Germany	Spruce and fir	Neutral
BELLO et al. (2019a)	Orléans state forest	*Quercus petraea* and *Pinus sylvestris*	Positive
SIDOR et al. (2018)	34 forest sites in Romania	*Pinus sylvestris L.* mixed with other species.	Plus
SOUSA-SILVA et al. (2018)	Belgium	*Fagus sylvatica*, *Quercus petraea*, and *Quercus robur*	Positive
KOTLARZ et al. (2018)	Poland	*Pinus sylvestris L.* and *Quercus robur L.*	Positive
ANDEREGG et al. (2018)	Fluxnet sites	Species were different in each forest types	Positive
GRANDA et al. (2018)	Agüero, northeast Spain	*Pinus halepensis*, *Pinus nigra subsp. Salzmannii* and *Pinus sylvestris L.*	Positive
METZ et al. (2016)	Three major geographic regions of Germany	*Fagus sylvatica* with other species	Positive
MÖLDER et al. (2014)	Hainich National Park, Germany	*Fagus sylvatica* with five other species	Positive
LEBOURGEOIS et al. (2013)	crystalline Vosges Mountains, France	*Abies alba* with *Fagus sylvatica* and with *Picea abies*	Positive
PRETZSCH et al. (2013)	South Germany	*Picea abies*, *Fagus sylvatica*, and *Quercus petraea*	Positive
VITALI et al. (2018)	Black Forest	Norway spruce, silver fir and Douglas fir	Both
FORRESTER et al. (2016)	Major European forest types	Species were different in each forest types	Both
GROSSIORD et al. (2014c)	Five forest types of Europe	Many	Both

negative effects of species diversity on the drought sensitivity of forests, three did not find any relationship, three reported positive and negative effects which differed from one site to another, and nine reported positive effects. In order to understand these differences in the results, we have tried to understand the effect of forest structural heterogeneity on carbon dioxide.

In order to estimate effect of structural heterogeneity of forests on drought response, we require an appropriate tool to quantify drought. In next section, we discuss different types of models that have been used to calculate soil water in the forests, a key parameter reflecting water availability to the trees.

1.4 Soil water models

Soil water availability is one of the major factors that limits productivity and decomposition or mineralisation of soil organic matter in forests (Paul et al., 2003). Recently, there has been an increasing reports on severe effects of water shortage on forests around the world (Allen et al., 2015). These impacts include episodes of large-scale diebacks, sudden drops in productivity after extreme droughts (Breshears et al., 2005) and chronic increases in tree mortality and growth decline (Bussotti et al., 2017). Understanding the effects of droughts on forest productivity and tree mortality is crucial to formulate adaptive forest management strategies (Lindner et al., 2014). Modelling forest production, drainage and turnover of organic matter and nutrients all need accurate predictions of soil water content (Paul et al., 2003).

Measurement of soil water content can be expensive, requires a lot of time, and is a complex process due to its inherent temporal and spatial variability. Therefore, a number of soil water simulation models have been developed during the last several decades with a wide range of sophistication (Jong et al., 1996). One of the earliest model was developed by Thornthwaite (1948). The model simulates soil water using a simple water balance approach in which mean monthly precipitation and soil water storage is balanced against estimated potential evapotranspiration. The budgeting procedures have slowly become more complicated by utilizing daily time steps, multi-layering of the soil profile and variable rates of extraction and movement of water from the various zones (Jong et al., 1996). In addition, several models simulate three interconnected components namely (i) the atmosphere (i.e. potential evapotranspiration), (ii) the crop (i.e. plant phenology) and (iii) the soil (i.e. root-zone water) such as models developed by Raddatz 1993.

Many of them are used to estimate soil water availability for forest growth which predict water content within the root zone of stands and water content within surface soil layers under forests Paul et al. (2003). Recently, many improvements have been made in soil water models for more accurate predictions and more suitable application. Here, we briefly describe a few recent soil water models used in the context of forest soils. First we describe few simple bucket models like simple water balance model (SWBM), Simple process-led algorithms for simulating habitats model (SPLASH), lumped water balance model (BILJOU), and soil water under forest (SWUF) followed by more complex vegetation models like Simulator for Mediterranean landscapes (SIERRA), coupled heat and mass transfer model for soil-plant-atmosphere systems (CoupModel), Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ), and CASTANEA.

Orth et al. (2013) modified simple water balance model (SWBM) proposed by Koster et al. (2012). The model considers evapotranspiration and run-off ratios as simple functions of soil moisture. The model shows that simple water balance model can be utilized together with precipitation, net radiation, and measurements to predict soil moisture and its controls even in the situation where direct soil moisture measurements are not present.

Simple process-led algorithms for simulating habitats (SPLASH) model offers robust estimations of key quantities at ecologically relevant time-scales. The model can be used to produce driving datasets for ecological and land-surface models (e.g., monthly carbon and water fluxes or seasonal plant functional trait distributions) from more readily available meteorological observations. The model shows promising results in spite of the model's simplifications and limited climatic drivers (Davis et al., 2017).

A lumped water balance model (BILJOU) was developed to quantify drought intensity and duration in forest stands (Granier et al., 1999). The information needed by the model includes daily potential evapotranspiration and rainfall as input climatic data. The site and stand parameters needed include maximum extractable soil water and leaf area index, the latter controlling (i) stand transpiration; (ii) forest floor evapotranspiration; and (iii) rainfall interception. Other informations such as root distribution and soil porosity can also be utilized if available. The robustness of the model and its easy parametrisation for a large range of species and soil types make it suitable for many ecological applications on both inter- and intra-annual basis (Granier et al., 1999).

Soil water under forest (SWUF) model was developed by Paul et al. (2003) which is used to predict daily water content within both surface soil layers and the sub-soil under a range of forest types. It is a simple cascading water bucket model which was mainly derived by combining algorithms from well-tested models for prediction of soil water under agriculture and extend them to account for interception by, and evaporation from, the dense canopy and litter layer, and the influence of site mounding, and weeds or understorey of forests, on soil water. The model can also be integrated in models of mineralisation of soil organic matter as well as models of forest production. The model was intentionally developed for simple and easy use. Therefore, it only requires easily obtainable data such as leaf area index, litter layer mass, irrigation applied, bulk density, and the upper and lower limit of water content.

Simulator for Mediterranean landscapes (SIERRA) was developed for particular use in Mediterranean-type communities subjected to large recurrent fires. The main property of the model is to utilize explicit functional processes to simulate vegetation dynamics based on fluxes of water and carbon. A spatial representation of the annual course of vertical structure of biomass and carbon fluxes coupled with the weekly soil water budget and evapotranspiration rates can be obtained using the model. The model shows that a weekly water budget is the main driver for primary production and inter-specific competition according to water availability, and at the same time simulates seasonal water stress of species. So far, the model has no limitation towards the species composition and it can be used as a practical tool for a large range of water limited ecosystems (Mouillot et al., 2001).

Coupled heat and mass transfer model for soil-plant-atmosphere systems (CoupModel) can be used to explain many problems regarding hydrological and/or thermal processes in the soil-plant-atmosphere system. Examples of the model application include simulation of regulating factors for biological and chemical processes in the soil, simulation of coupled biological and abiotic processes, simulation of coupled atmosphere and soil processes, generalisation of results to new soils, climates and time periods, and prediction of the influence of management e.g. soil heat extraction, mulching, drainage, irrigation and plant husbandry (Jansson et al., 2011).

The Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ) incorporates process-based large-scale representations of terrestrial vegetation dynamics and land-atmosphere carbon and water exchanges in a modular framework. The property of the model include feedback through canopy conductance between photosynthesis and transpiration and interactive coupling between these 'fast' processes and other ecosystem processes such as resource competition, tissue turnover, population dynamics, soil organic matter and litter dynamics and fire disturbance (Sitch et al., 2003).

Davi et al. (2005a) developed a new hybrid model, CASTANEA, described in Davi et al. (2005b), to simulate the carbon balance and the water cycle. The purpose of the model is to obtain net carbon and water fluxes of deciduous forest from half-hourly to multi-annual time scales and to accurately simulate ecosystem changes in biomass and soil organic matter from season to decades. The carbon balance input data includes canopy photosynthesis, autotrophic and heterotrophic respirations, net ecosystem exchange, wood and root growth. The water fluxes includes transpiration, soil evaporation, interception, drainage and soil water status. The model results simulates all the measured individual processes well, except the root respiration, which was underestimated during summer (Davi et al., 2005a). Therefore, the model suggests that more effort is needed on studying and modelling both root respiration and root turnover.

The described models are either not standalone soil water model but part of the land surface models (e.g. LPJ, CASTANEA, SIERRA, coupModel), or simple that does not take into account the soil and vegetation characteristics (e.g. SWBM, SPLASH). Models like SWUF and BILJOU are standalone model that takes into soil and vegetation characteristics. However, SWUF is built on MS-excel platform and BILJOU is online. Running these model for a single site or few years work excellently. But when we require the model to run for many sites with different sets of parameters both models become impractical. Additionally, modifying or improving the process is not possible in BILJOU as it is not open source and complicated in SWUF. Thus, an multi-layer soil model that can easily be used without many parameters and is open access is still missing.

1.5 Aims and organization of the thesis

Increase in anomalous events including droughts are predicted for future (Barriopedro et al., 2011; Greve et al., 2015). In this context, understanding adaptation and mitigation strategies for forests to cope with changing climate is essential. Forest structure can affect forest functions through niche complementarity, vertical and horizontal size diversity, etc. The effect of forest structure on drought sensitivity on forest functions are however not clear with different studies pointing to different directions. To understand the response of ecosystems to environmental and biotic disturbances, we can look at temporal stability and resistance of the ecosystems. Temporal stability of any ecosystem function (annual net ecosystem productivity and light saturated photosynthetic capacity in our case) is a measure of how much these functions fluctuate around its long-term mean between years (Tilman, 1999) and is related to ecosystem resilience (Holling, 1973). The resistance is the capacity of an ecosystem to remain unchanged after a disturbance (Grimm et al., 1997). In this thesis, we used the difference between observed values during an anomalous year and long-term mean of an ecosystem function, normalized by long-term mean to allow inter site comparison, to estimate resistance of forest ecosystem. The four major aims of this thesis are to:

- investigate the annual and seasonal carbon dioxide fluxes in two differently structured forest.
- assess the implications of forest structure on temporal stability of carbon dioxide fluxes.
- examine the effect of forest structure on resistance of carbon dioxide fluxes during droughts.
- report the flexible open source forest soil water model (FWSM).

This work, 'The effect of forest structures on carbon dioxide fluxes', provide insights on how forest heterogeneity modulates the temporal stability and resistance of carbon dioxide fluxes during droughts. We investigated the effects of forest structure on temporal variability of carbon dioxide fluxes and anomalies of photosynthetic capacity during droughts, and additionally reported a flexible soil water model (FWSM). Here we have made an first attempt to calculate the structural indices for forests for which the carbon dioxide fluxes are readily available in fluxnet dataset (`https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/`). Using inventory data along with the fluxnet data provides an unique opportunity to study the impact of forest structure on carbon dioxide fluxes using multiple sites when most of the studies use only few sites (see Table 1.1 and 1.2). Thus we combined approaches from two scientific community, i.e. forest structure from forestry and carbon dioxide fluxes from micrometeorology. Also the availability of meteorological data at different time-scales (half-hourly, daily, monthly and yearly), allows quantifying droughts at different temporal scales. Here, we took an opportunity to develop a open source soil water model capable of estimating drought at daily scale.

I start this thesis describing the background on structural indices, how forest structure modifies forest functions, and different soil water models available in present days in chapter 1. The introduction is followed by three scientific chapters presented as manuscript. After that in appendix I present two more scientific papers with a short description of the contribution I made. The five scientific studies are as following:

- **Implications of structural diversity for seasonal and annual carbon dioxide fluxes in two temperate deciduous forests** (chapter 2 of this thesis)

  Rijan Tamrakar, Mark B. Rayment, Fernando Moyano, Martina Mund, and Alexander Knohl

  published in *Agriculture and forest meteorology* (Tamrakar et al., 2018)

In this paper we studied two forests of similar mean stand age near-identical site conditions, and dominated by beech trees (*Fagus sylvatica*), but with a very different stand structure (including age, diameter distribution, stocks of dead wood and species composition) because of different management regimes. We observed higher annual net ecosystem productivity (NEP) in the managed, even-aged, and homogeneous forest, than in the unmanaged, uneven-aged, and structurally diverse forest. On the other hand, inter-annual variation was lower in the structurally diverse forest than homogeneous managed forests. The higher variability of NEP in the homogeneous forest was attributed to biotic factors such as fruit production and a time-dependent growth trend.

- **Effect of forest structure on drought response of forest canopy photosynthetic capacity** (chapter 3 of this thesis)
  Rijan Tamrakar, Mark B. Rayment, Fernando Moyano, and Alexander Knohl
  Manuscript to be submitted to *Biogeosciences*

  We expanded our analysis from the first paper (chapter 2) and included 19 more sites across temperate region to understand the effect of structural diversity on carbon fluxes. We looked at photosynthetic capacity (GPP_{1000}) instead of absolute fluxes in order to normalize the climate differences among the sites. We asked two questions in this paper, (a) Do structurally diverse forests have lower variation in annual GPP_{1000}? (b) Are structurally diverse forests more resistant to drought events?

- **A flexible forest soil water model (FWSM) in R**
  Rijan Tamrakar, Mark B. Rayment, Fernando Moyano, and Alexander Knohl (chapter 4 of this thesis)
  Manuscript to be submitted to *Environmental modelling and software*

  We have looked at annual carbon fluxes in chapter 2 and annual photosynthetic capacity in chapter 3. The signal of droughts might be lost at annual scale due to seasonality within a year. It is also important to understand how forest would respond to droughts at shorter time-scales (daily) and how these responses will be modulated by forest structure. However, an multi-layer soil model that can easily be used and is open access is still missing. Thus, we developed a flexible open source dynamic soil water model in R (forest soil water model, FWSM) which can also be translated to any other programming languages. In this chapter we describe a flexible open source soil water model for forests in R. We investigate how it performs in different fluxnet sites.

- **Difference in carbon uptake and water use between a managed and an unmanaged beech forest in central Germany**
  Mathias Herbst, Martina Mund, **Rijan Tamrakar**, Alexander Knohl (Appendix A of this thesis)

Published in *Forest ecology and management* (Herbst et al., 2015)

This paper assessed the net atmospheric carbon dioxide exchange (NEE), total evapotranspiration and net primary production of two neighbouring beech(Fagus sylvatica L.)forests in central Germany differing in site management. Though the inter-annual variability was higher in managed, even-aged stand, the unmanaged forest was weaker sink of carbon dioxide during a dry year. The study discusses the relative importance of tree and structural (age, size) diversity, leaf area index and regenerative growth as well as the temporal frame and extent of single weather extremes for the forest–atmosphere exchange. I supported in the preparation, analysis and discussions of figures A.2 and A.4 (section A.5.2) and contributed to the writing.

- **Stand age and species richness dampen inter-annual variation of ecosystem-level photosynthetic capacity**

  Talie Musavi, Mirco Migliavacca, Markus Reichstein, Jens Kattge, Christian Wirth, T. Andrew Black, Ivan Janssens, Alexander Knohl, Denis Loustau, Olivier Roupsard, Andrej Varlagin, Serge Rambal, Alessandro Cescatti, Damiano Gianelle, Hiroaki Kondo, **Rijan Tamrakar** and Miguel D. Mahecha (Appendix B of this thesis)
  Published in *Nature ecology and evolution* (Musavi et al., 2017)

  The study looked at the inter-annual variability (IAV) of photosynthetic capacity at light saturation, a key ecosystem functional property determining gross primary productivity. The study found that the older and species rich forest had reduced IAV of photosynthetic capacity at light saturation. In this paper, I provided data from the Hainich site and edits to the manuscript.

Finally, we conclude this thesis with a synopsis (chapter 5) - findings from three chapters and appendix chapters. Here, I also include broader discussion on the implications of forest structure on carbon fluxes and in particularly during droughts. Finally, I give an outlook on the future direction of research on effect of forest structure on drought response.

CHAPTER 2

Implications of structural diversity for seasonal and annual carbon dioxide fluxes in two temperate deciduous forests

Authors: **Rijan Tamrakar**, Mark Rayment, Fernando Moyano, Martina Mund, Alexander Knohl

Published in 'Agriculture and Forest Meteorology' (Tamrakar et al., 2018)
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2.1 Abstract

The effects of structural diversity on the carbon dioxide exchange (CO_2) of forests has become an important area of research for improving the predictability of future CO_2 budgets. We report the results of a paired eddy covariance tower study with 11 years of data on two forest sites of similar mean stand age, near-identical site conditions, and dominated by beech trees (*Fagus sylvatica*), but with a very different stand structure (incl. age, diameter distribution, stocks of dead wood and species composition) because of different management regimes. Here we address the question of how management and related structural diversity may affect CO_2 fluxes, and tested the hypothesis that more structurally diverse stands are less sensitive to variations in abiotic and biotic drivers. Higher annual net ecosystem productivity (NEP) was observed in the managed,even-aged, and homogenous forest (585 ± 57.8 g C m^{-2} yr^{-1}), than in the unmanaged, uneven-aged, and structurally diverse forest (487 ± 144 g C m^2 yr^{-1}). About two-third of the difference in NEP between the sites was contributed by a higher annual gross primary productivity (GPP, 1627 ± 164 vs 1558 ± 118 g C m^2 yr^{-1}) and one-third by a lower annual ecosystem respiration (Reco, 1042 ± 60 vs 1071 ± 96 g C m^2 yr^{-1}) in the homogenous forest. Spring (April - May) and summer (June – July) were the two main seasons contributing to the overall annual differences between the sites, also, the sensitivities of seasonal NEP and GPP to environmental variables were stronger in the homogenous forest during those periods. Inter-annual variation of NEP was higher in the homogenous forest (coefficient of variation (CV) = 25%) compared to the heterogeneous forest (CV = 12%). At annual time scale, the higher variability of NEP in the homogenous forest is attributed to biotic factors such as fruit production and a time-dependent growth trend, outweighing differences in environmental sensitivities.

2.2 Introduction

The carbon uptake of forests is affected by changes in both abiotic and biotic factors (Chen et al., 2015; Ciais et al., 2005). The former includes temperature, radiation, water and nutrient availability, and their intra and inter-annual variability. Biotic factors include plant functional traits such as nutrient status, structure, phenology, etc., that govern photosynthesis and respiration process (Jensen et al., 2017) as well as inter- and intra-specific competition. Identifying and under- standing the factors that contribute to the variability in net carbon dioxide (CO_2) uptake, i.e. net ecosystem productivity (NEP), between forest ecosystems and the atmosphere is crucial for understanding how forests will respond to and affect future climate (Baldocchi et al., 2001; Luo et al., 2015)as well as for answering questions relevant to forest management and ecology.

Many eddy covariance (EC) flux studies (e.g. Barr et al. 2007; Dragoni et al. 2011; Hui et al. 2017; Humphreys et al. 2011; Jensen et al. 2017; Kitamura et al. 2012; Richardson et al. 2009; Shao et al. 2015; Shao et al. 2016; Wu et al. 2013; Yuan et al. 2009) have attributed the inter-annual variability (IAV) of NEP variously to climatic variables, to phenological changes induced by climatic variables and to biotic changes, with Richardson et al. (2009) contending that, on an annual scale, variation in NEP is more strongly dominated by changes in biotic factors than by climate. To date, most studies have focused on under- standing effects of climate and biotic changes on CO_2 fluxes at single sites (Granier et al., 2008; Pilegaard et al., 2011; Wilkinson et al., 2012) or across contrasting ecosystem types (Baldocchi et al., 2005; Chu et al., 2016; Jensen et al., 2017; Ma et al., 2007; Novick et al., 2015; Pereira et al., 2007; Shao et al., 2014; Shao et al., 2015; Shao et al., 2016; Wu et al., 2012). Other studies have used multiple sites from across global and regional networks to understand the variability of CO_2 fluxes from different plant functional types and/or climatic zones (Beer et al., 2010; Chen et al., 2015; Law et al., 2002; Musavi et al., 2017). Such studies have been beneficial for understanding the underlying causes of variability in CO_2 uptake, but because flux stations are not closely located, there are typically very large differences in the environmental conditions be- tween sites, making it challenging to disentangle the effects of abiotic vs biotic factors. The short period of time analysed is also a limitation found in some studies (Anthoni et al., 2004; Hommeltenberg et al., 2014; Jensen et al., 2017). Only a few have investigated how structure and management scheme affect CO_2 fluxes (Herbst et al., 2015; Musavi et al., 2017) even though it is reasonable to suppose that these are important drivers of CO_2 fluxes and that they may interact with climate and biotic variables (Luyssaert, 2014). Here we present a case study that, in contrast, focuses on two forest sites that a) are characterized by similar site conditions, b) have a si- milar mean age, and c) are both dominated by beech trees (*Fagus sylvatica*) but differ in management regime and structure. We thus tackle the question of how management and related structural diversity may affect CO_2 fluxes, and directly test the hypothesis that more structurally diverse stands are less sensitive to variations in abiotic and biotic dri- vers. This study builds on the work of Herbst et al. (2015), which was done at the same sites and showed their difference in carbon uptake and water use. We seek to identify the major drivers of seasonal and inter-annual variability of net ecosystem productivity (NEP), gross primary productivity (GPP) and ecosystem respiration (Reco) of a structurally diverse and a structurally-homogeneous temperate broadleaf forest. We test two hypotheses: 1) The annual NEP and GPP of the homogeneous forest is more sensitive to variation in climate variables compared to the hetero- geneous forest. A study utilizing tree rings has shown that pro- ductivity of diverse temperate beech forests exhibited higher temporal stability than monoculture forests mainly due to lower inter-annual variation as well as due to overyielding because of asynchronous behaviour of different tree species and their interactions (Jucker et al., 2014). Grossiord et al. (2014c) observed higher water availability in mixed temperate beech forests than in single species forests during drought, which they speculate as result of niche partitioning and/or facilitation processes among the inter- acting species. 2) NEP and GPP of the homogeneous forest is more sensitive to in- trinsic species-determined characteristics such as fruit production. Synchronous fruit production, also known as masting, is a sink for plant resources that may compete with vegetative growth (Obeso, 2002) and a negative correlation between fruit production and ra- dial stem increment has been observed (Dittmar et al., 2003; Selås et al., 2002). Herbst et al. (2015) reported higher fruit production in the homogenous forest and here we will also quantify the effect of fruit production on annual NEP and GPP.

2.3 Material and methods

2.3.1 Site description

Data were obtained from two forest sites, Hainich (DE-Hai) and Leinefelde (DE-Lnf), located in central Germany (Figure 2.1). The two sites are ca. 30 km apart both at an altitude of 450 m mean above sea level. Soil at both sites is composed of Triassic limestone covered with variable Pleistocene loess deposits. The climate is suboceanic-submontane with a long-term annual mean air temperature of ca. 8 °C. General site characteristics are given in Table 2.1. The phenology of both sites is similar, with the dormant season lasting typically from November to March and growing season lasting from April to October.

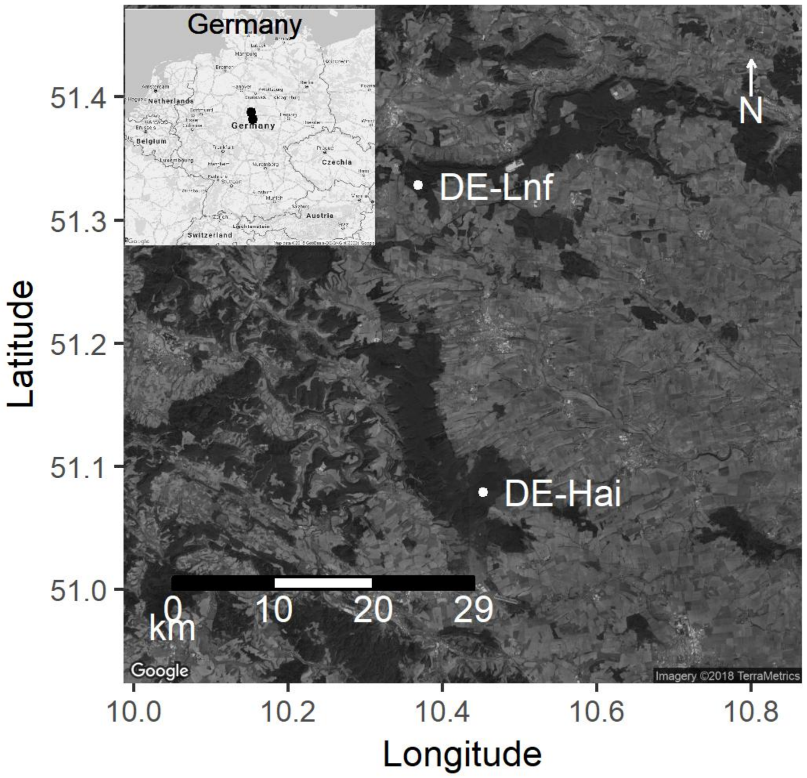


Figure 2.1: Map showing the location of the two study sites in the central Germany. Darker patches are forests and white dots show the positions of the eddy covariance flux towers at each site. Map of Germany in inset is not to scale.

Hainich: The Hainich site (DE-Hai) is an unmanaged forest with a heterogeneous structure, located in the central part of the Hainich National Park. Site details can be found in Anthoni et al. (2004) and Knohl et al. (2003). Until the end of the 19th century, it was managed as a coppice-with-standards system and was subjected to selective cutting until 1965. From 1965 to 1997, the area was used as a military training base and a large part of the forest was left untouched, with only single and very valuable trees being cut. The forest has never been clear felled and, as a result, it exhibits characteristics of

Table 2.1: Instrumentation and stand characteristics for the research sites. Hainich

Characteristics	Hainich (DE-Hai)	Leinefelde (DE-Lnf)
Latitude	51°04'45,36"N	51°19'41,58"N
Longitude	10°27'07,20"E	10°22'04,08"E
Altitude [m]	440	450
Soil	Pleistocene loess deposits with dominance of Cambisols	Pleistocene loess deposits with dominance of Luvisols
Instrumentation		
EC measuring height [m]	44	44
Displacement height [m]	22	22
Sonic anemometer	Gill Sonic Model R3	Gill Sonic Model R3
Infra-red gas analyser (IRGA)	Li6262	Li6262
Stand characteristics		
Primary species	*Fagus sylvatica L* (64)., *Fraxinus excelsior L.* (28), *Acer pseudoplatanus L* (7). and other species	*Fagus sylvatica L.* (single *Quercus petraea*)
Biomass [$\mathrm{t\,C\,ha^{-1}}$]	212	237
Plant density [$\mathrm{trees\,ha^{-1}}$]	334	224
Canopy height [m]	35	35
LAI [$\mathrm{m^2\ m^2}$]	5.1	4.2
Age [years]	Maximum up to 265, biomass weighted average = 140	130 ± 8

an unmanaged, old-growth forest with highly diverse horizontal and vertical structure, trees covering a wide range of age classes, up to a maximum of around 265 years, and large amounts of dead wood (both standing dead wood and coarse woody debris). The main tree species in the forest are beech (*Fagus sylvatica*, ca. 64% of tree biomass), ash (*Fraxinus excelsior*, ca. 28%), and sycamore (*Acer pseudoplatanus*, ca. 7%), with some single trees of European hornbean (*Carpinus betulus*), elm (*Ulmus glabra*), maple (*Acer platanoides*) and other deciduous species. The main ground vegetation in the forest includes *Allium ursinum*, *Mercurialis perennis* and *Anemone nemorosa* (Mund, 2004). The Hainich flux tower site is located on a gentle north facing slope (2–3 inclination) surrounded by forest for more than 3 km in the prevailing wind direction. The only change in the surface land use is a small clearing located about 800 m perpendicular to the prevailing wind, with only 5% contribution to the overall wind direction (Knohl et al., 2003).

Leinefelde The Leinefelde site (DE-Lnf) is an even-aged, about 130 years old, pure beech forest that was established and thinned as part of a regular shelterwood system with a rotation period of about 120-140 years. In recent years the management starts to transfer the shelterwood system towards a system of target diameter harvesting. Crown thinning – thinning of dominant trees to reduce crowding within the main canopy – is carried out regularly every 5-10 years. The thinning activity in the footprint area of the flux tower is presented in Figure 2.10. The ground vegetation includes *Galium odoratum*, *Melica nutans*, *Milium effusum*, *Oxalis acetosella*, and *Stellaria holostea*. The eddy covariance flux tower has been in operation since April 2002. No measurements were carried out in this site from 2007 to 2009 due to access limitation.

2.3.2 Eddy covariance and meteorological measurements

Fluxes of carbon dioxide, water vapor, sensible heat, and momentum along with standard meteorological variables were measured at the two study sites. The two sites had identical eddy covariance instrumental setup and data acquisition techniques. The eddy covariance measurement system consisted of a three-dimensional sonic anemometer (Solent R3, Gill Instruments Ltd., Lymington, UK) and a fast response closed-path CO_2/H_2O infrared gas analyser in absolute mode (LI-6262, LI-COR Inc., Lincoln, NE, USA). The tube connecting the gas inlet and gas analyser was 50 m. Data were collected on a field computer using the “EddySoft” software developed by O. Kolle from MPI-Biogeochemistry, Jena, Germany (Kolle and Rebmann, 2010). Detailed information about the instrumentation can be found in Anthoni et al. (2004) and Knohl et al. (2003). The turbulent fluxes were calculated using “EddyPro” software with same settings for both sites and all years. We followed Aubinet et al. (1999) and Foken et al. (2004) for quality control of the data collection and analyses. We used the “Fluxnet” online-tool (`http://www.bgc-jena.mpg.de/bgi/index.php/Services/REddyProcWeb`) and the REddyProc package in R (Wutzler et al., 2018) based on Reichstein et al. (2005) to obtain a continuous dataset of net ecosystem exchange and for partitioning this into gross primary production (GPP) and ecosystem respiration (Reco). Standard meteorological data were measured at both the sites. Anthoni et al. (2004) and Knohl et al. (2003) describe the details of the meteorological variables and instrumentation. We used the BILJOU model to calculate a water availability index (WAI). Details of this model are available in Granier et al. (1999).

2.3.3 Fruit production data

Periodical fruit production is an important characteristic of beech forests. In this study, we included fruit production as a biotic variable that is assumed to affect annual carbon fluxes. The fruits (seed and pericarp) were collected in litter traps (DE-Hai 25, DE-Lnf 21 traps of 0.25 m^2) distributed within the main footprint, dried at 70 °C and weighed. The traps were closed plastic funnels with a small sieve at the bottom for retaining fruits while allowing drainage. The funnels were fixed on a pillar about 50 cm above the ground so that herbivores (mostly mice) were kept out.

2.3.4 Statistical analysis

Data from April 2002 to 2006 and from 2010 to 2016, the period with complete flux and meteorological data, was used to investigate the effect of meteorological variables on seasonal fluxes. We calculated zero-order correlations and slopes of the simple linear regressions between seasonal fluxes and meteorological variables. We also tested the differences of the sensitivities of seasonal CO_2 fluxes to meteorological variables between sites (Lenth, 2017).

At annual scale, we used data from 2003 to 2006 and 2010 to 2016 (no fruit production data was available for 2002). Paired T-tests were applied to test for significant differences in annual CO_2 fluxes and meteorological variables between the sites. For selecting which predictor explained annual NEP, GPP and Reco, we conducted stepwise multiple linear regression (MLR) using the Akaike Information Criteria (AIC) (Field et al., 2012). The predictor variables considered for the study were mean annual air temperature (T_{air}), soil temperature (T_{soil}), global radiation (R_g), vapor pressure deficit (VPD), water availability index (WAI), spring air temperature, spring soil temperature, fruit production, growing season length, and time. The variable time was represented by calendar year. Thus, it integrates the effects of factors that vary and correlate with time, such as growth, effects of CO_2 fertilization (Fernández-Martínez et al., 2017), phenology (Baldocchi, 2018; Froelich et al., 2015; Granier et al., 2008; Pilegaard et al., 2011; Urbanski et al., 2007), and changes in nutrient deposition (Fernández-Martínez et al., 2017). To create a model applicable to both sites, we defined a MLR model using all the variables selected as significant during the per-site fits and fitted it again, this time to the combined data from both sites. To estimate the relative effects of model predictor variables on response variables, we calculated the 'product measure' which distributes the overall model R^2 to each of the predictors (Nathans et al., 2012). Product measure is the product of a predictor's β-coefficient (standardized slope) in a MLR model and its zero-order correlation. We also conducted simple regressions of predictors against the model residuals, i.e. after having removed the effects of other predictor variables via multiple linear regression. R version 3.4.3 was used for analyses (R Development Core Team, 2018).

2.4 Results

2.4.1 Meteorological characteristics

The two sites were meteorologically similar (Figure 2.2). Averaged yearly global radiation (R_g) from 2002 to 2016 was 122.4 ± 6.5 W m^{-2} (mean ± sd) in DE-Hai and 124.0 ± 7.2 W m^{-2} in DE-Lnf (Figure 2.2a). Mean annual temperature (T_{air}) during the study period was 8.34 ± 0.72 °C and 8.30 ± 0.7 °C for DE-Hai and DE-Lnf, respectively. This similarity was consistent for all years with no statistically significant differences between the sites. The mean annual soil temperature (T_{soil}) was 7.61 ± 0.36 °C and 8.23 ± 0.38 °C for DE-Hai and DE-Lnf, respectively. A systematically higher value of 0.62 °C was measured in DE-Lnf ($p < 0.001$), possibly resulting from differences in the measurement depth between the sites (5 vs 4 cm in DE-Hai and DE-Lnf, respectively, Figure 2.11). Mean annual vapor pressure deficit (VPD) was 3.45 ± 0.56 hPa and 3.28 ± 0.41 hPa at DE-Hai and DE-Lnf, respectively, with no statistical difference between the sites. Mean annual precipitation - based on a single pluviometer per site - was significantly lower ($p < 0.001$) in DE-Lnf (601 ± 154 mm) than in DE-Hai (744 ± 152 mm). Although DE-Lnf received less rainfall, the mean annual water availability index (WAI) was similar between the sites in most years, with average values of 0.86 and 0.84 in DE-Hai and DE-Lnf, respectively. We didn't observe temporal trend in any meteorological variables (Table 2.4).

2.4.2 Fruit production (masting) in the study sites

Figure 2.3 shows the fruit production (masting) data for DE-Hai and DE-Lnf from 1999 to 2016. Data for 2001 and 2002 was not available due to technical issues. The average fruit production for the entire period was 73.2 ± 77.9 g C m^2 yr^{-1} and 91.2 ± 113.1 g C m^2 yr^{-1} in DE-Hai and DE-Lnf, respectively. We define masting years as those when fruit production is more than 50 g C m^2 yr^{-1}. Masting years occurred every two or three years. Average fruit production during such years was 151 ± 46.3 g C m^2 yr^{-1} and 197 ± 91.8 g C m^2 yr^{-1} for DE-Hai and DE-Lnf, respectively, with the former being 76 % of the latter. The significant differences between DE-Lnf und DE-Hai are restricted to the extraordinarily high mast years (fruit production > 200 g C m^{-2}).

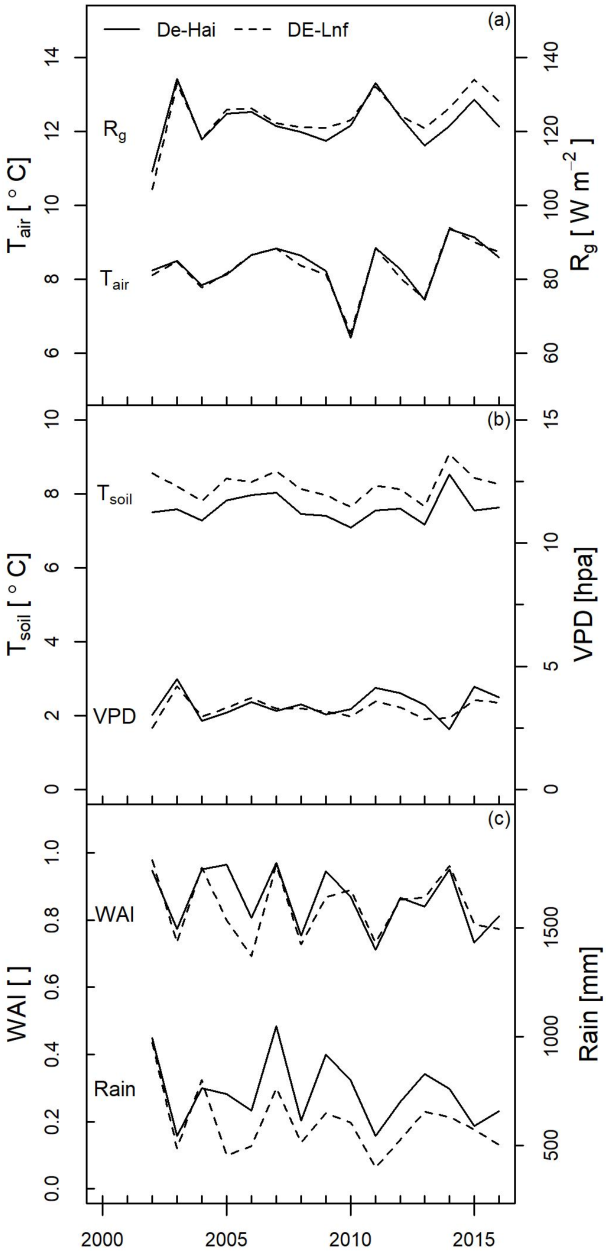


Figure 2.2: Mean annual values of (a) global radiation (R_g) and air temperature (T_{air}); (b) soil temperature (T_{soil}) and vapor pressure deficit (VPD); and (c) water availability index (WAI) and rainfall are shown from 2002 to 2016. T_{soil} was measured at 5 cm for DE-Hai and 4 cm for DE-Lnf.

2.4.3 Cumulative net ecosystem productivity (NEP)

Figure 2.4 shows gap-filled cumulative net ecosystem productivity (NEP) data calculated from eddy covariance measurements of fluxes. Positive values correspond to a cumulative net uptake of CO_2 by the vegetation (atmospheric sink) and negative values a net loss (atmospheric source). At the beginning of each year, both forests are sources of CO_2. The

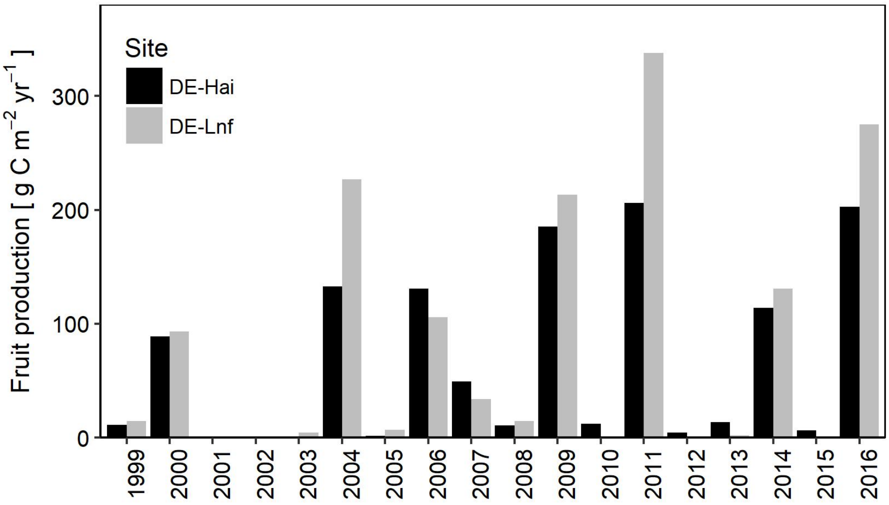


Figure 2.3: Total annual fruit production (g C m^2 yr^{-1}) in DE-Hai and DE-Lnf from 1999 to 2016. No data was recorded in 2001 and 2002.

average day of the year (doy) at which the net daily NEP switches from source to sink (i.e. shortly after leaf-out when the rate of change in the cumulative NEP goes from negative to positive) was 125 and 121 for DE-Hai and DE-Lnf, respectively (Table 2.5). But this was observed as early as doy 111 in DE-Hai and 112 in DE-Lnf in 2014, and as late as doy 134 in DE-Hai in 2010 and doy 130 in DE-Lnf in 2013. The forests continued to act as an overall C sink in average for 164 days and 168 days for DE-Hai and DE-Lnf, respectively. This

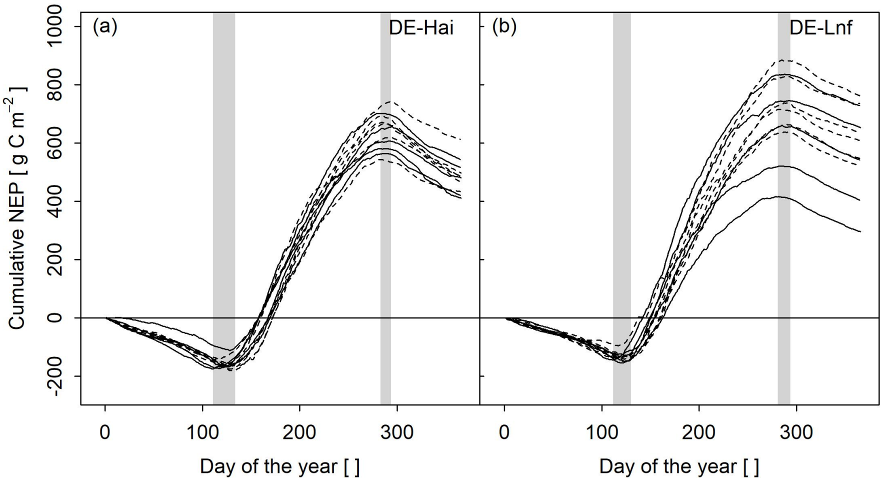


Figure 2.4: Cumulative net ecosystem productivity for (a) DE-Hai and (b) DE-Lnf. The solid lines indicate masting years and the dashed lines indicate remaining years. The vertical grey bars indicate the time of leaf out and leaf fall. The positive values of NEP indicate a cumulative carbon uptake by the ecosystem.

growing season length was significantly correlated with mean annual temperature (Figure 2.12). Longer growing season length and earlier start of growing season corresponded to higher annual carbon fluxes (Figure 2.13c, f, i).

Most of the variation in annual cumulative NEP occurred between the period of leaf out and leaf fall. The inter-annual variability in NEP during the growing season was larger in DE-Lnf compared to DE-Hai. On average, NEP in masting years was lower than in other years, with this difference being particularly visible in DE-Lnf (black solid lines in Figure 2.4b). The lowest cumulative NEP for both sites was measured in 2004, a year characterized by high fruit production but not the highest value observed during the study period.

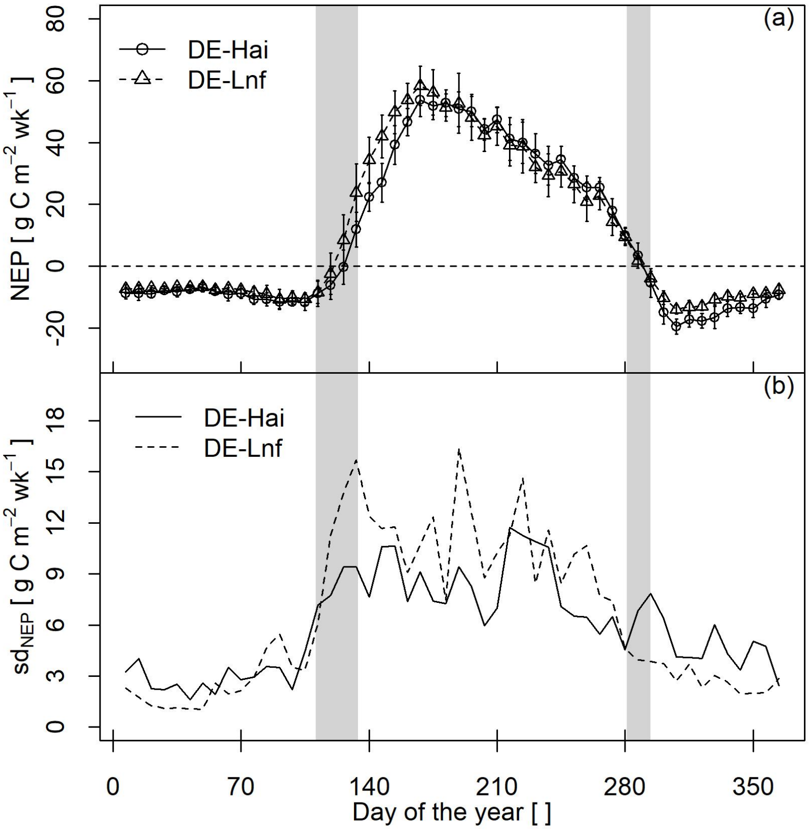


Figure 2.5: (a) The average annual NEP cycle, bar represents 95% confidence interval at 5% significance level and (b) standard deviation of weekly NEP. The grey horizontal bars show the range of the leaf out and leaf fall days of the two sites.

2.4.4 Seasonal variability of the CO_2 fluxes

Both sites have a similar average annual cycle of NEP (Figure 2.5a). Each point corresponds to the mean across years of weekly sums of NEP. Both forests reached the highest carbon uptake rate between doy 165 and 175. DE-Lnf showed a higher positive NEP at the start of the growing season, and DE-Hai was a stronger carbon source (black solid lines in Figure 2.5) from November to December.

Table 2.2: Zero-order correlation coefficients between seasonal carbon fluxes (NEP, GPP and Reco) and meteorological variables (mean of monthly values) for JFM (January - March), AM (April – May), JJ (June- July), A (August), SO (September – October) and ND (November – December) in DE-Hai and DE-Lnf. Bold numbers are statistical significant values at $p < 0.05$.

Season	site	T_{air}			T_{soil}			R_g			VPD			WAI		
		NEP	GPP	Reco	NEP	GPP	Reco	NEP	GPP	Reco	NEP	GPP	Reco	NEP	GPP	Reco
JFM	DE-Hai	-0.51		0.45	-0.52		0.58	-0.45		0.34	-0.55		0.41			
	DE-Lnf	-0.57		0.78	-0.49		0.71	-0.47		0.6	-0.66		0.8			
AM	DE-Hai	0.85	0.88	0.82	0.87	0.91	0.85	0.6	0.53	0.34	0.42	0.33	0.12			
	DE-Lnf	0.8	0.85	0.82	0.84	0.9	0.87	0.63	0.59	0.38	0.37	0.35	0.23			
JJ	DE-Hai	0.22	0.38	0.34	0.27	0.25	0.1	0.27	0.51	0.48	0.11	0.32	0.36	0	-0.07	-0.1
	DE-Lnf	0.11	0.24	0.37	-0.15	-0.04	0.2	0.57	0.54	0.21	0.16	0.23	0.24	-0.1	0	0.18
A	DE-Hai	-0.36	-0.27	-0.02	-0.36	-0.24	0.06	-0.38	-0.33	-0.15	-0.5	-0.49	-0.35	0.65	0.68	0.54
	DE-Lnf	-0.27	-0.24	0.06	-0.41	-0.34	0.13	-0.17	-0.17	-0.02	-0.23	-0.35	-0.3	0.08	0.37	0.65
SO	DE-Hai	0.75	0.83	0.74	0.79	0.86	0.73	0.87	0.88	0.55	0.65	0.69	0.53	-0.32	-0.33	-0.23
	DE-Lnf	0.62	0.7	0.81	0.7	0.77	0.86	0.76	0.8	0.75	0.46	0.52	0.59	-0.19	-0.18	-0.12
ND	DE-Hai	-0.76		0.79	-0.75		0.74	-0.78		0.79	-0.67		0.76			
	DE-Lnf	-0.69		0.75	-0.72		0.76	-0.61		0.64	-0.52		0.63			

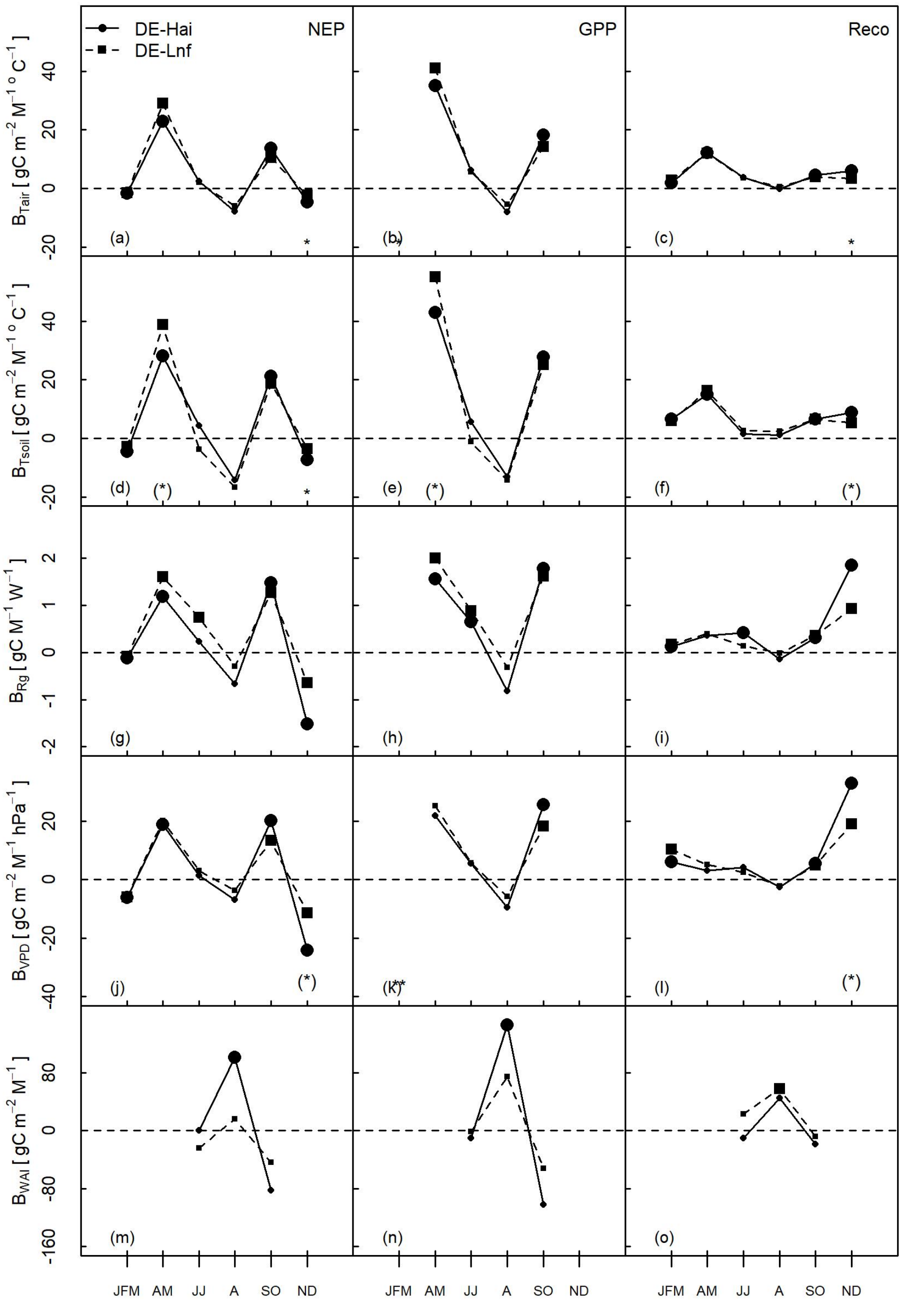


Figure 2.6: Slopes (B) between seasonal CO_2 fluxes (NEP - column 1, GPP - column 2 and Reco – column 3) and meteorological variables (mean of monthly values) for JFM (January - March), AM (April - May), JJ (June - July), A (August), SO (September – October) and ND (November - December). The larger circles and squares indicate slopes, which are significantly different from zero. *** indicate statistical significant difference of slopes between two sites at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$ at bottom of each figure (if any). The first letter of each month is used in the timescale.

Figure 2.5b shows the standard deviation of weekly NEP across years. The standard deviation of the early weeks of the year was low at both sites, and increased with the start of the growing season. A higher standard deviation in NEP was observed in DE-Lnf (dashed lines in Figure 2.5b) over the entire growing season. In DE-Hai (black solid lines in Figure 2.5b), the highest standard deviation was observed between doy 215 and 230. During the last days of the year, DE-Hai exhibited a higher standard deviation compared to DE-Lnf. For further analysis, we separated the year into different seasons, winter months (November – December: ND, January - March: JFM), spring (April – May: AM), summer (June- July: JJ), August (A) and fall (September – October: SO), to account for the different drivers and dynamcs of NEP in these periods. August was treated separately from the main growing season as it is a particularly dry month and large variability observed in this period (see Figure 2.5b and Table 2.2).

2.4.5 Meteorological factors controlling seasonal variability in CO_2 fluxes

For each site, Table 2.2 (correlation coefficients) and Figure 2.6 (absolute slopes) show the effect of measured meteorological factors on CO_2 fluxes for different seasons of the year (see section 2.4.4). In winter, NEP was correlated with T_{air}, T_{soil}, R_g, and VPD at both sites with stronger correlation in ND than JFM (Table 2.2). In ND, NEP was significantly sensitive (higher absolute slopes) to T_{air}, T_{soil} and VPD in DE-Hai than in DE-Lnf (Figure 2.6).

With the arrival of spring (April May, AM), T_{soil} became the most important factor controlling spring NEP, GPP and Reco in both sites, followed in importance by T_{air}, and R_g. A 1 °C change in spring T_{soil} changed the NEP by 28.07 ± 6.92 and 38.74 ± 11.19 $mathrmg\ C\ m^{-2}\ month^{-1}$ in DE-Hai and DE-Lnf, respectively. NEP was driven mainly by GPP, as seen by comparing $B_{TsoilGPP}$ (slope between T_{soil} and GPP, Figure 2.6e) and $B_{TsoilReco}$ (slope between T_{soil} and Reco, Figure 2.6f) for this period. NEP and GPP of DE-Lnf was more sensitive to T_{soil} than DE-Hai with significantly higher B_{Tsoil} NEP (Figure 2.6d) and B_{Tsoil} GPP (Figure 2.6e).

In summer (June – July, JJ), R_g remained a significant factor while other relationships weakened. In DE-Hai, R_g showed a weak relationship with NEP but significantly correlated with both GPP and Reco, while in DE-Lnf it was significantly correlated with NEP and GPP. The sensitivity of NEP and GPP to R_g was higher in DE-Lnf compared to DE-Hai. A change in 1 W m^{-2} of R_g increased NEP by 0.74 ± 0.47 ($p < 0.01$) g C m^2 $month^{-1}$ in DE-Lnf and about 0.23 ± 0.37 ($p = 0.11$) g C m^2 $month^{-1}$ in DE-Hai and the difference between the sites is significant ($p < 0.1$). In August (A), only the soil water availability index (WAI) correlated significantly with CO_2 fluxes, specifically with NEP, GPP and Reco in DE-Hai and only with Reco in DE-Lnf. In fall (September – October, SO), T_{air}, T_{soil}, R_g and VPD, again became significantly correlated with NEP, GPP and Reco in both sites, with high correlation values for the first three and slightly lower ones for VPD.

2.4.6 Seasonal differences in CO_2 fluxes between the two sites

In addition to slopes, we also looked at differences of average seasonal sums of NEP, GPP and Reco between sites (Figure 2.7). Significantly higher NEPs observed in DE-Lnf than in DE-Hai in JFM and ND (5.48 and 17.79 g C m^{-2} $month^{-1}$, Figure 2.7a) was due to lower

Reco in DE-Lnf (Figure 2.7c). DE-Lnf also acted as a stronger carbon sink in the spring (26 g C m^{-2} $month^{-1}$) which was mostly due to higher GPP of 24 g C m^{-2} $month^{-1}$. In JJ, difference between NEP in two sites were insignificant because both GPP and Reco in DE-Lnf were significantly higher by 19.08 g C m^{-2} $month^{-1}$ and 10.94 g C m^{-2} $month^{-1}$, respectively. During August, NEP and GPP were similar in both sites, however, a higher Reco was observed in DE-Lnf (10.04 g C m^{-2} $month^{-1}$). In the fall, NEP, GPP and Reco were lower in DE-Lnf but differences were insignificant.

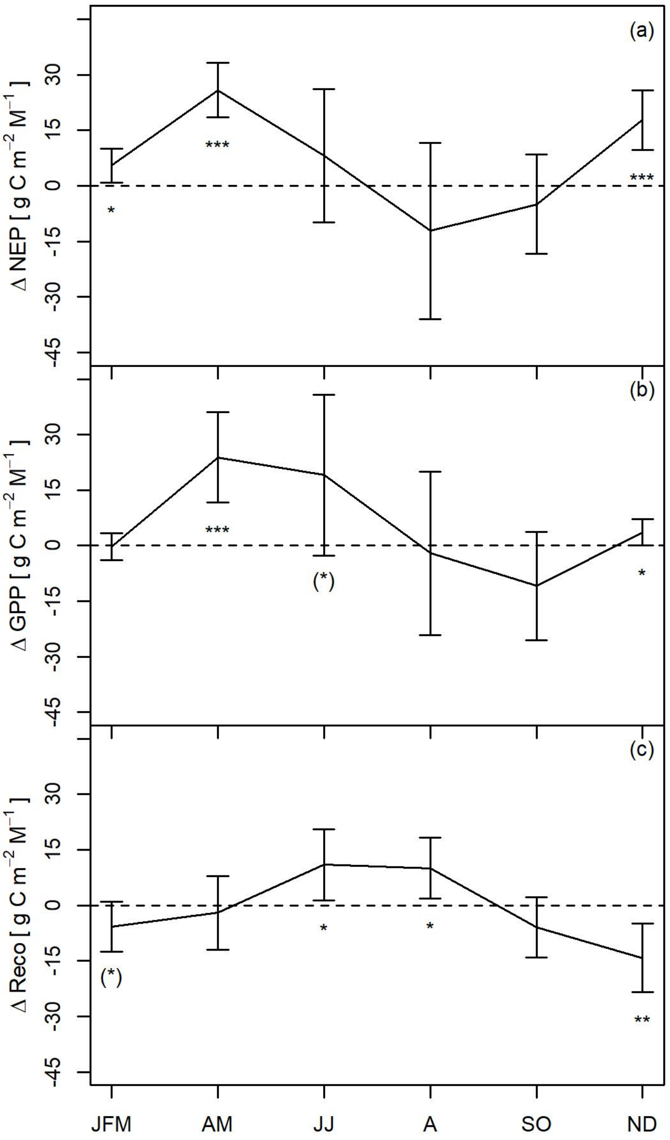


Figure 2.7: Difference in sum of (a) NEP, (b) GPP and (c) Reco between the two sites for JFM (January - March), AM (April – May), JJ (June- July), A (August), SO (September – October) and ND (November – December). The Y-axis represents X = XDE-Lnf – XDE-Hai (X being seasonal NEP, GPP or Reco). Bars represent 95% confidence interval. The dashed line marks the zero line (indicates no difference between the sites). *** indicate statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$.

2.4.7 Annual estimates of NEP, GPP and Reco

Annual gap-filled NEP, GPP and Reco for both sites are presented in Figure 2.8. Mean Annual NEP was 487 ± 57.8 (mean ± SD for the mean of all years) and 585 ± 144 g C m^{-2} yr^{-1} in DE-Hai and DE-Lnf, respectively. A paired t-test showed that difference between the sites was significant (98 g C m^{-2} yr^{-1}, $p < 0.05$). We observed the largest differences in NEP between the two sites from 2010 (Table 2.6). Annual NEP was significantly more variable in DE-Lnf (Levene's test with $p < 0.05$), with coefficients of variation (CV) being 12 % and 25 % in DE-Hai and DE-Lnf, respectively. A significant temporal trend of NEP was observed only for DE-Lnf, with an increase of 21.8 g C m^{-2} yr^{-1} ($p < 0.05$). The mean of annual GPP values at DE-Hai and DE-Lnf was 1559 ± 118 and 1627 ± 164 g C m^{-2} yr^{-1} respectively, with the difference being statistically significant ($p = 0.07$). Like NEP, significantly higher annual GPP was again observed in DE-Lnf from 2010 (Table 2.6). The variability in annual GPP was not significantly different between the two sites, with coefficients of variation (CV) equalling 7.5 % and 10 % in DE-Hai and DE-Lnf, respectively. As for annual NEP, no temporal trend in annual GPP was observed in DE-Hai, whereas a significant trend of 25.5 g C m^{-2} yr^{-1} ($p < 0.05$) was observed in DE-Lnf. The mean annual ecosystem respiration (Reco) was 1071 ± 96 and 1042 ± 60 g C m^{-2} yr^{-1} in DE-Hai and DE-Lnf, respectively with no significant difference between sites. In contrast to annual NEP and GPP, annual Reco was lower in DE-Lnf with no significant difference. Annual Reco showed a positive temporal trend at both sites but it was statistically insignificant (Table 2.4).

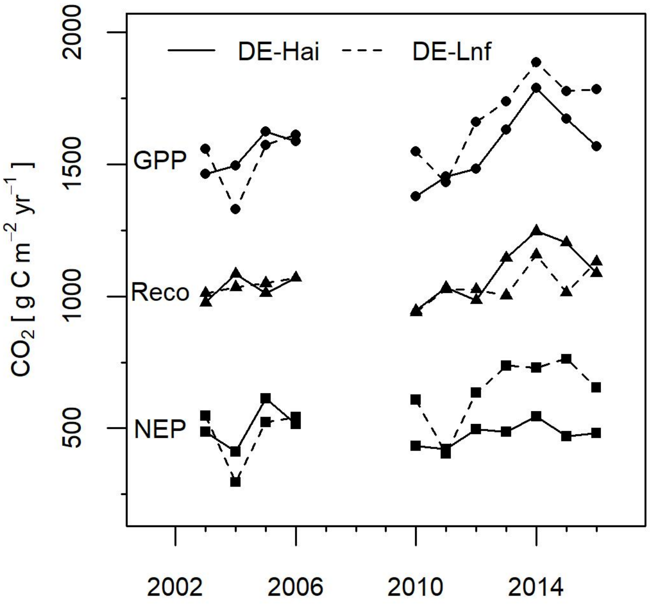


Figure 2.8: Annual sums of GPP, Reco and NEP from 2003 to 2016. Data from 2007 to 2009 was not measured in DE-Lnf.

2.4.8 Factors contributing to annual variability of NEP, GPP and Reco

Together, fruit production (FP), time (see the section 2.3.4) and mean annual soil temperature (T_{soil}) explained ca. 65 % and 92 % of the variation in annual NEP in DE-Hai and DE-Lnf, respectively (Table 2.3). In DE-Hai, T_{soil} was the most important factor, followed by FP (negative correlation). In the case of DE-Lnf, time and FP explained most of the variation. Results were similar for annual GPP, with a total R^2 of 0.62 and 0.88 in DE-Hai and DE-Lnf, respectively. T_{soil} was the only significant variable for DE-Hai, explaining most of the variation in GPP. In DE-Lnf, time was the strongest predictor variable, followed by T_{soil} and FP (negative correlation). A significant relationship between annual Reco was found only for DE-Lnf with T_{soil} as the only significant variable. Figure 2.9 shows the relationship between each of the three significant driving variables (T_{soil}, FP, time) and the three flux quantities (NEP, GPP, Reco) in terms of the residual variance remaining after the effects of the other two driving variables (e.g. FP and time, in the case of T_{soil}) have been removed. This analysis increased the amount of variation in NEP and GPP explained by T_{soil}. We tested the difference between the slopes of two sites obtained in Figure 2.9 (Table 2.7). The sensitivities of NEP on T_{soil} were similar between the sites when the effect of fruit production and time is removed. The result was similar for GPP. Similarly, fruit production was significantly correlated with residuals of NEP after removing effect of T_{soil} and time (Figure 2.9b) in both sites. We observed that residuals of GPP decreased with increased fruit production, but significant only for DE-Lnf and with a more than twice as large slope (Figure 2.9e and Table 2.7). Slope between residuals of annual Reco and fruit production was not significantly different from zero for both sites but had a positive slope for DE-Lnf. Only in DE-Lnf, we observed positive slope between time and residuals of NEP after removing the effect of T_{soil} and FP (2.9c and Table 2.7). We also observed higher slope of residuals of GPP (Figure 2.9f) compared to residuals of Reco (Figure 2.9i) to time. In DE-Hai, positive slope between time and residuals of GPP was negated by Reco, thus showing no effect in residuals of NEP.

Table 2.3: Major factors contributing to the variation of annual NEP, GPP and Reco. Var is the contribution of each predictor to total R^2 calculated with the product measure metric.

		DE-Hai			DE-Lnf		
Flux	Predictors	R2	Coefficients	Var	R2	Coefficients	Var
NEP		0.65			0.92		
	Tsoil +		110.48 *	0.49		79.94 (*)	0.07
	FP +		-0.34 (*)	0.15		-0.74 ***	0.34
	Time		-0.99	0		22.30 ***	0.51
GPP		0.62			0.88		
	Tsoil +		208.08 *	0.49		189.95 *	0.28
	FP +		-0.23	0		-0.60 **	0.13
	Time		8.93	0.13		22.57 *	0.46
Reco		0.45			0.79		
	Tsoil +		97.61	0.19		109.90 **	0.65
	FP +		0.02	0		0.14	0.14
	Time		9.92	0.25		0.27	0

*** significant at $p < 0.001$; ** $p < 0.01$; * at $p < 0.05$; (*) at $p < 0.1$

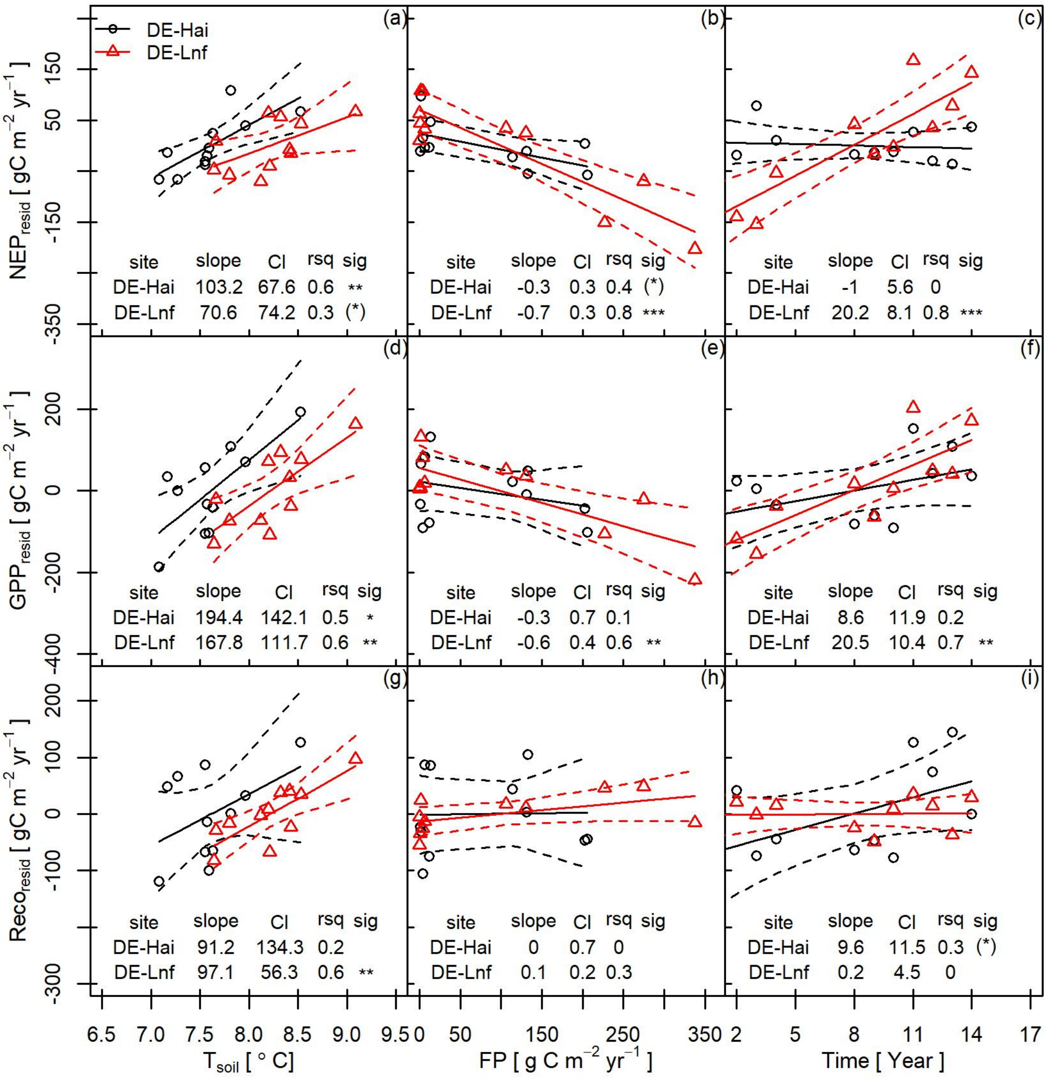


Figure 2.9: Simple linear regressions between residuals of different carbon fluxes after removing effect of fruit production and time (1st column, a, d, g), T_{soil} and time (2nd column, b, e, h) or T_{soil} and fruit production (3rd column, c, f, i). Here time is represented by number plus 2000 for clean graph. The solid lines represent linear regression lines and dashed lines confidence interval at 5 % significance level. *** indicate statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$.

2.5 Discussions

2.5.1 Meteorological controls of seasonal CO_2 fluxes

We observed stronger sensitivity of winter Reco to T_{soil} (Figure 2.6) resulting in higher Reco in DE-Hai than in DE-Lnf, thus, higher winter NEP in DE-Lnf (Figure 2.7). Higher ecosystem respiration is most likely driven by higher stocks of decaying dead wood and by higher rates of leaf litter decomposition caused by higher leaf litter quality (proportion of litter from ash and maple trees) and a higher biological activity in the soil (MUND, 2004). In spring, NEP, GPP and Reco strongly correlated with T_{air} and T_{soil} with higher correlation values for T_{soil} in both sites. The change of NEP with T_{soil} was mostly driven by the sensitivity of GPP to T_{soil}. Similar results were also observed in Borden forest, Canada, during the spring time (Froelich et al., 2015). Spring temperature is very important for leaf unfolding and we found that the growing season started earlier when spring air temperatures were higher (Figure 2.14). Also, warm soil means favourable growth conditions for roots (ALVAREZ-URIA et al., 2007), improving nutrient and water uptake and leading to increased photosynthesis. Along with GPP, Reco also increases with increased soil temperature, due to the increased activities of tree roots and microbes (DAVIDSON et al., 1998; GONZALEZ-MELER et al., 2013). DE-Lnf was a significantly stronger sink during spring, primarily driven by GPP (Figure 2.7). We further observed higher sensitivity of GPP to T_{soil} in DE-Lnf than in DE-Hai ($p < 0.1$). This could be explained by an earlier physiological activity in beech than in ash (COLE et al., 2017). DE-Lnf is a beech monoculture comprising mostly vital trees at their optimal age (optimal regarding wood growth and fruit production) whereas DE-Hai has 28% ash trees and includes many small, young, suppressed, very old, semi-dead and dead trees. In summer (June - July), R_g was the most important abiotic environmental factor controlling carbon fluxes of both sites. DE-Lnf was a stronger sink with higher GPP and Reco because it is full of optimally growing trees that may have capitalised the radiation more than DE-Hai. Similarly, the stronger sensitivity of summer GPP and Reco to R_g of DE-Lnf can be attributed to optimally growing trees of similar size and age that react to weather conditions in same direction and magnitude. August is of interest for DE-Hai where soil water availability (WAI) influences its CO_2 fluxes. DE-Hai is more affected than DE-Lnf by water availability because of ash trees that are still active when WAI drops below a critical value (e.g. 2003). Trees close their stomata as the soil water availability reduces to prevent water loss (CHAVES et al., 2002) also decreasing photosynthesis and respiration.

2.5.2 Annual CO_2 fluxes and its inter-annual variability

Before comparing DE-Lnf with DE-Hai, it is useful to discuss site management and history. DE-Lnf is an example of a managed even-aged forest that was established and thinned as part of a regular shelterwood system with a rotation period of about 120-140 years. In recent years the management starts to transfer the shelterwood system towards a system of target diameter harvesting. Currently, DE-Lnf represents a mature forest at its optimum phase. If parts of the forest were not certified for seed production, and if the eddy tower were not there, the forest might have been thinned more heavily. This means under a different thinning regime or at another point in time living biomass and/or NEP might be different. For a comparison of managed, even-aged forests with unmanaged forests a chronosequence of several even-aged stands covering the entire rotation period would be needed. We thus note that the heterogeneous stand is not being compared with the average managed beech forest in the region, but rather with a mature and productive stand. This must be considered before concluding on the general impact of management on carbon sequestration in forest ecosystems. Both the sites were strong carbon sinks despite one site being in an advanced stage of growth with trees as old as 265 years. The ranges of annual NEP were comparable with Oak Ridge forest in Tennessee, US (577 ± 63 g C m^{-2} yr^{-1}, Wilson et al. 2001), Ozarks forest in Missouri, US (479 ± 65 63 g C m^{-2} yr^{-1}, Shao et al. 2014), and Oak woodland forests, UK (486 ± 115 g C m^{-2} yr^{-1} , Wilkinson et al. 2012) but slightly higher than average annual NEP for temperate forests (350 ± 100 g C m^{-2} yr^{-1}, Table 2.8). Average annual GPP and Reco of both sites also fell within the range average annual GPP (1506 ± 214 g C m^{-2} yr^{-1}) and Reco (1181 ± 158 g C m^{-2} yr^{-1}) of temperate deciduous forests. A previous study of the same sites using seven years of data (Herbst et al., 2015) reported small but non-significant difference between the sites for NEP. However, by including four more recent years we found a significant difference in NEP between the two sites. The absolute difference in mean annual NEP (98 g C m^{-2} yr^{-1}) results from a higher mean annual GPP of 69 g C m-2yr-1 (2/3 of NEP) plus a lower mean annual Reco of 29 g C m^{-2} yr^{-1} (1/3 of NEP) in DE-Lnf. The higher mean annual values of NEP in DE-Lnf is due to higher annual NEP from 2010 than DE-Hai. From 2010, significantly higher GPP and lower Reco in DE-Lnf resulted in higher NEP. The higher carbon uptake in DE-Lnf was determined by the activities during winter, spring and summer (section 4.1). We observed lower coefficient of variation (CV) of annual NEP for both the sites compared to average CV of annual NEP of temperate forests. Average CV of annual NEP for temperate forests is 35 % (sd = ± 100 g C m^{-2} yr^{-1}, Baldocchi 2018 and Table 2.8) with the highest CV of 66 % observed in the Borden forest (Froelich et al., 2015) and Sorø forest (Pilegaard et al., 2011). Interestingly, the CV of annual NEP in DE-Hai was the lowest among reported results for temperate deciduous forests and remained similar even after adding four years of data. Also, the CV of annual GPP and Reco of both sites were lower than the average for temperate deciduous forests. Like annual NEP, CV of annual GPP in DE-Hai was lowest among all the temperate deciduous broadleaved forests following the results of Musavi et al., 2017 that reported older and diverse forests had less variation in saturated gross primary productivity (GPPsat). Between our sites, the managed, homogeneous forest showed a higher CV in NEP and GPP than the unmanaged, heterogeneous forest. Long-term studies conducted in temperate deciduous forests have identified many factors contributing to site-specific inter-annual variation of NEP. Some studies have found that growing season length explains inter-annual variation in NEP: the Borden forest in Canada (Froelich et al., 2015), Sorø forest in Denmark (Pilegaard et al., 2011), Hesse forest (Granier et al., 2008), Morgan-Monroe State Forest in Indiana (Dragoni et al., 2011). In our case, we observed positive correlation between growing season length and NEP and GPP (Figure 2.13e, f and g), and at the same time positive correlation between growing season length and temperatures (Figure 2.12). Among T_{air} and T_{soil}, we found stronger relationship of T_{soil} with NEP and GPP (Figure 2.15 and Figure 2.16), this could have led to selection of T_{soil} in multiple linear model selection using AIC criteria. At an annual scale, we found that sensitivities of T_{soil} to NEP and GPP were similar based on residual analysis conducted after removing effect of fruit production and time. Other two important factors that explained annual fluxes were fruit production and time. We will discuss them separately in section 4.3 and 4.4.

2.5.3 Effect of fruit production on CO_2 fluxes

Fruit production (FP) was negatively correlated with NEP at both sites (Figure 2.17). The negative slope of NEP vs fruit production was mostly the result of a reduction of GPP in high fruit production years, i.e. photosynthesis decreased with increasing fruit production. Many studies reported that tree ring growth was reduced in years of high fruit production (e.g. Holmsgaard 1955; Mund et al. 2010). Different mechanisms have been reported for this reduced growth in trees, including reduced photosynthetic rates in reproductive branches due to N or P depletion in those branches (Sala et al., 2012), smaller leaves (Innes, 1992), reduced leaf area (Ferretti et al., 1998), lower number of leaves during the mast year (Han et al., 2008) which could be due to diminished shoot growth and increased foliar bud mortality (Ishihara et al., 2009) as foliar buds are replaced by seeds (Innes, 1994). It is important to note that the effect was stronger in DE-Lnf - a homogeneous forests with trees in a similar fruit-producing age class (150 -170 years) (Herbst et al., 2015). On the other hand, DE-Hai has a heterogeneous structure with different species and a wide range of tree age from 0 to 265 years. Thus, beech fruit production does not occur in all trees (Figure 2.3).

2.5.4 Effect of time on CO_2 fluxes

Many studies report that CO_2 fluxes in temperate forests have been increasing (Fernández-Martínez et al. 2017; Froelich et al. 2015; Granier et al. 2008; Pilegaard et al. 2011, etc). A significant increasing temporal trend in CO_2 uptake has also been observed in ca. 80 year-old managed beech forest in Sorø, Denmark (-23 g C m^{-2} yr^{-1}, Pilegaard et al. 2011), ca. 40 year-old managed beech forest in Hesse, France (-43 g C m^{-2} yr^{-1}, Granier et al. 2008) and ca. 95 year-old managed maple, red oak and white oak Harvard forest in US (-16 g C m^{-2} yr^{-1}, Urbanski et al. 2007). We observed a similar temporal trend in NEP in DE-Lnf, a managed homogeneous forest, which was not visible when Herbst et al. (2015) reported 7 years' data. The NEP of DE-Hai was reported to be - 494 g C m^{-2} and - 490 g C m^{-2} for 2000 and 2001, respectively by Knohl et al. (2003) and the capacity remained in the same range for all 12 years described here, exhibiting no significant temporal trend. However, we observed positive trends in annual GPP and Reco at DE-Hai which might have cancelled resulting in no trend in NEP. The normal temporal trend in forest productivity is to follow a sigmoidal growth curve as individuals age. Overlaid on this, however, are the impacts of increasing atmospheric CO_2 concentration, decreasing sulphur deposition (Fernández-Martínez et al., 2017), increasing nitrogen deposition, as well as management activities such as thinning. Here we used time as a variable because it is hard to disentangle these effects. Thus, our observed temporal trend in DE-Lnf needs a careful interpretation because the trend appears to reflect an increase in CO_2 uptake starting from 2012 (Figure 2.8), and there was no significant temporal trend in any of the observed meteorological variables that could explain this increase (Table 2.4). We observed a positive trend in growing season length (0.75 days per year, $p < 0.05$) which explained about 19 % variability in NEP ($p = 0.16$) but not as high as it has been reported for Hesse (Granier et al., 2008), Sorø (Pilegaard et al., 2011), Borden forest (Froelich et al., 2015), and Morgan Monroe state forest (Dragoni et al., 2011). As an alternate hypothesis, we note that thinning operations were carried out in the main flux footprint area of DE-Lnf, and we speculate that because thinning has the effect of increasing productivity in the remaining trees, this might have impacted NEP subsequently. About 2850 g C m^{-2} of biomass was thinned from the footprint area from 2002 to 2006 (Figure 2.10) with the largest thinning carried out in 2004 (782 g C m^{-2}). For comparison, NEP in the period 2010 – 2016 was, in average, 171 g C m^{-2} yr^{-1} higher than in the period 2003 – 2006 (Table 2.6), amounting to 1197 g C m^{-2} of additional carbon in this period. Thus, it is likely that management is a strong driver of inter-annual variability in productivity, with the changes we observed being a response to thinning extended over several years. We note that Sorø was thinned about 20 % every 10 years (Pilegaard et al., 2011) and Hesse was thinned every five years (Granier et al., 2008), yet these authors did not report any significant effect of thinning on CO_2 fluxes. This could be due to the effects of thinning being seen only gradually over the following years as trees adjust to the new conditions, thus making the connection between C fluxes and thinning difficult to perceive or quantify.

2.6 Conclusions

We compared two temperate deciduous forest types with similar site and meteorological conditions but with different structure in terms of diameter distribution, age and species composition. We found that the homogeneous forest had a higher mean annual NEP than the heterogeneous forest due to lower respiration rates in winter and higher carbon uptake rates in spring and summer. CO_2 uptake by the homogeneous forest has increased in recent years playing a key role in determining differences between the forests. We identified an overall time-effect but could not disentangle possible contributing factors such as increasing atmospheric CO_2 concentrations or effects of silvicultural management. In the introduction section, we put forward two hypotheses. Regarding hypothesis one, i.e. higher sensitivity of carbon fluxes of homogenous forests to abiotic environmental variables, we concluded that the homogenous forest showed a stronger sensitivity to abiotic environmental variables during spring (T_{soil}) and summer (R_g) causing inter-annual differences between sites. At annual scale, however, the sensitivities of CO_2 fluxes to abiotic environment variables are similar due to stronger control by biotic factors. In case of the second hypothesis, i.e. a higher negative sensitivity of CO_2 fluxes of the homogenous forest to fruit production, we see that the NEP of the homogenous forest showed a stronger sensitivity to fruit production due to a higher negative sensitivity of GPP and higher positive sensitivity of Reco to fruit production. The relationships are weak; thus, we suggest that more data are required to confirm the hypothesis. Even though both forests are of same average age, structures of these forests vary. This leads to different responses of the CO_2 fluxes to abiotic and biotic factors. Thus, it is necessary that we include structural information along with species traits (fruiting characteristics) and management activities to be able to predict the CO_2 fluxes in response to future climate.

2.7 Supplementary materials

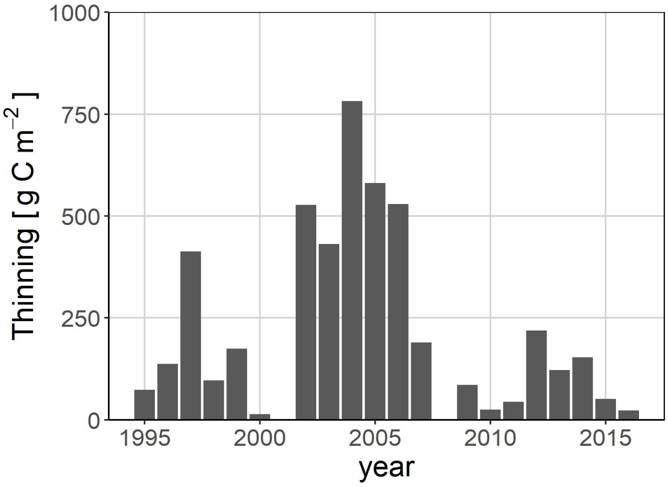


Figure 2.10: Annual footprint weighted thinning in eddy flux footprint area (calculated using Kljun et al., 2015) of DE-Lnf from 1995 to 2016. The highest thinning of 995 g C m-2 was conducted in 2005 from the footprint area.

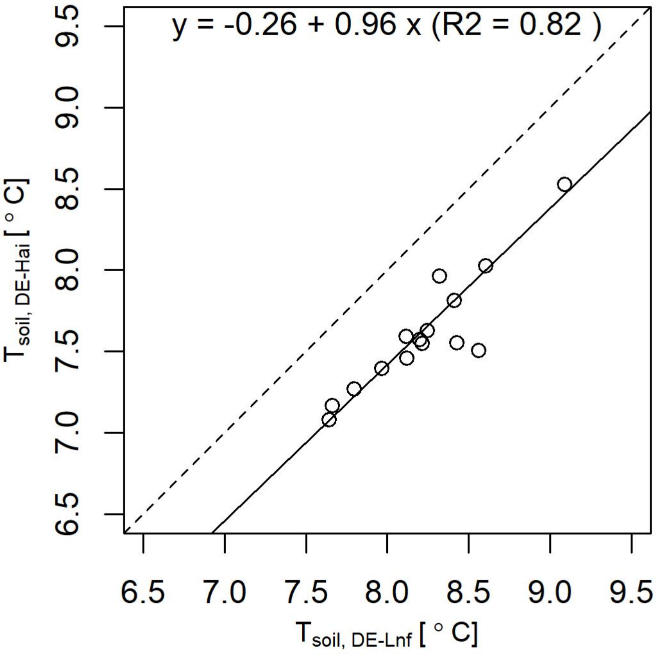


Figure 2.11: Linear regression between mean annual T_{soil} of DE-Lnf and DE-Hai. Dashed line represents a line with slope 1. Systematic difference between sites is due to difference in measurement depths (5 vs 4 cm in DE-Hai and DE-Lnf, respectively).

Table 2.4: Average Annual values (mean and sd) and the temporal trend during the study period for all dependent and selected predictor variables for both sites. Units for GSS (growing season start day), and GSE (growing season end day) is doy yr-1 where doy indicates Julian day of the year. Trend is the temporal trend and * indicates the statistically significant values at 5% significance level.

Variables	Units	DE-Hai		DE-Lnf	
		mean ± sd	trend	mean ± sd	trend
R_g	$W\ m^{-2}$	122 ±6.5	0.18	124 ±7.2	0.62
T_{air}	°C	8.34 ± 0.72	0.03	8.3 ±0.7	0.05
T_{soil}	°C	7.61 ± 0.36	0.01	8.23±0.38	0.02
VPD	hPa	3.45± 0.56	0.02	3.28±0.48	0
Rain	mm	744 ± 152	-6.76	601 ±154	-9.12
WAI	-	0.86 ± 0.09	-0.01	0.84±0.1	0
NEP	$g\ C\ m^{-2}\ yr^{-1}$	487 ± 57.8	-3.14	585 ± 144	21.8*
GPP	$g\ C\ m^{-2}\ yr^{-1}$	1558± 118	4.25	1627±164	25.5*
Reco	$g\ C\ m^{-2}\ yr^{-1}$	1071± 96	0.28	1042± 60	0.08
GSS	doy	125 ± 7	-0.42	121 ± 5	-0.29
GSE	doy	289 ± 4	-0.35	288 ± 5	0.45
GSL	day	164 ± 7	0.07	168 ± 6	0.75*

Table 2.5: Growing season start day (GSS), end day (GSE) and length (GSL) for DE-Hai and DE-Lnf during the study period.

Year	DE-Hai			DE-Lnf		
	GSS (doy)	GSE (doy)	GSL (days)	GSS (doy)	GSE (doy)	GSL (days)
2003	125	292	167	123	290	167
2004	123	288	165	121	281	160
2005	125	293	168	122	291	169
2006	127	294	167	126	294	168
2010	134	283	149	123	283	160
2011	117	288	171	114	285	171
2012	129	289	160	124	290	166
2013	131	288	157	130	292	162
2014	111	284	173	112	288	176
2015	114	284	170	117	293	176
2016	130	292	162	117	292	175
Average	125	289	164	121	289	168
Sd	7	4	7	5	4	6

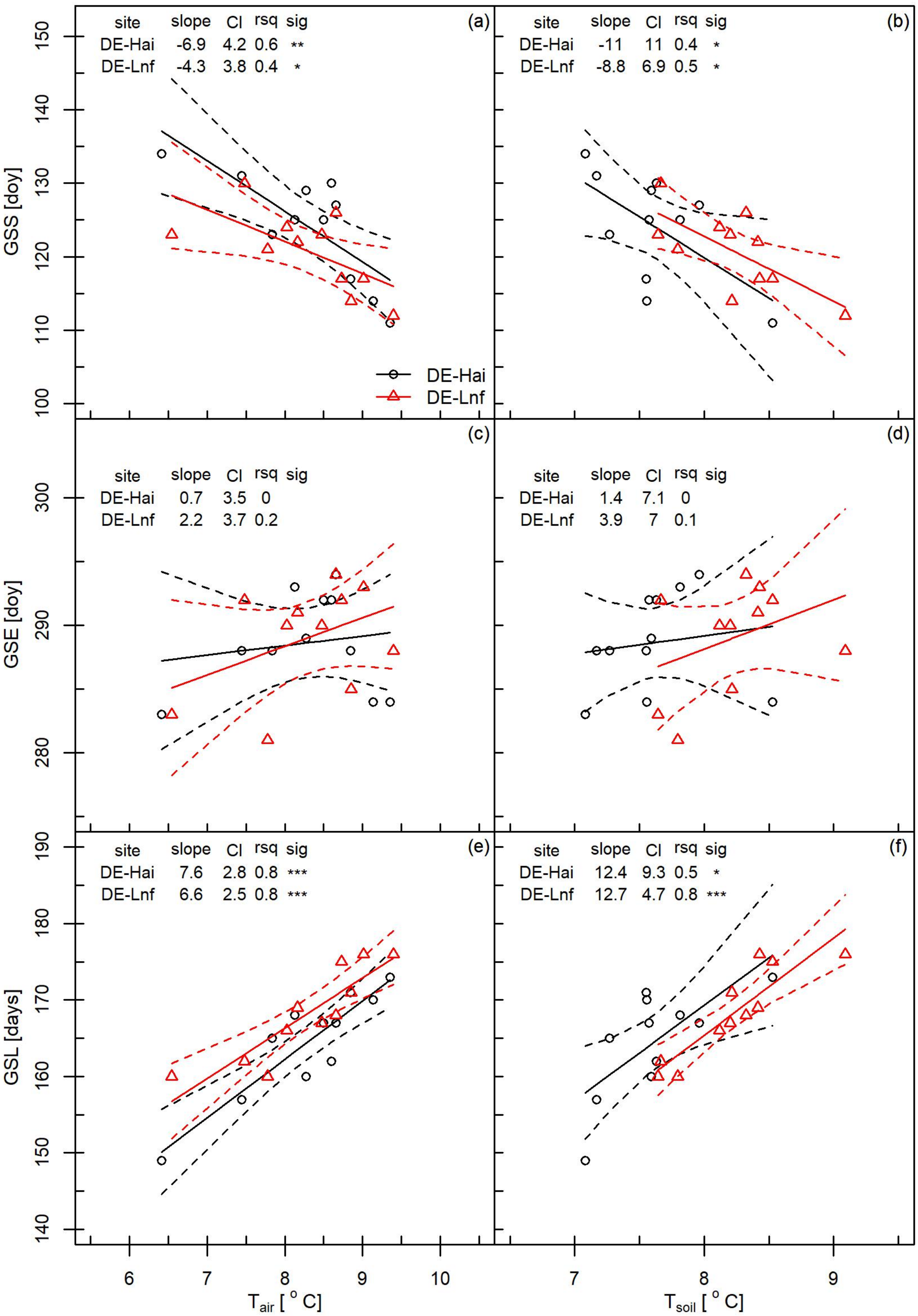
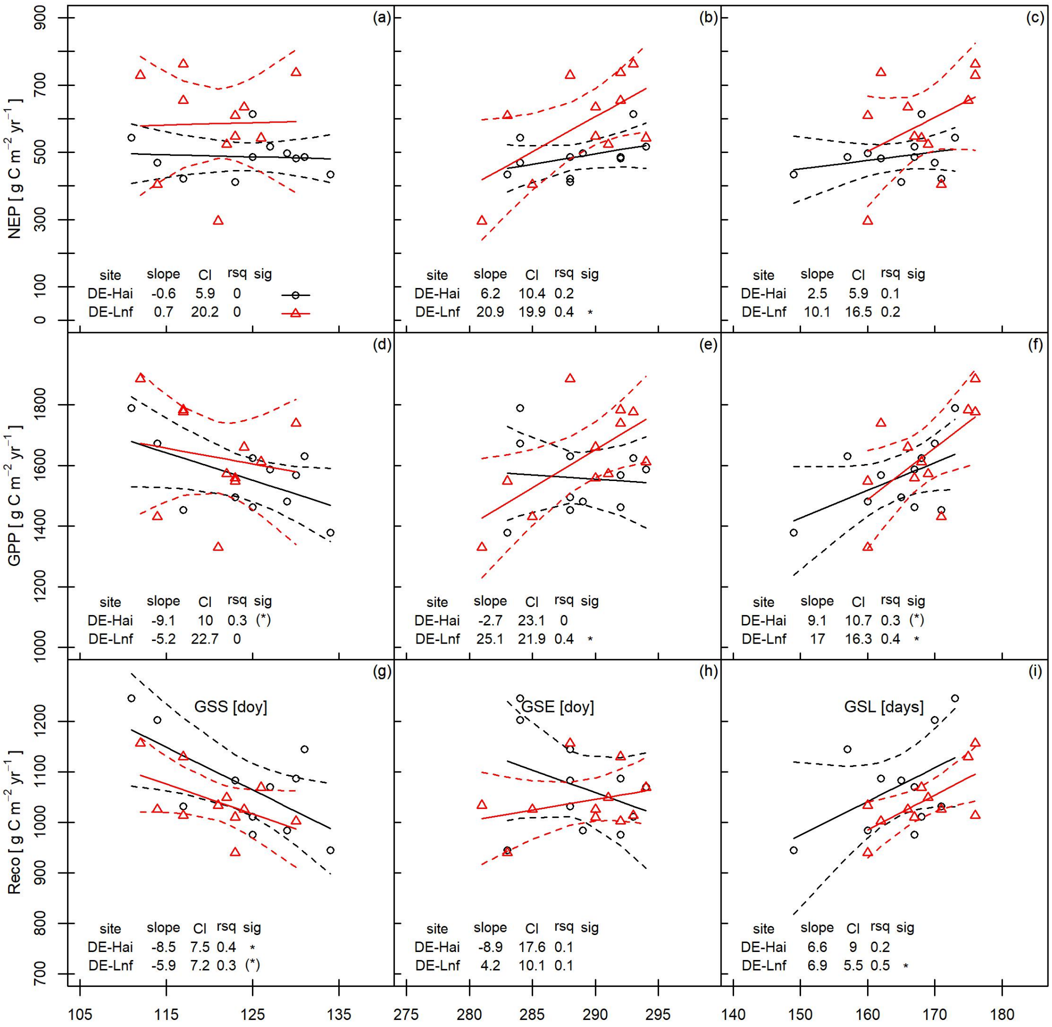


Figure 2.12: Relationship between T_{air} and T_{soil} with growing season matrix. GSS is growing season start day indicated by day of the year (doy), GSE is growing season end day indicated by day of the year (doy) and GSL is growing season length indicated by number of days. CI is 95% confidence interval of slope and rsq the coefficient of determination of linear regression, and sig its significance (*** indicates statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$). The solid lines represent linear regression lines and dashed lines 95 % confidence interval.



site	slope	CI	rsq	sig
DE-Hai	-0.6	5.9	0	
DE-Lnf	0.7	20.2	0	

site	slope	CI	rsq	sig
DE-Hai	6.2	10.4	0.2	
DE-Lnf	20.9	19.9	0.4	*

site	slope	CI	rsq	sig
DE-Hai	2.5	5.9	0.1	
DE-Lnf	10.1	16.5	0.2	

site	slope	CI	rsq	sig
DE-Hai	-9.1	10	0.3	(*)
DE-Lnf	-5.2	22.7	0	

site	slope	CI	rsq	sig
DE-Hai	-2.7	23.1	0	
DE-Lnf	25.1	21.9	0.4	*

site	slope	CI	rsq	sig
DE-Hai	9.1	10.7	0.3	(*)
DE-Lnf	17	16.3	0.4	*

site	slope	CI	rsq	sig
DE-Hai	-8.5	7.5	0.4	*
DE-Lnf	-5.9	7.2	0.3	(*)

site	slope	CI	rsq	sig
DE-Hai	-8.9	17.6	0.1	
DE-Lnf	4.2	10.1	0.1	

site	slope	CI	rsq	sig
DE-Hai	6.6	9	0.2	
DE-Lnf	6.9	5.5	0.5	*

Figure 2.13: Simple linear regression between NEP, GPP and Reco with growing season start day (GSS), growing season end day (GSE) and growing season length day (GSL). CI is 95% confidence interval of slope and rsq the coefficient of determination of linear regression, and sig its significance (*** indicates statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$). The solid lines represent linear regression lines and dashed lines 95 % confidence interval.

Table 2.6: Mean annual fluxes for two periods (2003-2006 and 2010-2016) and differences between two sites. Differences between sites were tested using paired t-test.

period	Flux	DE-Hai (mean ± sd)	DE-Lnf (mean ± sd) [g C m^{-2} yr^{-1}1]	$Diff_{Lnf-Hai}$ [g C m^{-2} yr^{-1}]
	NEP	506 ± 84	476 ± 122	30
2003-2006	GPP	1542 ± 76	1517 ± 128	25
	Reco	1035 ± 50	1040 ± 25	2
	NEP	476 ± 41	647 ± 121	171**
2010-2016	GPP	1568 ± 142	1689 ± 156	121**
	Reco	1092 ± 112	1042 ± 76	-50

Table 2.7: Difference between the two sites with respect to slopes between each of the three significant driving variables (T_{soil}, FP, time) and the three flux quantities (NEP, GPP, Reco) in terms of the residual variance remaining after the effects of the other two driving variables (e.g. FP and time, in the case of T_{soil}) have been removed.

CO_2 flux	Variable	Slope difference (DE-Hai – DE-Lnf)	SE
NEP	T_{soil}	32.6	44.5
GPP	T_{soil}	26.6	79.6
Reco	T_{soil}	-5.9	63.4
NEP	FP	0.4*	0.2
GPP	FP	0.3	0.3
Reco	FP	-0.1	0.3
NEP	Time	-21.2**	4.3
GPP	Time	-11.9(*)	7
Reco	Time	9.3(*)	5.5

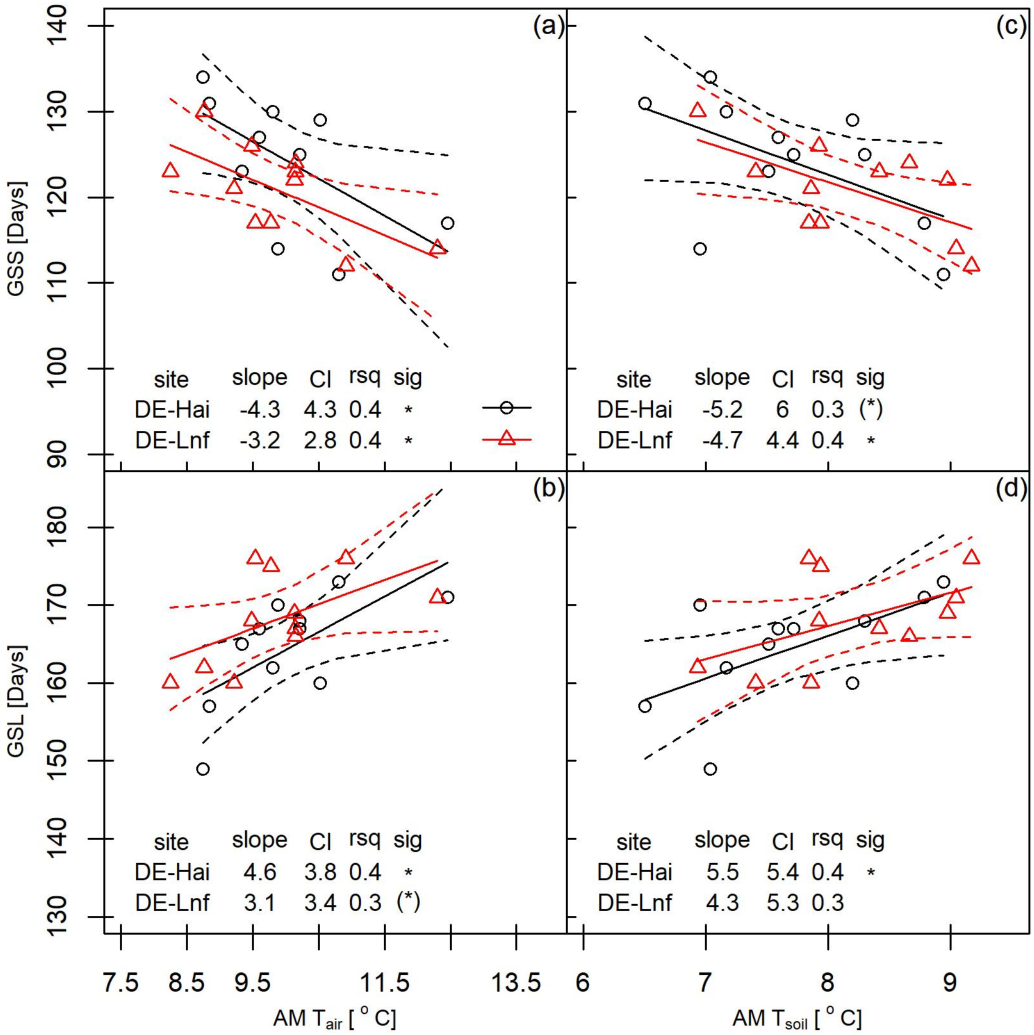


Figure 2.14: Relationship of growing season start day (GSS) and growing season length (GSL) with spring air (AM T_{air}) and soil temperature (AM T_{soil}). CI is 95% confidence interval of slope and rsq the coefficient of determination of linear regression, and sig its significance (*** indicates statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$). The solid lines represent linear regressions and dashed lines 95% confidence interval.

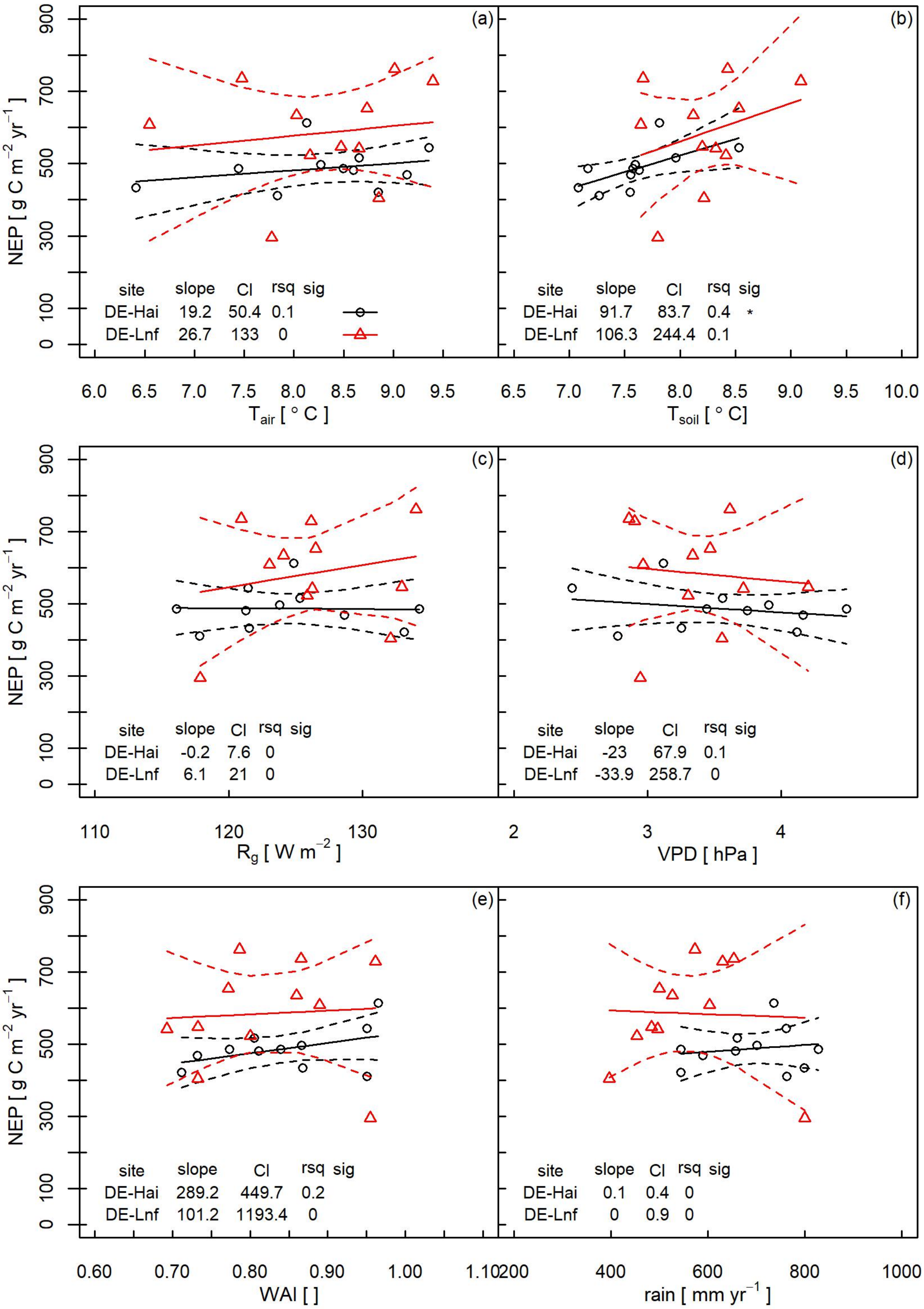


Figure 2.15: Regression between annual NEP and annual mean of meteorological variables (except for rain which was summed). CI is 95% confidence interval of slope and rsq the coefficient of determination of linear regression, and sig its significance (*** indicates statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$). The solid lines represent linear regressions and dashed lines 95% confidence interval.

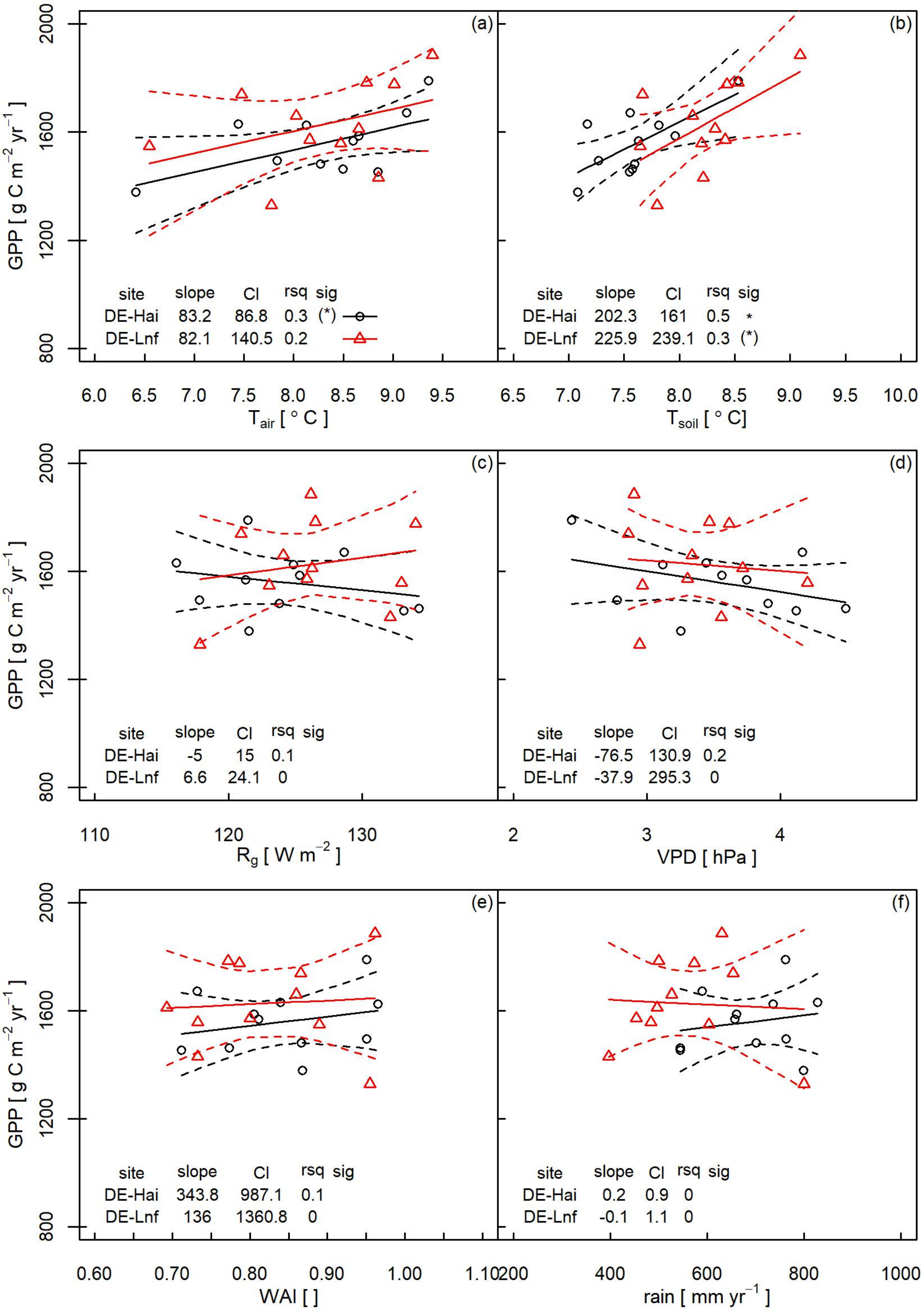


Figure 2.16: Regression between annual GPP and annual mean of meteorological variables (except for rain which was summed). CI is 95% confidence interval of slope and rsq the coefficient of determination of linear regression, and sig its significance (*** indicates statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$). The solid lines represent linear regressions and dashed lines 95% confidence interval.

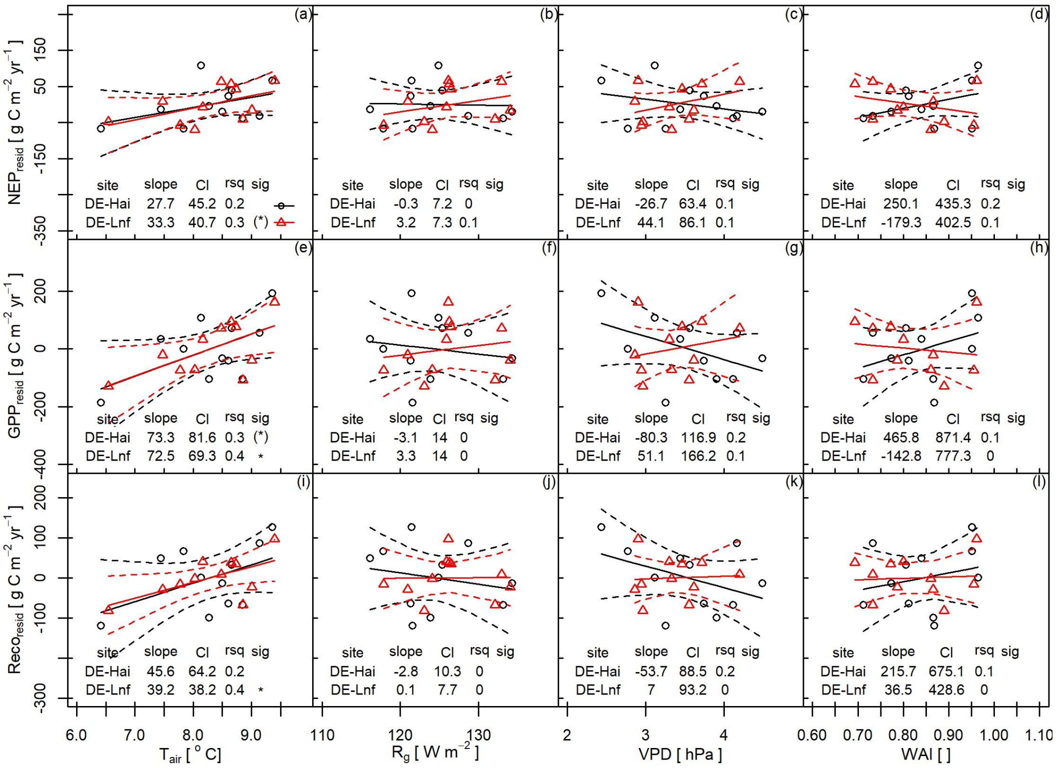


Figure 2.17: Linear regression between residual of NEP, GPP and Reco after removing the effect of time and fruit production (FP). CI is 95% confidence interval of slope and rsq the coefficient of determination of linear regression, and sig its significance (*** indicates statistical significance at $p < 0.001$; ** at $p < 0.01$; * at $p < 0.05$; and (*) at $p < 0.1$). The solid lines represent linear regression lines and dashed lines 95% confidence interval.

Table 2.8: Temperate broad-leaved deciduous forests with long term eddy covariance measurements. The table was modified after Baldocchi (2018). CV is coefficient of variation (standard deviation divided by mean).

Site	Country	n	NEP mean ± sd [g C m^{-2} yr^{-1}]	CV	GPP mean ± sd [g C m^{-2} yr^{-1}]	CV	Reco mean ± sd [g C m^{-2} yr^{-1}]	CV	Reference
Borden	Canada	18	177 ± 116	0.66	1373 ± 164	0.12	1196 ± 188	0.16	Froelich et al. (2015)
Soroe	Denmark	13	156 ± 103	0.66	1727 ± 136	0.08	1570 ± 97	0.06	Pilegaard et al. (2011)
Hesse	France	10	386 ± 171	0.44	1397 ± 192	0.14	1011 ± 137	0.14	Granier et al. (2008)
Takayama	Japan	9	237 ± 98	0.41	1110 ± 409	0.37	829 ± 264	0.32	Saigusa et al. (2005)
Straights Inclosure	UK	12	486 ± 115	0.24	1993 ± 275	0.14	1548 ± 192	0.12	Pilegaard et al. (2011)
Morgan-Monroe	US	13	351 ± 81	0.23	1452 ± 118	0.08	1098 ± 82	0.07	Sulman et al. (2016)
Harvard Forest, Petersham	US	13	245 ± 100	0.41	1400 ± 164	0.12	1153 ± 105	0.09	Urbanski et al. (2007)
Ozarks	US	5	479 ± 65	0.14	1125 ± 164	0.15	646 ± 121	0.19	Shao et al. (2014)
Duke Forest, Durham	US	8	402 ± 96	0.24	1982 ± 300	0.15	1580 ± 237	0.15	Novick et al. (2015)
Oak Ridge	US	5	577 ± 63	0.11	Na ± Na	Na	Na ± Na	Na	Wilson et al. (2001)
Average			350 ± 100	0.35	1506 ± 214	0.15	1181 ± 158	0.14	

CHAPTER 3

Effect of forest structure on drought response of ecosytem-level photosynthetic capacity

Manuscript to be submitted to 'Biogeosciences'

3.1 Abstract

Understanding the effect of forest stand structure on the temporal stability of ecosystem functions and resistance during droughts is key to understanding how forests may respond to climate change. Whilst many studies have looked at the effect of species, few have studied the effect of horizontal and vertical structural diversity. Here, we look at the effect of nine structural parameters (including species richness) on the temporal stability of ecosystem-level light-saturated photosynthetic capacity (GPP_{1000}) and its resistance to changes in water availability during droughts, with the aim of answering two questions, (a) Do structurally diverse forests have lower variation in annual GPP_{1000}? (b) structurally diverse forests more resistant to drought events? We found that unmanaged forests and forests managed as high forests with higher basal areas, which also tend to be older and more diverse in size, had more stable annual GPP_{1000}. Conversely, no structural parameters were found that explained GPP_{1000} anomalies during drought years. Instead, differences between sites in anomalies in GPP_{1000} were mostly explained by growing season air temperature. With relatively few flux sites having robust data on structural parameters, the statistical power of this type of analysis is limited, but we hope that with the availability of more canopy structural data from sites with long-term flux measurements we will be better able to understand the effect of structure on forest ecosystem functions.

3.2 Introduction

Forest structure – associated with the distribution of trees in space (both horizontally and vertically) and their variability in size – influences the local environmental conditions within stand (e.g. distribution of light and precipitation) affecting ecosystem functioning (e.g. ecosystem-level photosynthetic capacity). The changes in ecosystem functioning again modify the forest structure (see Figure 1 in Pretzsch et al. 2016). Forest structure plays thus an important role in determining ecosystem functioning and stand dynamics. Stand structural attributes like density, size distributions, size variation (of diameter and heights), spatial variation, age composition, species richness, canopy structure, etc. (McElhinny et al., 2005; Pommerening, 2002; Río et al., 2016; Seidl et al., 2017) are used to quantify stand structure. There exist numerous indices to quantify stand structure either using a single stand structural attribute or a combination of them (see review by Río et al., 2016). Several advantages of structurally heterogeneous forests have been listed by Schall et al. (2018), like, increase in productivity, promotion of biodiversity, resistance and resilience against disturbances and equally profitable as structurally less heterogeneous forests. Hence, understanding the effect of forest stand structure on ecosystem productivity (Firn et al., 2007; Gamfeldt et al., 2013; Lei et al., 2009; Liang et al., 2016; Mittelbach et al., 2001; Morin et al., 2011; Zhang et al., 2012) and stability (Jucker et al., 2014; Morin et al., 2014) has been an important area of research in the recent years.

In many cases, stand structure is the result of management regime, for e.g., old growth forests with high heterogeneity results from cessation of management and young forests with low heterogeneity from clear cut. Pommerening et al. (2013) highlighted that management activities like thinnings led to a high number of pairs of large and small trees close to each other.

Most studies have focused on the effect of tree species diversity (e.g. Gamfeldt et al., 2013; Liang et al., 2016; Zhang et al., 2012, etc) on ecosystem functions and few on other indices of stand structure (Lei et al., 2009; Lexerød et al., 2006; Long et al., 2010). In the case of temperate forests, where limited numbers of tree species grow (Schulze et al., 2016), understanding the effect of structural indices like age distribution, size distribution or canopy complexity may be key to understand the variability in stress response. The effect of structural diversity on ecosystem functions and its resistance or resilience to droughts have been less studied. But there are indications that increasing stand canopy complexity through a diverse age distribution improves the productivity of forest ecosystem (Hardiman et al., 2013). The forest structural indices based on diameter and height distribution had stronger positive effect on productivity than indices based on species diversity (Dănescu et al., 2016). Lei et al. (2009) have argued that structurally diverse could enhance resource use through niche complementaries, given the presence of different horizontal and vertical layers, both at the canopy and soil.

The biotic and abiotic factors that drive inter-annual variability of terrestrial CO_2 exchange (Chen et al., 2015; Ciais et al., 2005) is important for understanding how forests will respond to future climate and improve the predictability of global CO_2 budgets (Baldocchi et al., 2001; Luo et al., 2015). Biotic factors – functional traits of ecosystems such as nutrient status, phenology, maximum photosynthetic capacity etc., that govern photosynthesis and respiration process (Jensen et al., 2017) – have been shown to explain the inter-annual variability of CO_2 fluxes (Ma et al., 2011; Richardson et al., 2007). Maximum annual photosynthetic capacity of an ecosystem (GPP_{1000p}) – a biotic factor reflecting maximum ecosystem-level photosynthesis, is defined as the value of gross primary productivity (GPP) at saturating light under non-stressed conditions (Musavi et al., 2017). GPP_{1000p}, estimate of 90^{th} percentile of daily maximum photosynthetic capacity, is a key variable in understanding the inter-annual variation in CO_2 (Musavi et al., 2015). GPP_{1000p} highly correlates not only with annual GPP (Xia et al., 2015) but also with net CO_2 flux of ecosystems (Reichstein et al., 2014). The magnitude of inter-annual variability in GPP_{1000p} considerably varies across ecosystem (Musavi et al., 2016). Musavi et al. (2017) showed that the magnitude of inter-annual variability in GPP_{1000p} is strongly influenced by the age of the forest ecosystem – age is defined as the average tree age of the stand or the age of the stand since the last major disturbance that caused stand replacement. They reported lower magnitude of inter-annual variability GPP_{1000p} – indicating ecosystem functioning was not very sensitive to climatic variability – in older and diverse forests compared to younger forests. However, they do not offer a mechanistic explanation of their finding. Niche complementarity is driven by the forest structure and not just by age or species number. For example, light use among individual trees in a forest depends on tree architecture (Yachi et al., 2007). The niche partition of the light resource and the space in the forests are reflected by the correlation of the position and size of the tree canopy with light capture (Ishii et al., 2013).

In recent years climate warming has increased the frequency and severity of drought and heat-wave events. For the decade of 2006 to 2015, the observed global mean surface temperature was 0.87 °C (0.75 °C to 0.99 °C) higher than the average over the period of 1850 to 1900 and it is expected to reach 1.5 °C between 2030 to 2052 (IPCC, 2018). This increase in average surface temperature also means an increase in extreme events (IPCC, 2012). SCHLEUSSNER et al. (2017) showed an increase in the number of hot days and warm nights from the period of 1960 - 1979 to 1991 - 2010. Some of the heat extremes in the last years (COUMOU et al., 2013; HANSEN et al., 2012) include the European heat-waves of 2003 (CIAIS et al., 2005), 2006 (REBETEZ et al., 2009), and 2018, and the Russian heat-wave in 2010 (BARRIOPEDRO et al., 2011). BARRIOPEDRO et al. (2011) predicted a likelihood of an increase of extreme heatwaves by five to tenfold in Europe by the mid-21st century. These heatwaves are also intrinsically linked with drought, for example in 2003, the annual precipitation was 50 % below average. Model results predict an increase in dryness in temperate regions of the US and Europe in the future (GREVE et al., 2015).

Under the drought conditions, the photosynthetic capacity of forests decrease due to combined effects of stomatal, mesophyll and biochemical limitations (LIMOUSIN et al., 2010; STPAUL et al., 2012; ZHOU et al., 2015; ZHOU et al., 2014). However, the response varies with climate, species, forest types and structure (GROSSIORD et al., 2014c; JUCKER et al., 2016). In temperate regions, the mixing of different tree species has shown to increase resistance and resilience of ecosystem functions to drought due to differentiated functions or asynchrony of various species (FORRESTER et al., 2010; LEBOURGEOIS et al., 2013; PRETZSCH et al., 2013; RÍO et al., 2017). ANDEREGG et al. (2018) showed that the presence of diverse hydraulic traits decreases the drought sensitivity of forest ecosystems. In a forest with a mixture of beech and oak trees, the shallower rooting beech was relieved from drought stress by the hydraulic lift of water caused by the deep rooting oak (PRETZSCH et al., 2013; ZAPATER et al., 2011). A meta-analysis by GRIESS et al. (2011) showed that the mixing tree species dampened the lagged effect of drought (like secondary damages from insects, fungi and wind-throw). This means that on top of any positive effects of mixing on stress release and growth of trees, the reported avoidance or mitigation of secondary stress effects by species mixing can further improve the performance of mixed compared with pure stands. However, in Mediterranean and mountain climates, the mixing of tree species did not improve the resistance of forest ecosystems to drought (GROSSIORD et al., 2014a; GROSSIORD et al., 2014d) and was negative in the case of a Boreal ecosystem (GROSSIORD et al., 2014d). FORRESTER et al. (2016) also concluded that a reduction of drought stress in mixed-species forests is not a general pattern and might vary between sites even for a given species combination. Thus, we need to take into account environment differences while looking at the effect of forest structure or species mixing on forest ecosystem functions, like, $\mathrm{GPP_{1000p}}$ or its anomalies.

In this paper, we go further than MUSAVI et al. (2017) and look at the effects of diameter-based indices of forest structure on the $\mathrm{GPP_{1000p}}$. We are also interested in the effect of water limitation on ecosystem, thus we also calculated annual photosynthetic capacity of an ecosystem with the effect of hydrometeorological anomalies, represented by $\mathrm{GPP_{1000m}}$, calculated as mean of all daily maximum photosynthetic capacity within a year. The lower magnitude of inter-annual variability of $\mathrm{GPP_{1000m}}$ for an ecosystem indicated a very stable ecosystem functioning even during water limitation. Furthermore, we also investigated how the anomalies of $\mathrm{GPP_{1000p}}$ and $\mathrm{GPP_{1000m}}$ during the droughts differ among different forests with varying structure. We examined how diameter based indices, tree species diversity, stand age and management affect the temporal stability of an ecosystem function

(maximum photosynthetic capacity) and its resistance during droughts. We have tested two hypotheses in this paper:
(a) temporal stability of GPP_{1000} is higher in structurally diverse forests.
(b) resistance of GPP_{1000} during droughts is higher in structurally diverse forests.

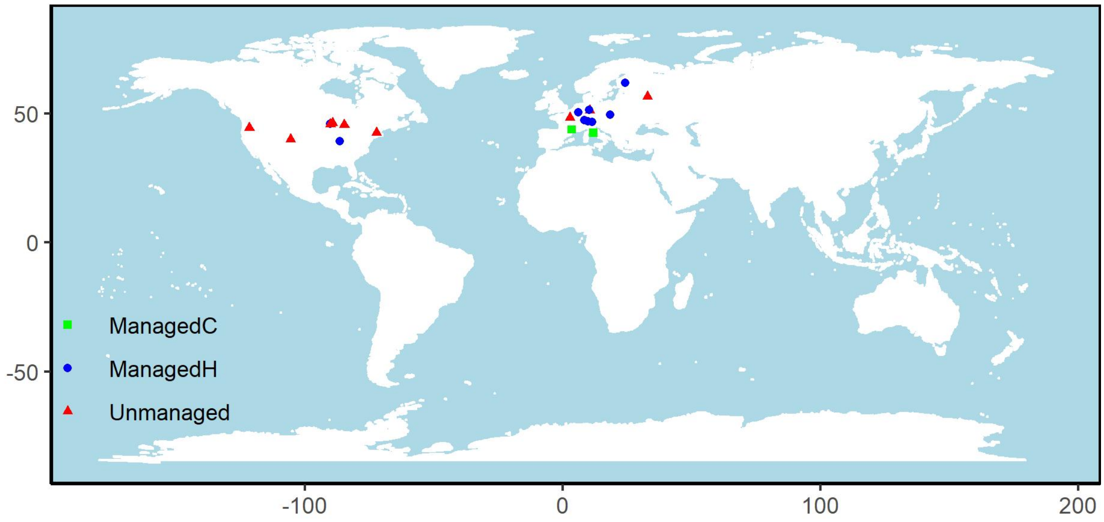


Figure 3.1: Map of the forest sites with flux tower used in this study. There were altogether 21 forest sites from temperate region. We included sites with inventory data and with at least 5 years of carbon dioxide flux data.

3.3 Material and methods

3.3.1 Sites

We requested inventory data from around 60 temperate eddy covariance flux sites. Finally, we had inventory data and carbon flux data from 21 temperate forest sites (Figure 3.1) with at least five years of flux data and that had forest inventory data. Details of the sites are given in Table 3.1. Flux data were retrieved from the ICOS 2019 (7 sites) and fluxnet 2015 database (14 sites) from `https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/`. There were nine deciduous broad-leaved forests (DBF), six evergreen forests (ENF), five mixed forests (MF), and one evergreen broad-leaved forest (EBF). Sites also represented a wide range of climatic zones. Sites were located between a latitude of 39.32 to 61.85 decimal degrees. IT-Ro1 had the shortest data on carbon flux from 2000 to 2008 and BE-Vie had the longest data from 1996 to 2018. Structure of a forest is usually the result of human intervention. We also collected data on history of management of each site (Table 3.8). Nine of the sites were unmanaged and twelve sites were managed. Out of 12 managed sites, three were managed as coppice forests (ManagedC) and nine as high forests (ManagedH).

3.3.2 Forest structure indices

We calculated nine stand structural indices from forest inventory data (Table 3.2). Age here refers to the age of forest stand since the last major disturbance that caused stand

Table 3.1: List of sites. We included data from different forest types (FT), DBF - deciduous broad-leaved forests, ENF - evergreen needle-leaved forests, EBF - evergreen broad-leaved forests, and MF - mixed forests. Sites also represented wide climatic zones, Bor - Boreal, Tmp - temperate, TmpC - temperate-continental with hot or warm summers, Sba - sub-artic and STM - sub-tropical Mediterranean. Forests were also classified based on management regime, Unmanaged, ManagedH - managed as high forests, ManagedC - managed as coppice forests.

Site	FT	Zone	Lat	Lon	Age	Years	Mgmt	References
BE-Vie	MF	Tmp	50.31	6.00	109	1996-2018	ManagedH	Hurdebise et al. (2017)
CH-Dav	MF	Tmp	46.82	9.86	244	1997-2018	ManagedH	Zweifel et al. (2010)
CH-Lae	MF	Tmp	47.48	8.37	175	2004-2018	ManagedH	Etzold et al. (2011)
CZ-BK1	ENF	TmpC	49.50	18.54	34	2004-2018	ManagedH	Sedlák et al. (2010)
DE-Hai	DBF	Tmp	51.08	10.45	260	2000-2018	Unmanaged	Knohl et al. (2003)
DE-Lnf	DBF	Tmp	51.33	10.37	145	2002-2012	ManagedH	Herbst et al. (2015)
FI-Hyy	ENF	Bor	61.85	24.29	53	1996-2018	ManagedH	Vesala et al. (2005)
FR-Fon	DBF	Tmp	48.48	2.78	152	2005-2014	Unmanaged	Otto et al. (2014)
FR-Pue	EBF	STM	43.74	3.60	74	2000-2014	ManagedC	Allard et al. (2008)
IT-Ren	ENF	Tmp	46.59	11.43	98	1998-2013	ManagedH	Papale et al. (2015)
IT-Ro1	DBF	STM	42.41	11.93	16	2000-2008	ManagedC	Papale et al. (2015)
IT-Ro2	DBF	STM	42.39	11.92	24	2002-2012	ManagedC	Hurdebise et al. (2017)
RU-Fyo	ENF	TmpC	56.46	32.92	195	1998-2018	Unmanaged	Milyukova et al. (2002)
US-Ha1	DBF	TmpC	42.54	-72.17	92	1991-2012	Unmanaged	Urbanski et al. (2007)
US-Me2	ENF	STM	44.45	-121.56	100	2002-2014	Unmanaged	Schwarz et al. (2004)
US-MMS	DBF	STM	39.32	-86.41	83	1999-2014	ManagedH	Ehman et al. (2002)
US-NR1	ENF	SbA	40.03	-105.55	103	1998-2014	Unmanaged	Monson et al. (2002)
US-PFa	MF	TmpC	45.95	-90.27	47	1995-2014	ManagedH	Davis et al. (2003)
US-Syv	MF	TmpC	46.24	-89.35	175	2001-2014	Unmanaged	Desai et al. (2005)
US-UMB	DBF	TmpC	45.56	-84.71	89	2000-2014	Unmanaged	Gough et al. (2007)
US-WCr	DBF	TmpC	45.81	-90.08	75	1999-2014	Unmanaged	Desai et al. (2005)

replacement normalized at the year 2015 - the year of release of fluxnet data. Further, we calculated the log of age. DBH is the mean tree diameter at breast height, but only counting those above 10 cm. BA is the average basal area per unit hectare of all trees above 7 cm DBH. We collected data for the average height of the canopy trees from the literature.

The Shannon Size index (ShnSz), the Simpson size index (SimSz), and the shape parameter of the Weibull function (ShWb) were calculated from the diameter distribution (e.g. 3.2). The Shannon size (ShnSz) and the Simpson size (SimSz) diversity indices were calculated using eq. 3.1 and 3.2, respectively using Rpackage 'vegan' (Oksanen et al., 2019).

$$ShnSz = -\sum_{i=1}^{R} p_i \, lnp_i \tag{3.1}$$

$$SimSz = \frac{1}{\sum_{i=1}^{R} p_i^2} \tag{3.2}$$

p_i in both equations is the proportion of trees in each diameter class, lnp_i is the natural log of p_i and R is the number of diameter size classes. We used a diameter size class width of 5 cm for our analysis. Higher values of ShnSz and SimSz indicate trees distributed in many different size classes and lower values indicated the trees concentrated in few diameter size classes.

Table 3.2: List of structural variables used.

Structural parameters	Description	Units
Age	Age of forest stand since the last major disturbance that caused stand replacement normalized at the year 2015	years
logAge	Log of age	-
BA	Total basal area	m^2 ha^{-1}
DBH	Diameter at breast height	cm
Height	The average height of canopy trees	m
ShnSz	Shannon size diversity index	-
SimSz	Simpson size diversity index	-
ShpWb	Shape Weibull parameter of the diameter distribution	-
SpNo	Number of species that makes up to 95 % of basal area	-

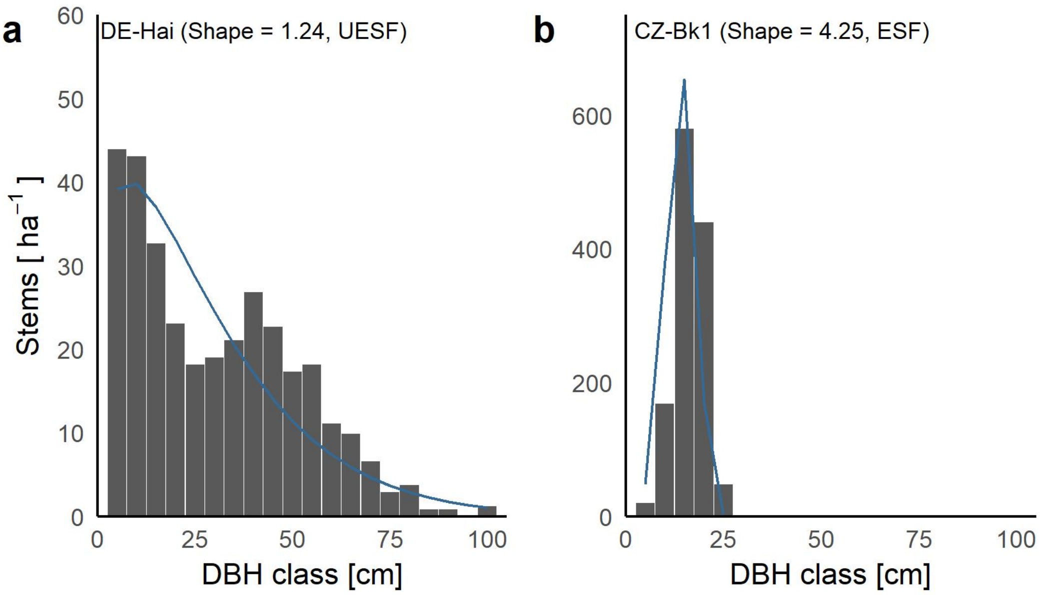


Figure 3.2: An example diameter distribution shown for (a) DE-Hai, an unevenly structured forest (ESF) and (b) CZ-Bk1, an evenly structured forest (ESF). The blue line represents the fitted Weibull function. 'Shape' is the shape parameter of the fitted Weibull function.

We calculated the shape parameter (k) of the Weibull function (eq. 3.3) fitted to the diameter distribution (the blue line in Figure 3.2). λ is the scale parameter of the Weibull function.

$$y = \frac{k}{\lambda}\left(\frac{x}{\lambda}\right)^{k-1} exp^{(-\frac{x}{\lambda})^k} \tag{3.3}$$

The sites were categorized as (a) unevenly structured forests (UESF) if the values of k were around one indicating a higher frequency of trees in smaller diameter size classes and a decreasing frequency of trees with increasing diameter size class (DE-Hai in Figure 3.2a), and (b) evenly structured forests (ESF) if the values were greater than one indicating uniform forests with trees concentrated in few diameter classes (CZ-Bk1 in Figure 3.2b).

Finally, species number (SpNo) is the number of tree species which add up to 95 % of basal area.

3.3.3 Environmental data

We used average annual and growing season (May - September) values of five environmental variables, namely air temperature (TA), global radiation (R_g), vapour pressure deficit (VPD), precipitation (P), and standardized precipitation and evapotranspiration index (SPEI). We obtained the data for the first four environmental variables from the fluxnet 2015 and ICOS 2019 databases. We downloaded the SPEI data for each site from SPEIbase, a new global database that covers the period 1901–2015 at a 0.5-degree resolution (Beguería et al., 2017). SPEI is the climatic water balance (precipitation minus potential evapotranspiration) over different timescales (from monthly to 24 monthly) expressed as a standardized Gaussian variate with a mean of zero and a standard deviation of one (Beguería et al., 2010) at a location. We used the R-codes provided by Beguería (2017) to extract the SPEI values for each site.

To present the environmental condition of the sites we estimated the mean and standard deviation of annual and growing season values across years for all environmental variables. The mean and standard deviation of annual values across years for each environmental variable is indicated by subscript mean and sd (for e.g. TA_{mean} and TA_{sd}), respectively. Similarly, the mean and values of growing season across years is indicated by GS_{mean} and GS_{sd} (for e.g. TA_{GSmean} and TA_{GSsd}), respectively. We included growing season values because photosynthesis mostly occur during this period of the year. Therefore, there were altogether 20 different environmental indicators for each site.

3.3.4 Annual light-saturated gross primary productivity (GPP_{1000})

First we investigated daily values of net ecosystem exchange (NEE) for all sites and removed all the periods when the data had problems.

Second, we quantified daily GPP_{1000} by fitting rectangular hyperbolic light-response curve (LRC) including the effect of vapour pressure deficit as suggested by Lasslop et al. (2010) (eq. 3.4 and eq. 3.5).

$$NEE = \frac{\alpha\,\beta\,R_g}{\alpha\,+\,\beta}\,+\,\gamma \tag{3.4}$$

$$\beta = \begin{cases} \beta_0\,exp(-k(VPD - VPD_0)) & \text{if VPD} > VPD_0 \\ \beta_0 & \text{if VPD} < VPD_0 \end{cases} \tag{3.5}$$

where NEE is net ecosystem exchange (μ mol m^{-2} yr^{-1}), α is the canopy light utilization efficiency and represents the initial slope of the light–response curve, β (μ mol m^{-2} yr^{-1}) is the maximum CO$_2$ uptake rate of the canopy at light saturation, γ (μ mol m^{-2} yr^{-1}) is the ecosystem respiration and R$_g$ is the downward shortwave radiation (W m^{-2}). The effect of high VPD on the LRC was included by replacing β by an exponentially decreasing function as shown in eq. 3.4. We fixed the value of VPD_0 to 10 hPa as in (Lasslop et al., 2010).

We estimated α, β_0, k and γ using 5 days of not gap-filled daytime (R$_g$ $>$ 4 W m^2) half-hourly data selected with a moving window approach. We used the R package 'FME' for fitting the LRC (Soetaert et al., 2016). We then computed the GPP (the first part of eq. 3.4) at 1,000 W m^2 of R$_g$ (corresponding to PAR of 2,110 μ mol m^{-2} yr^{-1}) and 10 hPa of VPD, which is daily GPP$_{1000}$. This GPP$_{1000}$ was assigned to the day in the middle of the 5-day window. We did not use parameters of model fits with R^2 lower than 0.6. We calculated GPP$_{1000}$ from May to September to include the most photosynthetically active period for all forest types. We calculated two types of annual GPP$_{1000}$, GPP$_{1000p}$ and GPP$_{1000m}$. GPP$_{1000m}$ is the mean of all daily values of GPP$_{1000}$ which includes effect of drought events if any occurred (see Figure 3.3). Similarly, GPP$_{1000m}$ is 90th percentile of all daily values of GPP$_{1000}$ which excludes any hydrometeorological anomalies, thus is the maximum photosynthetic capacity of the forests.

3.3.5 Drought estimation

We used the standardized precipitation–evapotranspiration index (SPEI) to identify and quantify drought events across flux tower sites at the annual scale. SPEI values are available for monthly to 24 monthly timescales, represented by a number after SPEI. For e.g. SPEI12

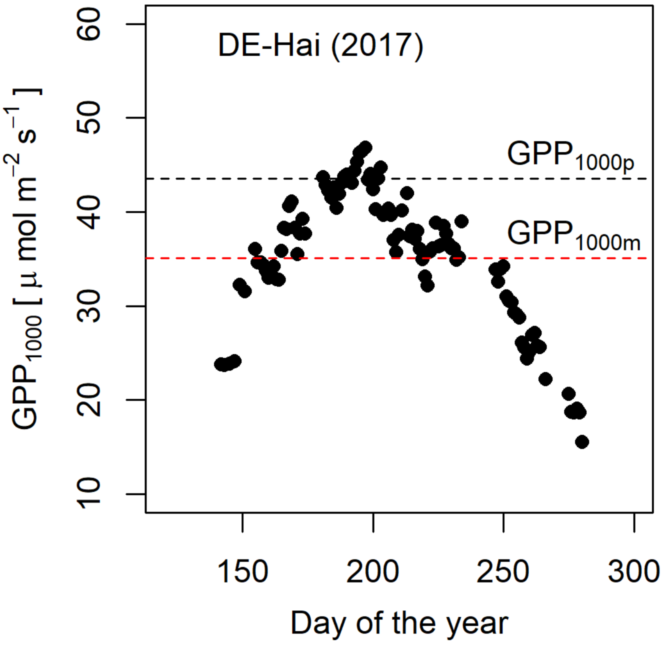


Figure 3.3: An example of timeseries for light-saturated GPP (GPP$_{1000}$) in DE-Hai for 2017. The black dashed line represents the annual GPP$_{1000p}$, 90th percentile , and the red dashed line GPP$_{1000m}$, the mean of all values.

values represent SPEI value for a period accumulated over 12 months. In our case, we required annual SPEI spanning from January to December which is SPEI12 for December (hereafter, SPEI12).

Negative values of SPEI indicate drier conditions. For our study, we defined drought years as those when SPEI12 values lie below the lower 10 percentile of 115 years long SPEI data i.e. value less than or equal to -1.28. We present an example of DE-Hai in Figure 3.4. Here, SPEI12 in 2003 is -1.28 which means an annual drought (shown by the value of 12 and the water balance is accumulated from January 2003 to December 2003) with the probability of occurring once a decade has occurred. Altogether there were 24 events of droughts identified in 21 sites (2^{nd} row in Table 3.9).

3.3.6 Statistical analysis

We used software R-3.5.1 (R Development Core Team, 2018) for the analysis. The R codes and data for this chapter are available in `https://doi.org/10.25625/KO7YTE`.

Coefficient of variation of GPP_{1000}

In order to better compare the temporal variability of forest ecosystem function, we calculated the coefficient of variation (CV) of $\text{GPP}_{1000\text{p}}$ ($\text{CV}_{\text{GPP1000p}}$) and $\text{GPP}_{1000\text{m}}$ ($\text{CV}_{\text{GPP1000m}}$) for each site, i.e. the standard deviation divided by the mean across years (eq. 3.6), thus obtaining a normalized measure for all sites. Additionally, we conducted an analysis using the standard deviation of GPP_{1000} across all years. Table 3.9 gives mean and standard deviation of different carbon dioxide fluxes across different years.

Ten of the sites showed temporal trends in $\text{GPP}_{1000\text{p}}$ or $\text{GPP}_{1000\text{m}}$ (for e.g. see Figure 3.5 and last column in Table 3.9), likely due to tree growth or increasing atmospheric carbon dioxide concentrations (Fernández-Martínez et al., 2017). Thus, we also the calculated

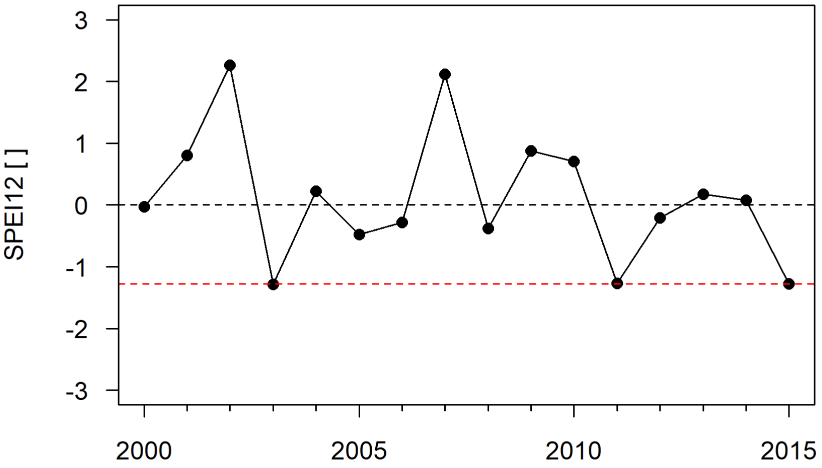


Figure 3.4: Annual standardized precipitation and evapotranspiration index (SPEI12) values for DE-Hai from 2000 to 2015. The positive values indicate wetter years and negative drier years. SPEI12 values at or below -1.28, the red dashed line, indicate drought events as defined for this study and have a return period of ten years on average.

coefficient of variation after removing any significant trends ($p < 0.05$). As an example for sites with and without annual trend, we have plotted annual values of GPP_{1000m} for US-MMS (without trend) and US-UMB (with trend) in Figure 3.5. We observed significant temporal trend in GPP_{1000m} of 0.35 μ mol m^{-2} yr^{-1} in US-UMB (dashed line in the Figure 3.5). In such case, we detrended the data represented by the dotted line in the same figure.

Thus, there were four variation of CV of GPP_{1000}:- $CV_{GPP1000mWT}$ - from mean with trend; $CV_{GPP1000mWoT}$ - mean without trend; $CV_{GPP1000pWT}$ - percentile with trend; $CV_{GPP1000pWoT}$ - percentile without trend. We also calculated the coefficient of variation of growing season gross primary productivity (GPP) and ecosystem respiration (Reco).

$$CV_{GPP1000} = \frac{sd_{GPP1000}}{mean_{GPP1000}} \tag{3.6}$$

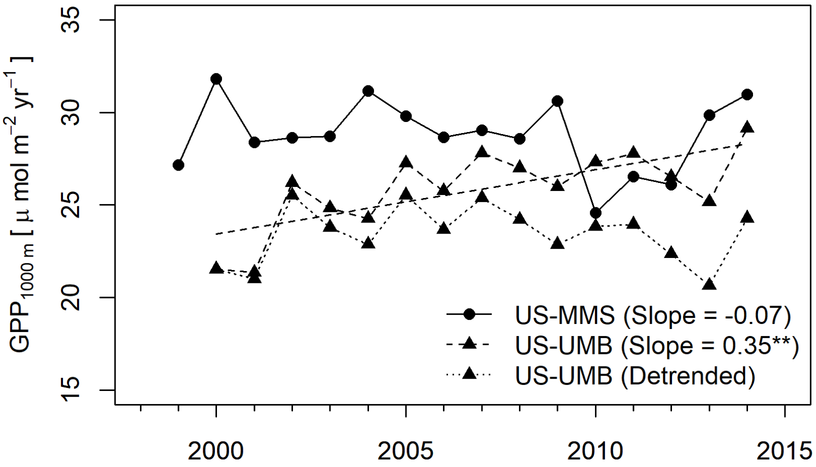


Figure 3.5: Example of annual GPP_{1000m} for US-MMS and US-UMB. The straight lines represent annual trend for US-UMB for which the temporal trend is significant. Detrended GPP_{1000m} is also shown for US-UMB. ** is significant at p = 0.01.

Anomalies of GPP_{1000}

For understanding the resistance of forest ecosystems to drought, we calculated the anomalies of GPP_{1000p} and GPP_{1000m} for dry years as shown in eq. 3.7, where GPP_{1000i} is the GPP_{1000} for an i^{th} dry year of a site and $mean_{GPP1000}$ is the mean across years for the same site. Like CV of GPP_{1000p}, we also calculated anomalies after removing long term trends. Thus, there were also four variations of anomalies of GPP_{1000}, $Ano_{GPP1000mWT}$ - from mean with trend; $Ano_{GPP1000mWoT}$ - from mean without trend; $Ano_{GPP1000pWT}$ - from percentile with trend; and $Ano_{GPP1000pWoT}$ - from percentile without trend.

$$Anomaly_{GPP1000} = \frac{GPP_{1000i} - mean_{GPP1000}}{mean_{GPP1000}} \tag{3.7}$$

Step-wise regression with meteorological and structural variables

We calculated the Pearson correlation of each $\mathrm{CV}_{\mathrm{GPP1000}}$ and $\mathrm{Anomaly}_{\mathrm{GPP1000}}$ with meteorological and structural variables. For each case, we then chose only the variables which were significant at the 0.05 level and management regime for including in a stepwise regression, which was performed without any interaction effect. All continuous predictors were standardized with mean and sd 1 before stepwise regression. Models were evaluated by sequential comparison (forward and backward selection) based on Akaike Information Criterion (AIC) and maximum likelihood likelihood (ML) estimation, using the stepAIC function in R (R Development Core Team, 2018). We then calculated the variation inflation factor (VIF) for each explanatory variable selected by stepwise regression, using the vif function from car package (Fox et al., 2019). High values of VIF of an explanatory variable indicated a high correlation with other explanatory variables in the multiple linear regression. The final model was then established by discarding the variables with VIF values higher than 2. The model result was also plotted with effect of single environmental variable and structure or management.

3.4 Results

3.4.1 Structural characteristics of sites

Table 3.3 shows the values of the structural parameters for all forest sites. The youngest forest was IT-Ro1, forest regenerating after clear cut via coppicing in December 1999. The site with oldest trees was DE-Hai, an unmanaged deciduous forest. BA was smallest in IT-Ro2 (a young forest managed as coppice-with-standards) and largest in US-NR1 (an unmanaged forest). FR-Pue, an evergreen broad-leaved coppice forest, and BE-Vie, a managed mixed forest, had the smallest and largest DBH, respectively. Tree height was lowest in FR-Pue and highest in DE-Hai and DE-Lnf. The coppice forests (FR-Pue, IT-Ro1 and IT-Ro2) had the lowest values ShnSz and SimSz, whereas BE-Vie had the highest. US-MMS and US-PFa have the highest species diversity, and seven sites have only one species. Based on ShWb values, ten forests were categorised as unevenly structured forests (UESF) and remaining as evenly structured forests (ESF).

Table 3.3: Values of nine structural parameters for all sites.Mean and sd are the mean and standard deviation across sites, respectively. Based on the Shape of Weibull function (ShWb) forests are categorised as unevenly structured forests (UESF) or evenly structured forests (ESF) forests.

Site	Age	logAge	BA	DBH	Height	ShnSz	SimSz	SpNo	ShWb
-	(Years)	-	(m^2 ha^{-1})	(cm)	(m)	-	-	-	-
BE-Vie	109	4.69	37.3	44.15	33	2.72	0.93	5	UESF
CH-Dav	244	5.5	49.31	25.4	25	2.1	0.86	1	ESF
CH-Lae	175	5.16	37.5	28.7	31	2.46	0.9	8	UESF
CZ-BK1	34	3.53	26.4	14.54	14	0.96	0.56	1	ESF
DE-Hai	260	5.56	37.84	33.45	35	2.62	0.92	3	UESF
DE-Lnf	145	4.98	36.03	44.06	35	1.77	0.79	1	ESF
FI-Hyy	53	3.97	25.73	17.33	14	1.55	0.77	3	ESF
FR-Fon	152	5.02	49.5	33.2	30	2.61	0.88	2	UESF
FR-Pue	74	4.3	27.16	10.24	6	0.86	0.54	1	ESF
IT-Ren	98	4.58	32	20.56	29	2.1	0.83	3	UESF
IT-Ro1	16	2.77	23.69	11.81	18	1.18	0.63	1	ESF
IT-Ro2	24	3.18	11.73	11.97	16	1.33	0.66	1	UESF
RU-Fyo	195	5.27	30.5	24.29	28	1.95	0.84	2	ESF
US-Ha1	92	4.52	37.31	25.61	23	2.06	0.85	9	UESF
US-Me2	100	4.61	41.27	31.82	18	1.7	0.76	1	ESF
US-MMS	83	4.42	41.23	33.1	31	2.46	0.9	14	ESF
US-NR1	103	4.63	54.77	14.76	12	1.56	0.75	3	UESF
US-PFa	47	3.85	22.02	19.87	20	1.68	0.76	14	UESF
US-Syv	175	5.16	23.29	25.6	27	2.31	0.88	4	UESF
US-UMB	89	4.49	24.87	19.24	26	1.95	0.83	7	UESF
US-WCr	75	4.32	31.82	19.84	24	1.86	0.83	4	ESF
Mean	111.57	4.5	33.39	24.26	23.57	1.89	0.79	4.19	-
Sd	68.05	0.73	10.47	9.81	8.15	0.54	0.11	4.03	-

Figure 3.6 shows the histogram (diagonal plots) of six selected structural parameters and correlation between them except for ShWb. We plotted boxplots for ShWb against other variables (the last row of Figure 3.6). Distributions of most of the structural parameters were non-uniform and skewed (diagonal plots in Figure 3.6). Study sites belonged to a wide range of ages (16-260) with 90 % sites below 200 years. In the case of BA, the sites were mostly between 20 to 40 m^2 ha^{-1}. The DBH of sites were uniformly distributed between 10 to 35 cm and two sites with DBH higher than 40 cm. The SimSz values of sites were mostly between 0.7 and 0.9. Ten sites i.e. about 47 % of total sites had a maximum of 2 species.

Age, BA, DBH and SimSz are significantly correlated with each other (figures on the left side of diagonal plots of Figure 3.6 and corresponding correlation values on the right side of the diagonal plots). For example, the correlation between SimSz and DBH is 0.71 ($p < 0.001$) meaning that the forests with thicker stems also have trees distributed in more size classes. SpNo did not correlate with any other structural parameter. The boxplots of ShWb with other structural parameter showed that unevenly structured and evenly forests did not differ (last column of Figure 3.6) in age, BA, DBH, SimSz or SpNo, though the median values were always slightly higher for unevenly structured forests.

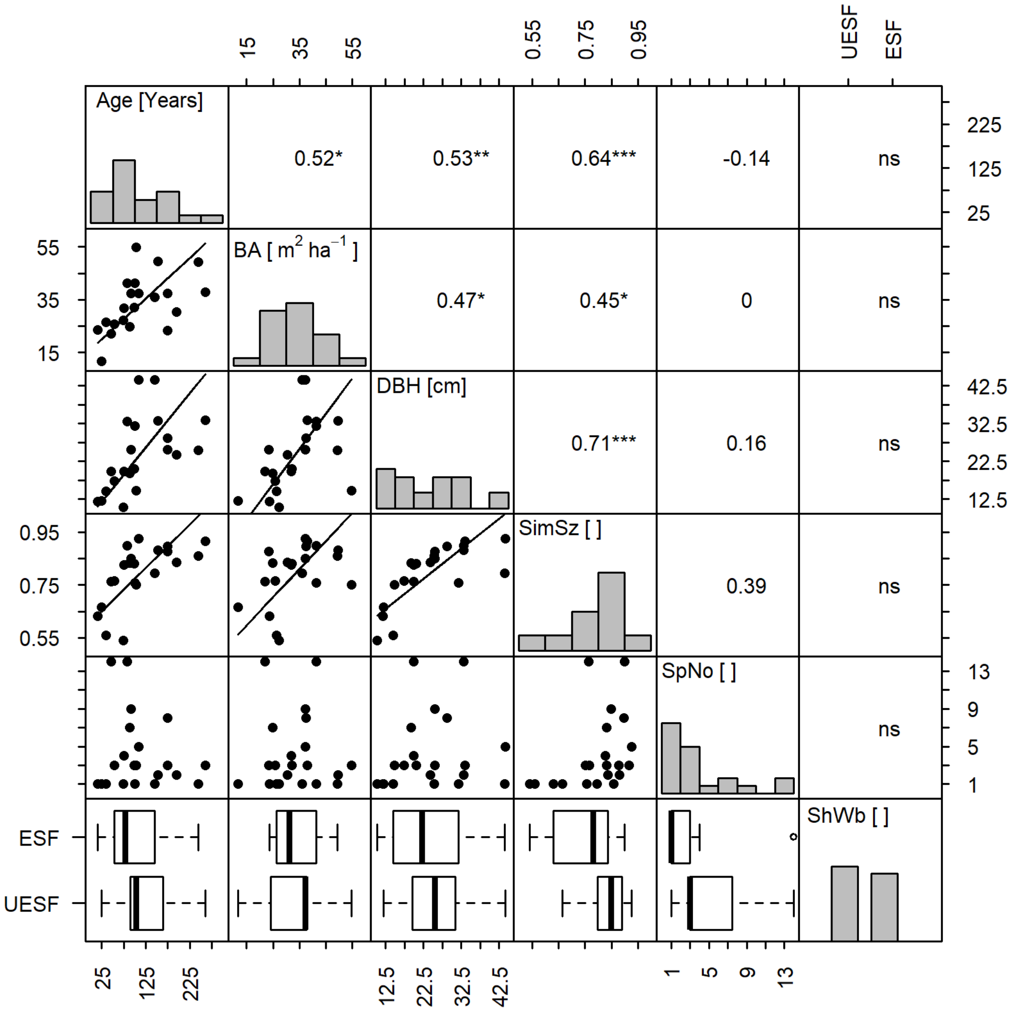


Figure 3.6: Chart showing histogram (barpot in the case of ShWb) and relationship between different structural parameters. Only six are included to increase the clarity of the figure. Histograms of each structural parameter are on the diagonal, with scatter plots between variables on one side and the respective correlation coefficients on the opposite side. The last row is presented as boxplot for categorical variable ShWb (UESF - unevenly structured forests, ESF - evenly structured forests). The stars represent the level of significance: *** for p=0.001, ** for p=0.01, and * for p=0.05. The line in the scatter plots is the linear relationship of significant correlations.

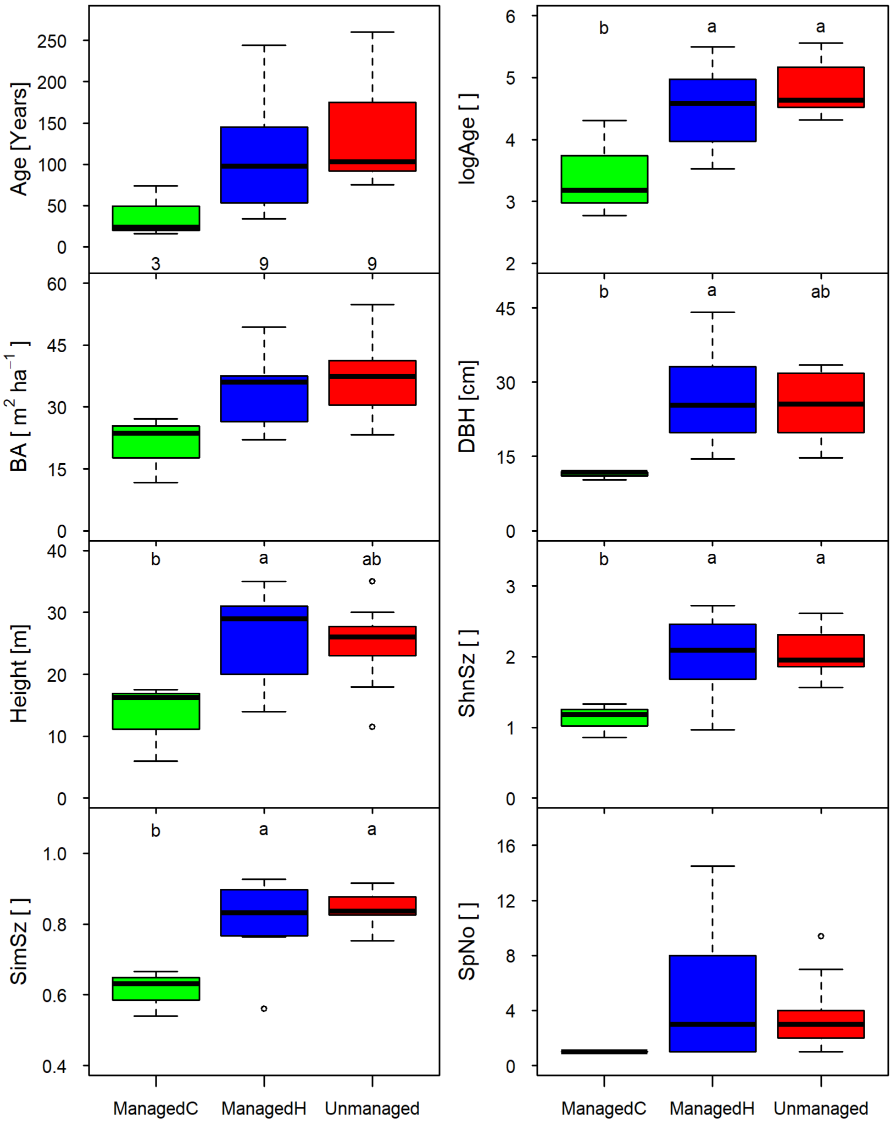


Figure 3.7: Effect of forest management on different structural parameters. The values on the bottom of first plot are the number of forests in each management regime. The different letters on top of each plot represent significant difference (at $p < 0.05$) between sites categorized by management regime.

The forest structure results from human intervention mostly via silvicultural operations. Figure 3.7 shows the effect of forest management on different structural parameters. Most of the structural parameters were lower for coppice forests (FR-Pue, IT-Ro1 and IT-Ro2) compared to forest managed as high forests and unmanaged forests. logAge, DBH, height, ShnSz and SimSz were significantly lower. The structural parameters for managed and unmanaged forests however did not differ.

3.4.2 Factors explaining inter-site variability in $CV_{GPP1000}$

Table 3.4: Zero-order correlation of environmental and structural variables with $CV_{GPP1000}$ calculated from mean and percentile with (WT) and without trend (WoT). *** is significant at $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$.

Variables	Correlation of			
	$CV_{GPP1000m}$		$CV_{GPP1000p}$	
	WT	WoT	WT	WoT
Environmental parameters				
TA_{mean}	0.41	0.51*	0.26	0.27
Rg_{mean}	0.37	0.34	0.41	0.4
VPD_{mean}	0.46*	0.49*	0.45*	0.39
P_{mean}	0.18	0.18	0.12	0.03
$SPEI_{mean}$	-0.41	-0.39	-0.39	-0.36
TA_{GSmean}	0.38	0.46*	0.27	0.28
Rg_{GSmean}	0.42	0.37	0.45*	0.41
VPD_{GSmean}	0.43*	0.44*	0.42	0.35
P_{GSmean}	-0.06	-0.11	-0.06	-0.07
$SPEI_{GSmean}$	-0.41	-0.31	-0.45*	-0.39
TA_{sd}	0.17	0.16	0.14	0.25
Rg_{sd}	0.52*	0.33	0.39	0.34
VPD_{sd}	0.37	0.34	0.21	0.29
P_{sd}	0.52***	0.44*	0.46*	0.41
$SPEI_{sd}$	0.06	-0.07	0.16	0
TA_{GSsd}	-0.16	-0.15	-0.19	-0.16
Rg_{GSsd}	0.25	0.13	0.2	0.16
VPD_{GSsd}	0.22	0.25	0.08	0.14
P_{GSsd}	0.61***	0.61***	0.58***	0.61***
$SPEI_{GSsd}$	0.06	0	0.04	-0.08
Structural parameters				
Age	-0.26	-0.23	-0.29	-0.27
logAge	-0.35	-0.35	-0.33	-0.37
BA	-0.57***	-0.48*	-0.5*	-0.47*
DBH	-0.44*	-0.44*	-0.54***	-0.5*
DBH_{sd}	-0.18	-0.18	-0.3	-0.26
Height	-0.35	-0.33	-0.52***	-0.4
ShnSz	-0.43*	-0.43*	-0.54***	-0.45*
SimSz	-0.47*	-0.47*	-0.56***	-0.44*
SpNo	-0.15	-0.1	-0.16	-0.07

Table 3.4 lists the zero-order correlation of $CV_{GPP1000mWT}$, $CV_{GPP1000mWoT}$, $CV_{GPP1000pWT}$ and $CV_{GPP1000pWoT}$ with environmental and structural variables. Among environmental variables, the standard deviation of growing season rainfall sum (P_{GSsd}) showed the strongest significant correlation and in the case of structural variables, BA, DBH, ShnSz and SimSz correlated in similar magnitude with all metrics of $CV_{GPP1000}$. The positive correlation of $CV_{GPP1000}$ with P_{GSsd} means that sites with a higher inter-annual variation in their growing season rainfall have higher variability in GPP_{1000}. On the other hand, the BA, DBH, ShnSz and SimSz were negatively correlated with $CV_{GPP1000}$ meaning denser

forests with thick stems and higher size diversity showed less variability in GPP_{1000}.

We also looked at the correlation of standard deviation of annual GPP_{1000} ($Sd_{GPP1000}$) with environmental and structural variables (Table 3.10). $Sd_{GPP1000}$ correlated positively with the standard deviation of growing season rainfall (P_{GSsd}) and negatively with basal area (BA) for $CV_{GPP1000}$. Furthermore, we also looked at the correlation of coefficient of variation of GPP (CV_{GPP}) and Reco (CV_{Reco}) with all structural and environmental parameters (Table 3.11). CV_{GPP} correlated with P_{GSsd}, and Simpson size diversity index (SimSz).

Table 3.5: Stepwise regression coefficients for four metrics of $CV_{GPP1000}$ with environmental and structural parameters. Predictor estimates were normalized with mean 0 and standard deviation 1, hence their magnitude is proportional to the effect size. Note that the intercept (a) indicates the response of unmanaged forests, while managedH indicates forests managed as high forests and managedC as coppice. *** is significant at $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ and (*) $p < 0.1$.

Model	Fixed effects	R^2	$adjR^2$	Estimate ± se
1.$CV_{GPP1000mWT}$ =	a +	0.66	0.58	-0.25 ± 0.23
	b ManagedH +			0.14 ± 0.32
	c ManagedC +			1.32 ± 0.54*
	d P_{GSsd} +			0.33 ± 0.17(*)
	e BA +			-0.24 ± 0.17
2.$CV_{GPP1000mWoT}$ =	a +	0.71	0.64	-0.4 ± 0.21(*)
	b ManagedH +			0.26 ± 0.3
	c ManagedC +			2.04 ± 0.49***
	d P_{GSsd} +			0.47 ± 0.19*
	e P_{sd} +			-0.25 ± 0.2
3.$CV_{GPP1000pWT}$ =	a +	0.61	0.51	-0.29 ± 0.25
	b ManagedH +			0.29 ± 0.34
	c ManagedC +			1.13 ± 0.59(*)
	d P_{GSsd} +			0.35 ± 0.18(*)
	e Height +			-0.29 ± 0.19
4.$CV_{GPP1000pWoT}$ =	a +	0.56	0.48	-0.37 ± 0.25
	b ManagedH +			0.36 ± 0.35
	c ManagedC +			1.52 ± 0.54*
	d P_{GSsd} +			0.36 ± 0.18(*)

Table 3.5 shows the result of stepwise regression of four metrics of $CV_{GPP1000}$ with environmental and structural variables. Model 1 and 2 use $CV_{GPP1000m}$ with and without trend, respectively. Similarly, model 3 and 4 use $CV_{GPP1000p}$ with and without trend, respectively. P_{GSsd} and management regime were selected as predictors in all four models. The effect of unmanaged stand on $CV_{GPP1000}$ (intercepts in Table 3.5) was negative indicating that inter-annual variation of GPP_{1000} was lowest in unmanaged stands (also see Figure 3.8). The higher $CV_{1GPP000}$ was observed in forests growing in climates with higher variation in growing season rainfall (Figure 3.8). The coppice forests (ManagedC) had significantly higher $CV_{1GPP000}$ compared to the forests managed as high forests and unmanaged forests in every case (Figure 3.8). The unmanaged forests had the lowest $CV_{1GPP000}$ but did not differ from forests managed as high forests.

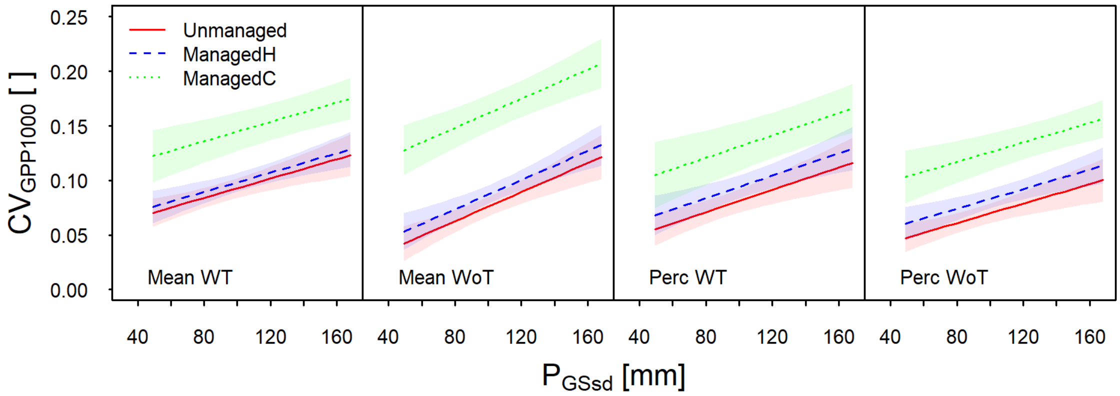


Figure 3.8: Effect of different forest management regimes on four metrics of $CV_{GPP1000m}$. Lines correspond to the predicted response based on mixed-effects models presented in Table 3.5) and shaded areas indicate the 95 % confidence interval. The remaining predictors estimate were fixed at their mean values.

3.4.3 Factors affecting GPP_{1000} anomalies during droughts

Like in section 3.4.2, we looked at the zero-order correlation of environmental and structural variables with the four metrics of GPP_{1000} anomaly ($Ano_{GPP1000}$, Table 3.6). The negative anomaly means large drought effect. The correlation was significant with two structural parameters (BA and logAge) and numerous environmental variables (also see Figure 3.10). We observed the highest correlation (0.67 - 0.74) with mean growing season air temperature (TA_{GSmean}) among environmental variables and with the basal area (0.60 - 0.67) among structural variables. A positive correlation generally denotes a less negative $Ano_{GPP1000}$ with an increase in the explanatory variable. For example, the positive relationship between basal area and $Ano_{GPP1000}$ indicates that a higher basal area correlates with a less pronounced decrease in GPP_{1000}. The positive significant relationship between logAge and $Ano_{GPP1000}$ is driven by coppice forests (leftmost plot in Figure 3.10). The relationship is however opposite for unmanaged forests.

We also looked at the correlation of GPP and Reco anomalies with all independent variables. GPP anomalies strongly correlated with the basal area (0.52), the standard deviation of annual and the growing season radiation (-0.52 and -0.53), and mean growing season temperature (-0.46) as shown in Table 3.12.

Table 3.7 shows the results of stepwise regressions of four $Ano_{GPP1000}$ metrics. Results show that the mean growing season air temperature (TA_{GSmean}) is the most important variable. Other explanatory variables differed from model to model. In the case of model 1, management was selected as an explanatory variable. The intercept in model 1 indicates the effect of unmanaged forest. The effect is negative indicating that reduction in $GPP_{1000mWT}$ was more pronounced in unmanaged forests during droughts (Figure 3.9). However, when the effects of any other predictors is not considered, we observed more negative values of $Ano_{GPP1000}$ in coppice forests during drought events compared to unmanaged forests (the last plot in Figure 3.10).

Table 3.6: Zero-order correlation of environmental and structural variables with $\mathrm{Ano}_{\mathrm{GPP1000}}$ calculated from mean and percentile with (WT) and without trend (WoT). *** is significant at $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$.

Variables	Correlation of			
	$\mathrm{Ano}_{\mathrm{GPP1000m}}$		$\mathrm{Ano}_{\mathrm{GPP1000P}}$	
	WT	WoT	WT	WoT
Environmental parameters				
$\mathrm{TA}_{\mathrm{mean}}$	-0.59***	-0.62***	-0.69***	-0.66***
$\mathrm{R}_{\mathrm{gmean}}$	-0.15	-0.14	-0.31	-0.26
$\mathrm{VPD}_{\mathrm{mean}}$	-0.49*	-0.51***	-0.55***	-0.5***
$\mathrm{P}_{\mathrm{mean}}$	0.1	0.03	-0.12	-0.17
$\mathrm{SPEI}_{\mathrm{mean}}$	0.15	0.23	0.13	0.17
$\mathrm{TA}_{\mathrm{GSmean}}$	-0.67***	-0.7***	-0.74***	-0.7***
$\mathrm{R}_{\mathrm{gGSmean}}$	-0.35	-0.34	-0.48*	-0.41*
$\mathrm{VPD}_{\mathrm{GSmean}}$	-0.51***	-0.54***	-0.54***	-0.5***
$\mathrm{P}_{\mathrm{GSmean}}$	0.46*	0.46*	0.32	0.27
$\mathrm{SPEI}_{\mathrm{GSmean}}$	0.38	0.48*	0.26	0.32
$\mathrm{TA}_{\mathrm{sd}}$	-0.19	-0.16	-0.24	-0.23
$\mathrm{R}_{\mathrm{gsd}}$	-0.66***	-0.64***	-0.66***	-0.61***
$\mathrm{VPD}_{\mathrm{sd}}$	-0.63***	-0.68***	-0.62***	-0.65***
P_{sd}	-0.11	-0.21	-0.3	-0.35
$\mathrm{SPEI}_{\mathrm{sd}}$	0.2	0.2	0.21	0.21
$\mathrm{TA}_{\mathrm{GSsd}}$	-0.31	-0.24	-0.3	-0.24
$\mathrm{R}_{\mathrm{gGSsd}}$	-0.63***	-0.62***	-0.64***	-0.61***
$\mathrm{VPD}_{\mathrm{GSsd}}$	-0.64***	-0.7***	-0.56***	-0.58***
$\mathrm{P}_{\mathrm{GSsd}}$	0.05	-0.01	-0.13	-0.16
$\mathrm{SPEI}_{\mathrm{GSsd}}$	-0.26	-0.24	-0.31	-0.29
Structural parameters				
Age	0.36	0.37	0.38	0.37
logAge	0.42*	0.47*	0.46*	0.49*
BA	0.67***	0.66***	0.63***	0.6***
DBH	0.19	0.23	0.28	0.28
$\mathrm{DBH}_{\mathrm{sd}}$	-0.11	-0.05	-0.18	-0.14
Height	0.07	0.15	0.14	0.16
ShnSz	0.11	0.19	0.13	0.16
SimSz	0.17	0.26	0.2	0.24
ShWb	0.32	0.24	0.4	0.31

While structural parameters were not selected in stepwise regression, Table 3.4) shows positive correlations between $\mathrm{Ano}_{\mathrm{GPP1000}}$ and age, logAge and BA, with BA being the strongest. However, the relationship between logAge and $\mathrm{Ano}_{\mathrm{GPP1000}}$ is caused by a very young site and two old sites (on the leftmost plot of Figure 3.10), and most of the remaining points forms a cloud without any distinct pattern. The effect of basal area looks convincing (the middle plot of Figure 3.10) however, we see that BA and $\mathrm{TA}_{\mathrm{GSmean}}$ have reciprocal effects (size of the dots in the figure).

Table 3.7: Stepwise regression coefficients for four metrics of $\mathrm{Ano}_{\mathrm{GPP1000}}$ with environmental and structural parameters. Predictor estimates were normalized with mean 0 and standard deviation 1, hence their magnitude is proportional to the effect size. Note that the intercept a in model 1 indicates the response of unmanaged forests, while managedH indicates forests managed as high forests and managedC as coppice. *** is significant at $p < 0.001$, ** $p < 0.01$, * $p < 0.05$ and (*) $p < 0.1$.

Model		R^2	$\mathrm{adj}R^2$	Estimate ± se
1.$\mathrm{Ano}_{\mathrm{GPP1000mWT}}$ =	a +	0.78	0.71	-0.31 ± 0.19
	b $\mathrm{TA}_{\mathrm{GSmean}}$ +			-0.49 ± 0.16**
	c $\mathrm{R}_{\mathrm{gsd}}$ +			-0.59 ± 0.13***
	f $\mathrm{P}_{\mathrm{GSmean}}$ +			0.25 ± 0.17
	d ManagedH +			0.41 ± 0.32
	e ManagedC +			0.73 ± 0.42(*)
2.$\mathrm{Ano}_{\mathrm{GPP1000mWoT}}$ =	a +	0.73	0.69	0 ± 0.11
	b $\mathrm{TA}_{\mathrm{GSmean}}$ +			-0.38 ± 0.14*
	c $\mathrm{R}_{\mathrm{gGSsd}}$ +			-0.49 ± 0.13***
	d $\mathrm{P}_{\mathrm{GSmean}}$ +			0.33 ± 0.13*
3.$\mathrm{Ano}_{\mathrm{GPP1000pWT}}$ =	a +	0.75	0.71	0 ± 0.11
	b $\mathrm{TA}_{\mathrm{GSmean}}$ +			-0.47 ± 0.13**
	c $\mathrm{R}_{\mathrm{gGSmean}}$ +			-0.25 ± 0.12(*)
	d $\mathrm{R}_{\mathrm{gGSsd}}$ +			-0.45 ± 0.12**
4.$\mathrm{Ano}_{\mathrm{GPP1000pWoT}}$ =	a +	0.66	0.61	0 ± 0.13
	b $\mathrm{TA}_{\mathrm{GSmean}}$ +			-0.46 ± 0.15**
	c $\mathrm{R}_{\mathrm{gGSsd}}$ +			-0.42 ± 0.14**
	d $\mathrm{R}_{\mathrm{gGSmean}}$ +			-0.2 ± 0.14

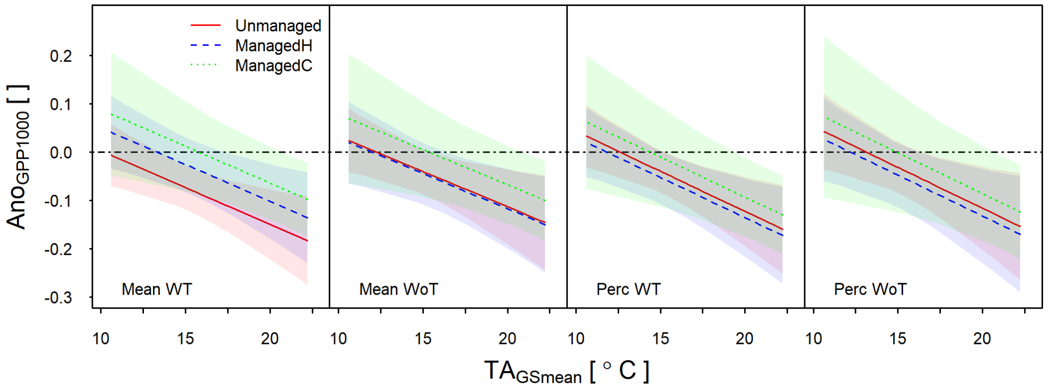


Figure 3.9: Effect of different forest management regimes on four metrics of $\mathrm{Ano}_{\mathrm{GPP1000m}}$. Lines correspond to the predicted response based on models presented in Table 3.7 (we added management as an additional predictor when it was not selected) and shaded areas indicate the 95 % confidence interval. The remaining predictors estimate were fixed at their mean values.

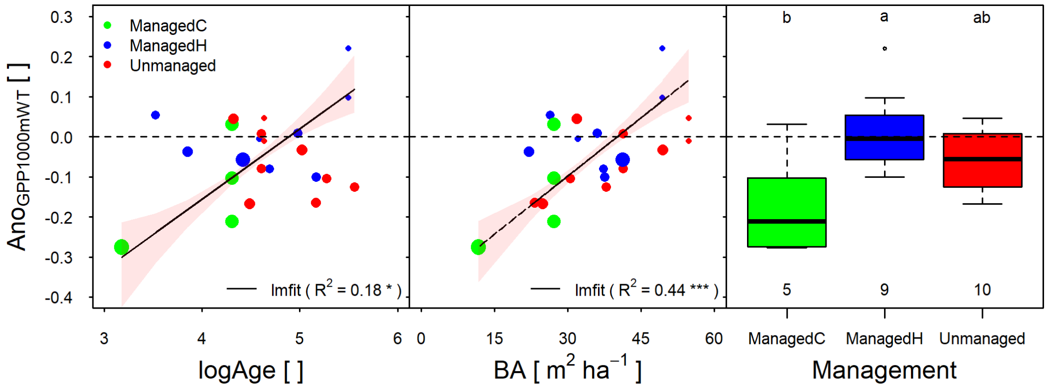


Figure 3.10: The first and second plot shows the relationship of logAge and basal area (BA) with $\text{Ano}_{\text{GPP1000mWT}}$. The size of the dots corresponded with the growing season mean temperature ($\text{TA}_{\text{GSmean}}$). The last plot shows the effect of management on $\text{Ano}_{\text{GPP1000mWT}}$ without removing effect of any other predictor variables. The different letters on the top of the last plot indicates the significant differences at $p < 0.05$.

3.5 Discussion

3.5.1 Temporal stability of GPP_{1000}

We found that forests from climates with low variability in growing season rainfall and unmanaged forests had stable GPP_{1000} i.e. lower inter-annual variation in GPP_{1000}. Our results differ from those of (Musavi et al., 2017) which showed higher stability in older

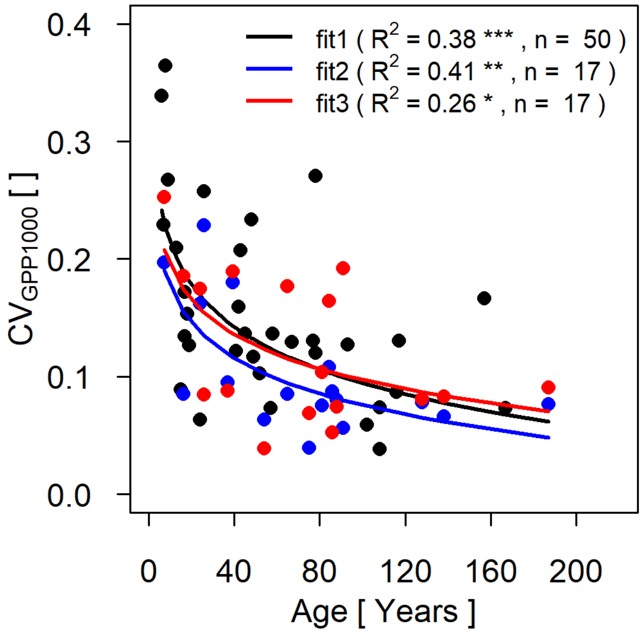


Figure 3.11: Relationship between age and $\text{CV}_{\text{GPP1000}}$ using a subset of sites from Musavi et al. (2017) but using an extended time period. fit1 is the line as published by Musavi et al. (2017), fit2 is a subset of data from fit1 for which extended data was available and fit3 uses longer time series data.

and species diverse forests. They showed that stand age was the strongest predictor of $\mathrm{CV}_{\mathrm{GPP1000p}}$. Forest age itself results from human intervention or cessation of human intervention mostly via silvicultural operations, the unmanaged forests are older than managed forests and significantly older than coppice forests (Figure 3.7). On the other hand, the relationship between age and $\mathrm{CV}_{\mathrm{GPP1000p}}$ strengthens or weakens based on the number of sites and length of data available. We had fewer sites (50 v 21) but a longer time series for each site. Figure 3.11 shows the change in the strength of the relationship between stand age and $\mathrm{CV}_{\mathrm{GPP1000}}$ when using fewer sites (blue) and longer time-series data (red). When taking a subset of 17 sites, the relationship improved from R^2 of 0.38 to 0.41 (from black to blue). However, when longer time series of those same sites were used, R^2 decreased from 0.41 to 0.26 (from blue to red). We used different sites than those used in their paper (due to inventory data availability), our relationship was in the same direction but weaker. Additionally, we see the effect of variability in growing season rainfall on $\mathrm{CV}_{\mathrm{GPP1000p}}$ because GPP_{1000} is normalized for radiation and vapour pressure deficit but without taking into account effect of water limitation (see eq. 3.4). The change in rainfall amount during growing season thus affect the photosynthetic capacity (see Table 3.13).

BA, logAge, ShnSz and SimSz negatively correlated with $\mathrm{CV}_{\mathrm{GPP1000}}$ indicating lower inter-annual variation in GPP_{1000} and thus more stable GPP_{1000}. EHBRECHT et al. (2017) showed that structurally more forests had lower daily fluctuations in temperature and vapour pressure deficit which could be the result of higher enhanced stand transpiration in such forests (FORRESTER, 2015; GEBAUER et al., 2012). Thus, more stable climate conditions in the structurally complex could have contributed to more stable GPP_{1000}.

The management regime had significant effect on these structural parameters (Figure 3.7). (SCHALL et al., 2018) also showed that forest management controlled forest structure. Coppice forests usually had lower values for all different structural parameters because they are usually recently created via clear cut. These forests also show higher inter-annual variation in GPP_{1000} (Figure 3.8) indicating that their functioning sensitive to environmental conditions. On the other hand, we note that the unmanaged forests and managed high forests (ManagedH) are older, have higher DBH and size diversity. In terms of structural diversity managed high forests (ManagedH) and unmanaged forests are not different (Figure 3.7).

With time, the forest adapts to their habitat by widening their size distribution, increasing the inequality of tree sizes, extending the canopy space occupation, increasing stand density and diversifying the boundaries between crowns of different species (PRETZSCH et al., 2016). Larger trees also have higher root mass (BOLTE et al., 2004; DREXHAGE et al., 1999) that facilitates absorbing nutrients and soil water. Since the forests with the higher basal area also have more diverse sizes of trees, we can assume a higher variation in root distribution as well as in canopy distribution. The higher variation in root distribution will increase the complementary use of nutrients and water. Similarly, higher horizontal differentiation can lead to better use of light resources. Thus, the ecosystem-level photosynthetic capacity (GPP_{1000}) was more stable in unmanaged forests than which structurally diverse forests which are also

3.5.2 Effect of forest structure on GPP_{1000} anomalies

The stepwise regression results showed that $\mathrm{Ano}_{\mathrm{GPP1000}}$ was mostly driven by environmental conditions, $\mathrm{TA}_{\mathrm{mean}}$ being the most important. The sites with lower temperatures have shown positive anomalies during droughts meaning that, under drier conditions, these forests actually increase their CO2 uptake. Environmental and site conditions have been reported to modulate the relationship between forest productivity and species diversity (Jucker et al., 2016; Potter et al., 2014).

Though the regression analysis did not choose logAge and BA as a predictor variable, simple correlation showed that BA and logAge significantly correlated with $\mathrm{Ano}_{\mathrm{GPP1000mWT}}$, with more positive $\mathrm{Ano}_{\mathrm{GPP1000mWT}}$ in the forests with higher basal area. Mausolf et al. (2018) reported that forests that are unmanaged for more than 50 years were less sensitive to spring drought compared to managed forests. Older forests could have deeper and heterogeneously distributed roots. One of the most effective strategies for plants to deal with drought is to have deep, ramified and dense root system as it provides trees with access to larger soil water reserves (Bréda et al., 2006). Since, in our case effect of $\mathrm{TA}_{\mathrm{mean}}$ and BA are reciprocal, we can not confirm that forests with higher basal area have lower values of GPP_{1000} during droughts.

We have looked at the direct effect of droughts on forest ecosystems, i.e. we have analysed the disturbances in ecosystem-level photosynthetic capacity during the year when droughts have occurred. Ten drought events did not affect GPP_{1000}, we speculate that these droughts could have occurred without temperature stress. The effect of drought is strong when drought co-occurred with temperature stress (Ciais et al., 2005; Von Buttlar et al., 2018). Light use efficiency of temperate forests were less or non sensitive to droughts (Stocker et al., 2018). But the GPP_{1000} of coppice forests in Sub-tropical Mediterranean region (IT-Ro2 and FR-Pue) show strong response to drought and listed as drought sensitive forests by Stocker et al. (2018).

Also the effect of management on $\mathrm{Ano}_{\mathrm{GPP1000mWT}}$ during droughts was not clear though management was selected in case of $\mathrm{Ano}_{\mathrm{GPP1000mWT}}$ only. The coppice forests had more positive $\mathrm{Ano}_{\mathrm{GPP1000mWT}}$ compared to other management regimes. The coppice forests in our case were from the relatively warmer regions (indicated by dots in Figure 3.10). Thus we arrive to this result after removing the effect of climate which was stronger than management. The effect of droughts on GPP_{1000} was higher in unmanaged forests than managed high forests but statistically insignificant (Figure 3.10 when we did not remove effect any other factor. The managed forests are regularly thinned, the thinning has shown to increase the resistance against drought in the forests (Magruder et al., 2013; Sohn et al., 2016). It hint us towards the point that forests management, particularly appropriate thinning activities, can decrease the effect of drought on forests. More studies can aid us in comfirming this, studies including droughts in 2018 and 2019 in Europe will give us further hint.

3.5.3 Limitations of the study

The main question addressed here is if the response of photosynthetic C fluxes to climate variation and drought is affected by the structural characteristics of forests. An ideal situation to understand the effect of structural parameters on any functional parameter of forests (e.g. GPP_{1000}) would be to have uniformly distributed sites over a wide range of structural parameter values, i.e. an equal number of sites in each structural parameter classes. For example, the effect of age on GPP_{1000} can be best understood if we have an equal number of forests in a wide range of age classes. In our case, our sites were not equally distributed across structural parameter classes. Similarly, this study is limited by the lower number of samples but high number of predictors. Regressions using this kind of data (independent variable concentrated in some parameter classes) could be biased or otherwise unreliable.

3.5.4 Outlook

Here, we have used only the structural parameter calculated from single structural attributes. However, to classify different forest along the axes of stand structures we need to have indices that combine multiple structural attributes (Gossner et al., 2014; Schall et al., 2018). Use of these more complex stand structural indices to understand the relationship between stand structure and forest resistance/resilience could be an interesting area of research in future. Recently, new and promising methods have been developed to characterize three-dimensional forest structure, such as terrestrial laser scanning (TSL)(Ehbrecht et al., 2016). Using the structural data from these techniques can further hint us on the effect of forest structure on resilient and resilience of forest ecosystem functions.

3.6 Conclusions

Our findings suggests that in addition to the effects of structural and environmental parameters on the stability of ecosystem functioning, inclusion of management activities is necessary. Here, we find that management regimes dominates the structural indices. Regarding our two hypotheses presented in the introduction section, we could confirm our first hypothesis. The unmanaged forests which had more diverse stand structure had higher temporal stability of ecosystem functioning (here measured in the response of inter-annual variation of GPP_{1000}). Whereas we could not confirm second hypothesis regarding the higher resistant of photosynthetic capacity (GPP_{1000}) of diverse forests during drought. However, we observe the indication that forests with higher basal area were more resistant during droughts.

3.7 Competing interests

We declare that we have no conflict of interest.

3.8 Acknowledgements

We would like to thank Erasmus Mundus Joint Doctorate Programme Forest and Nature for Society (EMJD FONASO) and University of Goettingen Scholarship for funding this research. We are grateful to all the PIs for providing inventory data.

3.9 Supplementary materials

Table 3.8: Brief management history of the sites.

Site	Management Regime	Reference
BE-Vie	Forest was thinned at the beginning of 2001, in mid-2003 and at the end of 2004.	Hurdebise et al. (2017)
CH-Dav	From 1987 to 2008, only seven of 500 trees on the 0.6 ha long-term ecosystem monitoring plot were removed from the site, mostly following a severe storm in 1990. In October 2006, an area of 1750 m^2 within the north-east part of the eddy covariance (EC) footprint was harvested.	Zweifel et al. (2010)
CH-Lae	The southern part of the EC footprint has been managed according to the forest stewardship council (FSC) since 1998 and the northern part is left unmanaged as a nature reserve since 2001	Etzold et al. (2011)
CZ-BK1	Norway spruce planted in 1981.	Sedlák et al. (2010)
DE-Hai	The old-growth beech forest.	Knohl et al. (2003)
DE-Lnf	The pure beech forest and thinned under regular shelterwood system with a rotation period of about 120-140 years.	Tamrakar et al. (2018)
FI-Hyy	Scots pine planted in 1962 and thinned in early 2002.	Ilvesniemi et al. (2009) and Vesala et al. (2005)
FR-Fon	Forest stand located in protected reserve.	Koop et al. (1987) and Otto et al. (2014)
FR-Pue	This forest has been managed as a coppice for centuries and the last clear cut was performed in 1942.	Allard et al. (2008) and Pita et al. (2013)
IT-Ren	The site is of natural origin and is used for wood production.	Papale et al. (2015)
IT-Ro1	The site is in the initial developmental stages after the forest cut via coppicing in December 1999	Papale et al. (2015)
IT-Ro2	The forest is managed as coppice-with-standards with a rotation cycle ranging 15-20 years and arranged in 15 sequentially aged compartments.	Hurdebise et al. (2017)
RU-Fyo	The site is located in reserve without any commercial disturbance since 1960s.	Milyukova et al. (2002)
US-Ha1	Some selective harvesting in site was done 300 m to the S-SE but not in a direction sampled by EC tower.	Urbanski et al. (2007)
US-Me2	The site was clear-cut in 1914 and then allowed to regenerate naturally.	Schwarz et al. (2004)
US-MMS	The forest is a secondary successional broadleaf forest. Timber has been harvested around EC tower based on selection and seed tree methods on a 20–25 years rotation for several decades	Ehman et al. (2002)
US-NR1	The sub-alpine forest is recovering from early twentieth century logging.	Monson et al. (2002)
US-PFa	The parts of forest has been thinned and clear-cut within the past few decades.	Davis et al. (2003)
US-Syv	It is unmanaged old-growth site which has never been logged.	Desai et al. (2005)
US-UMB	The stand was disturbed by harvest and fire once in the early 20th century and was not disturb later.	Gough et al. (2007)
US-WCr	The site is mature upland forest. The forests were harvested extensively in early 1990s.	Desai et al. (2005)

Table 3.9: Dry years, and annual mean ± sd values of different fluxes (NEE, GPP, Reco, GPP_{1000p} and trend of GPP_{1000p} - T_{GPP100}) for sites.

Site	Dry years	NEE	GPP	Reco	GPP_{1000}	T_{GPP100}
–	–	g C m^{-2} yr^{-1}	g C m^{-2} yr^{-1}	g C m^{-2} yr^{-1}	⁻ mol m^{-2} yr^{-1}	⁻ mol m^{-2} yr^{-1}
BE-Vie	2003	-477 ± 157	1816 ± 186	1385 ± 242	27.41 ± 2.41	0.26***
CH-Dav	2003, 2015	-78 ± 183	1055 ± 92	853 ± 157	16.91 ± 2.08	-0.1
CH-Lae	2015	-673 ± 395	1867 ± 177	1678 ± 315	32.19 ± 3.12	0.4*
CZ-BK1	2015	-858 ± 120	1914 ± 155	968 ± 169	29.18 ± 2.68	0.45**
DE-Hai	2003	-544 ± 84	1541 ± 143	1153 ± 104	29.3 ± 2.92	-0.19
DE-Lnf	2003	-597 ± 167	1659 ± 107	1127 ± 78	29.21 ± 2.6	0.03
FI-Hyy		-227 ± 55	1106 ± 109	924 ± 92	21.15 ± 1.5	0.18***
FR-Fon	2005	-633 ± 91	1678 ± 178	1026 ± 242	30.15 ± 1.51	0.01
FR-Pue	2005, 2006, 2012	-232 ± 86	1224 ± 257	970 ± 240	14.65 ± 2.96	-0.33
IT-Ren	2005	-678 ± 143	1503 ± 248	991 ± 243	24.42 ± 3.3	0.59**
IT-Ro1		-226 ± 194	1646 ± 122	1352 ± 178	21.53 ± 2.59	0.87
IT-Ro2	2007, 2012	-682 ± 258	1631 ± 163	1011 ± 195	23.29 ± 4.38	-0.31
RU-Fyo	2002	105 ± 127	1351 ± 133	1413 ± 102	23.86 ± 1.54	0.11*
US-Ha1		-226 ± 208	1551 ± 232	1274 ± 268	26.72 ± 2.54	0.21*
US-Me2	2002, 2013	-550 ± 265	1656 ± 152	1190 ± 271	19.93 ± 1.82	0.37**
US-MMS	1999	-427 ± 73	1644 ± 114	1231 ± 133	28.79 ± 1.97	-0.07
US-NR1	2002, 2012	-170 ± 29	910 ± 49	766 ± 55	16.1 ± 0.82	0.01
US-PFa	2006	-12 ± 114	903 ± 236	810 ± 149	20.39 ± 2.59	0.04
US-Syv	2006	-74 ± 113	1184 ± 266	947 ± 146	21.59 ± 2.53	0.64**
US-UMB	2000	-269 ± 65	1319 ± 138	1071 ± 114	25.86 ± 2.19	0.35**
US-WCr	2006	-260 ± 153	1272 ± 139	1043 ± 171	25.58 ± 3.15	0.13

Table 3.10: The zero-order correlation of environmental and structural variables with $\mathrm{Sd}_{\mathrm{GPP1000}}$ calculated from mean and 90^{th} percentile with and without trend. *** is significant at p = 0.001, ** p = 0.01, and * p = 0.05.

Variables	Correlation of			
	$\mathrm{Sd}_{\mathrm{GPP1000m}}$		$\mathrm{Sd}_{\mathrm{GPP1000p}}$	
	WT	WoT	WT	WoT
Environmental parameters				
$\mathrm{TA}_{\mathrm{mean}}$	0.43*	0.56***	0.33	0.43*
$\mathrm{R}_{\mathrm{gmean}}$	0.12	0.15	0.3	0.3
$\mathrm{VPD}_{\mathrm{mean}}$	0.2	0.3	0.3	0.34
$\mathrm{P}_{\mathrm{mean}}$	0.27	0.17	0.22	0.06
$\mathrm{SPEI}_{\mathrm{mean}}$	-0.31	-0.29	-0.34	-0.3
$\mathrm{TA}_{\mathrm{GSmean}}$	0.4	0.52*	0.39	0.46*
$\mathrm{R}_{\mathrm{gGSmean}}$	0.2	0.2	0.37	0.34
$\mathrm{VPD}_{\mathrm{GSmean}}$	0.18	0.26	0.29	0.31
$\mathrm{P}_{\mathrm{GSmean}}$	0.11	-0.05	0.07	-0.09
$\mathrm{SPEI}_{\mathrm{GSmean}}$	-0.3	-0.22	-0.45*	-0.32
$\mathrm{TA}_{\mathrm{sd}}$	0.35	0.34	0.38	0.41
$\mathrm{R}_{\mathrm{gsd}}$	0.57***	0.31	0.51*	0.32
$\mathrm{VPD}_{\mathrm{sd}}$	0.49*	0.44*	0.36	0.35
P_{sd}	0.43*	0.33	0.46*	0.3
$\mathrm{SPEI}_{\mathrm{sd}}$	-0.2	-0.34	-0.07	-0.28
$\mathrm{TA}_{\mathrm{GSsd}}$	0.05	0.06	-0.04	0.02
$\mathrm{R}_{\mathrm{gGSsd}}$	0.31	0.18	0.33	0.2
$\mathrm{VPD}_{\mathrm{GSsd}}$	0.29	0.33	0.16	0.23
$\mathrm{P}_{\mathrm{GSsd}}$	0.46*	0.47*	0.55***	0.48*
$\mathrm{SPEI}_{\mathrm{GSsd}}$	0	-0.12	0	-0.17
Structural parameters				
Age	-0.2	-0.11	-0.35	-0.28
logAge	-0.31	-0.27	-0.42	-0.39
BA	-0.61***	-0.44*	-0.66***	-0.52*
DBH	-0.17	-0.16	-0.45*	-0.38
$\mathrm{DBH}_{\mathrm{sd}}$	-0.01	-0.01	-0.21	-0.17
Height	0.06	0.04	-0.28	-0.19
ShnSz	-0.14	-0.15	-0.42	-0.33
SimSz	-0.21	-0.2	-0.44*	-0.33
SpNo	-0.03	0.02	-0.07	0.01

Table 3.11: The zero-order correlation of environmental and structural variable with mean annual GPP and Reco calculated with and without trend. *** is significant at p = 0.001, ** p = 0.01, and * p = 0.05.

Variables	Correlation of			
	GPP		Reco	
	WT	WoT	WT	WoT
Environmental parameters				
TA_{mean}	0.41	0.55***	0.29	0.19
R_{gmean}	0.19	0.2	0.26	0.18
VPD_{mean}	0.38	0.47*	0.19	0.01
P_{mean}	0.23	0.21	0.31	0.34
$\text{SPEI}_{\text{mean}}$	-0.41	-0.39	-0.23	-0.11
$\text{TA}_{\text{GSmean}}$	0.37	0.44*	0.19	0.08
$\text{R}_{\text{gGSmean}}$	0.28	0.28	0.3	0.17
$\text{VPD}_{\text{GSmean}}$	0.4	0.46*	0.16	-0.04
P_{GSmean}	-0.02	-0.14	0.15	0.29
$\text{SPEI}_{\text{GSmean}}$	-0.38	-0.23	-0.09	0.06
TA_{sd}	0.11	-0.09	0.09	0.09
R_{gsd}	0.43*	0.38	0.05	0.02
VPD_{sd}	0.2	0.25	0.03	0.08
P_{sd}	0.38	0.39	0.19	0.15
SPEI_{sd}	0.1	0.02	0.05	-0.02
TA_{GSsd}	-0.23	-0.24	-0.2	-0.14
R_{gGSsd}	0.19	0.24	-0.01	0.03
VPD_{GSsd}	0.15	0.27	-0.1	-0.09
P_{GSsd}	0.45*	0.48*	0.2	0.15
$\text{SPEI}_{\text{GSsd}}$	0.18	0.07	0.18	0.18
Structural parameters				
Age	-0.3	-0.17	-0.06	0.01
logAge	-0.35	-0.26	-0.07	-0.04
BA	-0.54***	-0.39	0.03	0.13
DBH	-0.44*	-0.36	-0.16	-0.1
DBH_{sd}	-0.1	0	0.47*	0.56***
Height	-0.42	-0.32	-0.17	0
ShnSz	-0.47*	-0.38	0	0.13
SimSz	-0.58***	-0.49*	-0.16	0.01
SpNo	-0.18	-0.34	-0.07	-0.09

Table 3.12: The zero-order correlation of GPP and Reco anomalies of dry years with environmental and structural variables. Anomalies were also estimated with trend and after removing trend. *** is significant at p = 0.001, ** p = 0.01, and * p = 0.05.

Variables	Correlation of			
	Ano_{GPP}		Ano_{Reco}	
	WT	WoT	WT	WoT
Environmental parameters				
TA_{mean}	-0.3	-0.33	-0.06	-0.05
R_{gmean}	-0.32	-0.22	-0.06	0.07
VPD_{mean}	-0.44*	-0.39	-0.07	0.02
P_{mean}	0.03	-0.15	-0.15	-0.34
$SPEI_{mean}$	0.02	0.13	-0.15	-0.15
TA_{GSmean}	-0.46*	-0.45*	-0.18	-0.18
$R_{gGSmean}$	-0.43*	-0.34	-0.09	0.05
VPD_{GSmean}	-0.44*	-0.41*	-0.06	0.02
P_{GSmean}	0.28	0.19	-0.1	-0.27
$SPEI_{GSmean}$	0.34	0.43*	0.05	0.09
TA_{sd}	-0.08	-0.07	-0.22	-0.24
R_{gsd}	-0.53***	-0.51***	-0.35	-0.32
VPD_{sd}	-0.45*	-0.49***	-0.19	-0.25
P_{sd}	-0.21	-0.35	-0.17	-0.29
$SPEI_{sd}$	-0.14	-0.11	-0.02	-0.08
TA_{GSsd}	-0.18	-0.16	-0.3	-0.24
R_{gGSsd}	-0.51***	-0.54***	-0.35	-0.37
VPD_{GSsd}	-0.41*	-0.46*	-0.13	-0.16
P_{GSsd}	-0.09	-0.14	-0.13	-0.25
$SPEI_{GSsd}$	-0.36	-0.33	-0.16	-0.3
Structural parameters				
Age	0.37	0.38	0.2	0.21
logAge	0.38	0.43*	0.19	0.26
BA	0.53***	0.51***	0.32	0.37
DBH	0.33	0.34	0.11	0.19
DBH_{sd}	0.11	0.17	0.19	0.27
Height	0.24	0.29	0.01	0.05
ShnSz	0.24	0.31	0.06	0.15
SimSz	0.24	0.33	0.03	0.14
SpNo	-0.03	0.02	-0.18	-0.15

Table 3.13: The distance correlation values of GPP_{1000m} and GPP_{1000p} with yearly growing season rainfall (TA_{GSmean}.

site	$GPP_{1000m}VsTA_{GSmean}$	$GPP_{1000p}VsTA_{GSmean}$
BE-Vie	0.43	0.45
CH-Dav	0.45	0.39
CH-Lae	0.32	0.38
CZ-BK1	0.45	0.50
DE-Hai	0.57	0.36
DE-Lnf	0.38	0.45
FI-Hyy	0.37	0.28
FR-Fon	0.53	0.37
FR-Pue	0.64	0.65
IT-Ren	0.37	0.37
IT-Ro1	0.58	0.53
IT-Ro2	0.71	0.43
RU-Fyo	0.34	0.35
US-Ha1	0.43	0.41
US-Me2	0.62	0.48
US-MMS	0.59	0.52
US-NR1	0.35	0.37
US-PFa	0.52	0.32
US-Syv	0.53	0.52
US-UMB	0.35	0.43
US-WCr	0.52	0.42

CHAPTER 4

A flexible forest soil water model (FWSM) in R

Manuscript to be submitted to 'Environmental modelling and software'

4.1 Abstract

Soil water availability is one of the most important determinants of vegetation characteristics. To estimate soil water in forest soils, a new model (forest soil water model - FSWM), suitable for a range of forest soils, is developed in the R environment. This new open-source model incorporates the Gash model for interception, the Ritchie model for soil evaporation and the Richards equation for soil water movement. Model performance, evaluated against soil water measurements at 12 sites, was good for deciduous broadleaf forests ($R^2 = 0.68$), moderate for mixed forests ($R^2 = 0.57$) and evergreen needle leaf forests ($R^2 = 0.45$). Performance when simulating evapotranspiration was better, with R^2 from values 0.52 to 0.88. FSWM is also flexible for simulating soil horizons with different depths and helps when comparing modeled with observed values at different soil depths. The above characteristics make FSWM a flexible and freely available tool for the ecosystem and hydrological research.

4.2 Introduction

Soil water availability is one of the most important determinants of vegetation characteristics (Clark et al., 2016; Stephenson, 2002), including vegetation health (Hu et al., 2017; Lantschner et al., 2019; Liu et al., 2018), and productivity (Huang et al., 2012; Reichstein et al., 2007; Wang et al., 2016). The increasing frequency of drought events in recent years (Spinoni et al., 2019) has increased interest within the scientific community towards better understanding the associated impacts on terrestrial ecosystems.

Various drought indices have been proposed to quantify droughts (see review by Speich, 2019). Some indices use precipitation data alone (e.g. the standardized precipitation index - SPI by McKee et al., 1993; the standardized precipitation and evapotranspiration index - SPEI by Vicente-Serrano et al., 2010) while other use physiological parameters along with meteorological variables (e.g. the water stress integral - WSI by Myers, 1988). Soil water in forests can be calculated either from sub-modules of process-based land surface models, as found in FORCLIM (Bugmann et al., 1998), FOREST-BGC (Running et al., 1988), SPA (Williams et al., 1996), FORSKA (Prentice et al., 1992), SIERRA (Mouillot et al., 2001), LPJ–DGVM (Sitch et al., 2003), CASTANEA (Davi et al., 2005b), CoupModel (Jansson et al., 2011), and others, or from soil water balance models like Site Water Balance - SWB (Grier et al., 1977), the Simple Water Balance Model - SWBM (Orth et al., 2013), SPLASH (Davis et al., 2017), BILJOU (Granier et al., 1999), SWUF (Paul et al., 2003), and others. Process-based land surface models usually involve a large number of parameters and the estimation of these parameters requires detailed field and experimental data. If soil water content or drought indices are required, water balance models using simple soil and stand parameters and climatic data are often adequate (Granier et al., 1999).

Jong et al. (1996) categorized water balance models into budget models, semi-dynamic models and dynamic models and pointed out the main advantages and disadvantages of each. Most simple budget models consider the soil profile as a bucket into which water flows until it is full and surplus water is then either runoff or drainage beneath the root zone (Davis et al., 2017). The advanced budget models have the soil profile divided into multiple layers (O'Leary et al., 1985). In the case of semi-dynamic models, the rate of water movement of each layer varies as a function of infiltration amount, the relative water content, percolation coefficient, drainage rate coefficients, etc. (Granier et al., 1999; Paul et al., 2003). In dynamic models, the physical factors governing water movement in soil – for example, the soil water potential, the differential water capacify, the hydraulic conductivity, etc. of each soil layer – control infiltration and redistribution of water (Jong et al., 1996).

Stocker et al. (2018) used three different water budget models (SPLASH, SWBM and ET-driven bucket) and two different water holding capacities to quantify soil water content of many different ecosystem types. Their results showed that in most of the temperate forests analyzed (eg. Hainich, Tharandt, Soroe, Loobos, Hyytiala, etc) soil moisture had little to no influence on light use efficiency (LUE). Contrary to that, Granier et al. (2007), using the semi-dynamic soil water model (BILJOU), showed that soil moisture for the same temperate sites had a strong influence on gross primary productivity (GPP) in the heat-wave of 2003. We note that Stocker et al. (2018) used longer-term data including 2003. Such inconsistencies in reported drought effects can arise from a number of factors, such as errors in the calculation of soil moisture indices, differences in the temporal data coverage (only one year in the case of Granier et al. (2007)), different types of models, and different functional properties of forest stands. Such uncertainties can make it difficult to address ecological questions about the sensitivity of functional properties (e.g. LUE) of temperate forests to drought or to derive meaningful drought indices.

One approach is to use semi-dynamic or dynamic models that allow calculating water dynamics of entire soil profiles over multiple years, spatial and temporal levels at which direct measurements are rarely available (and in any case prone to large errors). The resulting data can be more effectively used to test if functional properties of temperate forests have been more or less affected by soil moisture content in a given period. These models can utilize site-specific soil parameters and vegetation characteristics to quantify forest soil moisture indices.

Although there are many models (as listed above) that calculate soil water dynamics using a variety of approaches, it is difficult to find soil water models that are open source, easily accessible and practical to implement. The latter requires models that are stand-alone, meaning they are independent and can be run with a minimal set of vegetation, soil and climate data. Models also do not always have the structural flexibility to simulate different soil vertical resolutions, thus making them more easily comparable to the variety of site-level moisture data available.

The BILJOU model (Granier et al., 1999), a semi-dynamic model, is a useful tool for such purposes because it requires simple soil and stand parameters, in addition to climatic data. BILJOU can be run for single years using the online platform `https://appgeodb.nancy.inra.fr/biljou/`. There are a few disadvantages of this model. First, running the model for multiple years in such a platform is impractical and quickly becomes tedious and time-demanding. Second, the model code is closed source, making it impossible to know precisely how calculations are performed or to modify the code if changes in parameter values or processes are desired. Thus, we recognized the need to build a model using a familiar and accessible platform, for which we chose R (R Development Core

TEAM, 2018). Making the code open-source facilitates the improvement and further development of the model by the research community.

Here we present the forest soil water model (FSWM) that runs at a daily time scale. Our model is based on the same general principles underlying BILJOU (GRANIER et al., 1999) while improving a number of processes and adding functionality for the quantification of soil water in temperate forests. These improvements include (1) the use of soil texture data, to estimate field capacity, wilting point and hydraulic conductivity (SAXTON et al., 2006); (2) the use of net radiation whenever possible instead of solar radiation; (3) an optional function to calculate root distribution in different soil layers (GALE et al., 1987); (4) the Ritchie formulation for soil evaporation (RITCHIE, 1972); (5) the Gash model of interception (GASH et al., 1995); and (6) the Richards equation to calculated soil water movement (RICHARDS, 1931).

4.3 Materials and methods

4.3.1 Model description

FSWM runs at a daily scale and calculates transpiration, interception, throughfall, soil evaporation, soil moisture and drought indices – relative extractable water (REW) at a daily scale and annual drought index (ADI) at an annual scale – using the input data shown in Table 4.1. Soil can be represented in multiple layers. Saturation point, field capacity, wilting point, and hydraulic conductivity of different soil layers are calculated using soil texture data following SAXTON et al. (2006). Field capacity, however, can also be given as input data by estimating it from the measured long-term soil moisture data. Changes in daily soil water content (Δ) SW, eq. 4.1) are calculated as the balance between total rainfall (P), interception (I), transpiration (T), soil evapotranspiration (E) and drainage (D). The model assume no run-off. Symbols and parameters used in the model are listed in Table 4.2 and 4.3, respectively.

$$\Delta SW = P - I - T - E - D \tag{4.1}$$

Distribution of roots

We used the model presented by GALE (1987) for the vertical distribution of root. In this model, lower values of the parameter β represent higher abundance of roots on the shallower soil layers. Jackson et al. (1996) listed β values for different ecosystems between 0.914 and 0.975 (β = 0.976 and 0.966 for temperate coniferous and deciduous forests, respectively). Whenever data for root mass in different soil layers is available, we can calculate site-specific β values.

$$Y = 1 - \beta^d \tag{4.2}$$

Here, Y is the cumulative root fraction from the surface to any depth (d) in centimeters.

Table 4.1: List of inputs required for the model, site data, soil layer data, phenological, and climatic data.

Symbols	Description
Site data	
Ele	site elevation [m]
FT	forest type – Deciduous, Evergreen or Mixed
Lat	latitude [decimal degrees]
Site	name of the site
TRD	total rooting depth [cm]
M_H	wind speed measurement height [m]
Data for each soil layer	
BD	bulk density [g cm^{-3}]
Clay	clay [g g^{-1}]
DL	depth of layer lower boundary [cm]
DU	depth of layer upper boundary [cm]
DUL	the volumetric water content of drained soil [v v^{-1}] (optional)
Gravel	gravel [g g^{-1}]
RF	root fraction (optional)
Sand	sand [g g^{-1}]
SOM	soil organic matter content [g g^{-1}]
Phenological data	
GSE	Julian day when the all the leaves fall
GSS	Julian day when the first leaves appear
Lai	maximum leaf area index for the year [m^2 m^{-2}]
Climatic data	
P	daily sum of rainfall [mm]
R_g	daily short-wave radiation [Mj m^{-2} day^{-1}] (if R_n not available)
RH_{max}	maximum daily relative humidity [%]
RH_{min}	minimum daily relative humidity [%]
R_n	daily net radiation [Mj m^{-2} day^{-1}]
T_{max}	maximum daily temperature [°C]
T_{mean}	mean daily temperature [°C]
T_{min}	minimum daily temperature [°C]
WS_{MH}	wind speed at measurement height [m]

Temporal variation of leaf area index (LAI) and light reaching the ground

Forests in the model can be either evergreen, deciduous or mixed. For evergreen forests, we maintain a constant LAI over the year. For deciduous forests, LAI is 0 during the non-leaved period and linearly increases after the start of leaf-out over the course of 45 days, after which it reaches a maximum. Based on our experience in a deciduous unmanaged Hainich forest, Germany, the underground vegetation starts growing nearly two weeks before the tree leaves start coming out and tree leaves took around thirty days to come out completely. For mixed forests, LAI is divided into an evergreen and a deciduous fraction, with the dynamics of each fraction being as described for each forest type. LAI for the evergreen part is constant over the entire year and we follow the same principle for the deciduous part as in the deciduous forest. LAI remains maximum for both deciduous and

Table 4.2: Symbols of variables used in the model.

Symbols	Description
C	canopy cover (0 to 1)
D	sub-surface drainage [mm day^{-1}]
Δ	slope of the saturation vapour pressure curve [kPa °C]
Dep	depth of the soil layer [cm]
$\mathrm{dz_i}$	thickness of soil layer i [mm]
E	soil evaporation [mm day^{-1}]
FC	field capacity [mm]
γ	psychrommetric constant [kPa °C]
I	rainfall interception [mm day^{-1}]
K	empirical unsaturated hydraulic conductivity function [mm s^{-1}]
LAI	leaf area index [m^2 m^{-2}]
λ	latent heat of vaporization [MJ kg^{-1}]
$\mathrm{L_g}$	proportion of light at canopy
$\mathrm{L_g}$	proportion of light reaching ground
P	daily sum of rainfall [mm day^{-1}]
PET	potential evapotranspiration [mm day^{-1}]
$\mathrm{P_s}$	canopy saturating rainfall [mm]
ψ	empirical soil hydraulic capillary head function [mm]
r	ratio of $\mathrm{TR_{max}}$ to PET
REW	relative extractable water
T	transpiration [mm day^{-1}]
t	time [s]
θ_i	volumetric soil water content of layer i [m^3 m^{-3}]
$\mathrm{TR_{max}}$	transpiration without water stress [mm day^{-1}]
WP	Wilting point [mm]
$\mathrm{WS_{2m}}$	wind speed at 2 m height [m s^{-1}]
Y	cumulative root fraction
z	vertical coordinate (positive downward) [mm]

mixed forest until leaves start falling in autumn. LAI starts to decrease 45 days before all the leaves shed.

The proportion of light reaching the ground ($\mathrm{L_g}$) is estimated with the Beer-Lambert function using a light extinction coefficient (k) and LAI as shown in eq. 4.3. The fraction of light intercepted by the canopy is the remaining fraction (eq. 4.4) and also considered as canopy cover (C).

$$L_g = e^{-k*LAI} \tag{4.3}$$

$$L_c = C = 1 - L_g \tag{4.4}$$

Canopy interception

We used the Gash model (Gash et al., 1995) for quantifying canopy interception (I) where daily rainfall is considered to fall in a single event. First, the minimum amount of rainfall required to saturate the canopy ($\mathrm{P_s}$) is calculated based on canopy storage (S), rate of evaporation during the rainfall event (ER) and canopy cover (C) (eq. 4.5). Canopy storage

Table 4.3: Symbols of parameters and their values used in model.

Parameter	Description	Value	Reference
β	Root distribution parameter	0.92 - 0.97	Jackson et al., 1996
CSC	Canopy water storage capacity	0.10 - 1 [mm LAI^{-1}]	Bittner et al., 2010; Cáceres et al., 2015; Klaassen et al., 1998
ER	The ratio of the evaporation rate to rainfall rate during the rainfall event	0.05 - 0.25	Bittner et al., 2010; Cáceres et al., 2015
g	Desorptivity values	2-8 [mm day$^{-1/2}$]	Kustas, 2016; Paul et al., 2003
k	Light extinction coefficient	0.5	

on a particular day is calculated as the product of canopy storage capacity (CSC) and LAI. Intercepted water is then calculated as shown in eq. 4.6.

$$P_s = \frac{S}{C\,ER}\,ln(1 - ER) \tag{4.5}$$

$$I = \begin{cases} C\,P_s + C\,ER(P - P_s) & \text{if P} > P_s \\ C\,P & \text{if P} <= P_s \end{cases} \tag{4.6}$$

Transpiration

Transpiration is a function of PET, LAI and relative extractable water (REW). The model first calculates the potential evapotranspiration (PET) with the Penman-Monteith equation (Zotarelli et al., 2010) requiring daily net radiation ($\mathrm{R_n}$), mean temperature ($\mathrm{T_{mean}}$), vapour pressure deficit (VPD), and wind speed at 2 m height ($\mathrm{WS_{2m}}$) as shown in eq. 4.7. If ($\mathrm{R_n}$) is not available it is estimated from the global radiation ($\mathrm{R_g}$). $\mathrm{WS_{2m}}$ is calculated using eq. 4.8.

$$PET = \frac{0.408\varDelta\;R_n + \gamma\frac{900}{Tmean+273}\;WS_{2m}\;VPD}{\varDelta + \gamma\;(1 + 0.34\;WS_{2m})} \tag{4.7}$$

$$WS_{2m} = WS_{MH}\;\frac{4.87}{ln(67.8\;M_H - 5.42)} \tag{4.8}$$

Secondly, the model estimates r, the ratio of maximum stand transpiration (transpiration without water limitation - $\mathrm{TR_{max}}$) to PET as the function of LAI (eq. 4.9). A soil water limitation to transpiration is estimated by calculating REW, which is the ratio of available water (available soil water -SW minus wilting point - WP) to maximum available water (field capacity - FC minus wilting point - WP) for plants (eq. 4.10). Actual transpiration (T) is then calculated as the product of r and PET when soil water is not limited or as a function dependent on r, REW and PET when soil water is limited (eq. 4.11).

$$r = \frac{TR_{max}}{PET} = \begin{cases} 0.75 & \text{if LAI >= 6} \\ 0.125\ LAI & \text{if LAI < 6} \end{cases} \tag{4.9}$$

$$REW = \frac{SW - WP}{FC - WP} \tag{4.10}$$

$$T = \begin{cases} r\ PET & \text{if REW > 0.4} \\ PET\ \frac{r\ REW + 0.15\ (0.4 - REW)}{0.4} & \text{if REW <= 0.4} \end{cases} \tag{4.11}$$

Understorey evapotranspiration

Understorey evapotranspiration is the minimum between soil water supply ($\mathrm{S_{soil}}$) from the topsoil layer and potential soil evaporation. $\mathrm{S_{soil}}$ is based on Ritchie (1972). First, the time required to evaporate the water deficit (i.e. the difference between field capacity (FC1) and soil water (SW1) - $\mathrm{t_{def}}$), from the topsoil layer is calculated (eq. 4.13) and is dependent on desorptivity parameter (γ). Then, the soil water supply is calculated (eq. 4.14).

$$E_{soil} = min\ (S_{soil}, PET_s) \tag{4.12}$$

$$t_{def} = \left[\frac{FC_1 - SW_1}{\gamma} \right]^2 \tag{4.13}$$

$$S_{soil} = \gamma\ (\sqrt{t_{def} + 1} - \sqrt{t_{def}}) \tag{4.14}$$

Potential evaporation from the understorey $\mathrm{PET_s}$ is calculated using the same formulation as for the canopy (eq. 4.7). The net radiation reaching the ground was estimated as the product of fraction light reaching the ground (eq. 4.3) and net radiation at the canopy $\mathrm{R_n}$. Wind speed under the canopy was estimated from eq. 4.15. During the non-leaved period, the $\mathrm{R_n}$ reaching the ground was assumed to be 0.3 as used by BITTNER et al. (2010).

$$WS_{2m} = WS_{MH}\ exp\big[\ a(\frac{2}{M_H} - 1)\big] \tag{4.15}$$

Water movement in soil

The model divides the soil into at least two layers: the top layer (0-10 cm) from where soil evaporation occurs and bottom layer(s). The number of soil layers (nsl) depends on the soil details available. The Richards equation (RICHARDS, 1931) is applied for vertical water flow through unsaturated porous medium to estimate the change in soil moisture in each soil layer (eq. 4.16). The unsaturated conductivity (K_θ) and tension (ψ_θ) at soil moisture (θ) is quantified following Saxton and Rawls (2006), and linearized about change in volumetric soil water content (d_θ). A tridiagonal system of equations is used to solve d_θ, as implemented in the R package LimSolve(SOETAERT et al., 2016). The solution conserves water as shown in eq. 4.17.

$$\frac{d\theta}{dt} = \frac{d}{dz}\left[-K_\theta \, \frac{d(\psi_\theta + z)}{dz}\right] \tag{4.16}$$

$$\begin{aligned}\left[\theta_1 \cdot dz_1 + ... + \theta_{nsl}\, dz_{nsl}\right]_{n+1} = \left[\theta_1\, dz_1 + ... + \theta_{nsl}\, dz_{nsl}\right]_n + \\ (q_{infl} - q_E - q_T - q_D)\, dt\end{aligned} \tag{4.17}$$

where, θ_i is volumetric soil water content of layer i [$m^3\ m^{-3}$]
d_z is thickness of i^{th} soil layer [mm]
n is the number of the timestep (day of the year in our case)
q_{infl} is the infiltration rate (mm s^{-1})
q_E is the soil evaporation rate(mm s^{-1})
q_T is the transpiration rate (mm s^{-1})
q_D is the drainage rate (mm s^{-1})
dt is the number of seconds in a timestep (86400 seconds in our case)

The lower and upper boundaries for daily soil water content are given by wilting point (WP) and field capacity (FC), respectively. As a more reliable alternative to pedotransfer functions, FC can be directly taken from long-term measurement of soil moisture that captures maximum field values. Temperate forests typically show periods of stable high soil water levels, indicating a well-drained maximum (see Fig. 4.3). This value, also known as the drained upper limit (DUL), can be used as FC. WP, on the other hand, was estimated using the soil texture data following Saxton et al. (2006). Water exceeding FC is percolated from a soil layer down to lower layers. Any excess water in the last soil layer is lost as sub-surface drainage.

Drought indices

REW is the index for daily drought. At the annual scale, we calculate annual drought days (ADD) and annual drought intensity as drought index (ADI). ADD is calculated as the numbers of days when REW is below 0.4 (based on threshold value given by Granier et al., 1999) and ADI as:

$$ADI = \frac{\sum max[\frac{0.4-REW}{0.4},\ 0]}{365} \tag{4.18}$$

where ADI is dimensionless and ranges between 0 (when daily REW is always above 0.4) and 1 (when daily REW is 0 in all days of a year).

4.3.2 Data

We compiled data from twelve forest sites within the fluxnet2015 eddy covariance data set (Fluxnet, 2017). Data consisted of daily climate (temperature, humidity, precipitation, radiation), latent energy fluxes, soil moisture and soil texture of four deciduous broad-leaved forests (DBF), four evergreen needle-leaved forests (ENF) and four mixed forests (MF)(Table

4.4). Soil data (sand, clay, bulk density, gravel, soil organic material) were obtained from fluxnet2015, euroflux (http://www.europe-fluxdata.eu/) and from relevant literature. Data and model for this chapter are available at `https://doi.org/10.25625/3DVVVN`.

Table 4.4: Sites used in this study.

Site	Forest Type	Latitude	Elevation	Reference
DE-Hai	DBF	51.08	431	Knohl et al. (2003)
DE-Lnf	DBF	51.33	450	Herbst et al. (2015)
DK-Sor	DBF	55.49	40	Pilegaard et al. (2001)
US-MMS	DBF	39.32	293	Schmid et al. (2000)
DE-Tha	ENF	50.96	295	Grünwald et al. (2007)
IT-Lav	ENF	45.96	1319	Papale et al. (2015)
NL-Loo	ENF	52.17	26	Schelhaas et al. (2004)
US-Me2	ENF	44.45	1234	Irvine et al. (2004)
BE-Bra	MF	51.31	16	Janssens et al. (1999)
BE-Vie	MF	50.31	495	Aubinet et al. (2001)
CH-Lae	MF	47.48	674	Etzold et al. (2011)
US-Syv	MF	46.24	533	Desai et al. (2005)

4.3.3 Model parameterizations

Four model parameters namely deabsorbity (γ), canopy storage capacity (CSC), rate of canopy evaporation to rainfall rate (ER) and the root distribution coefficient (β) were optimized by minimizing the difference between modelled evapotranspiration and evapotranspiration calculated from the observed corrected latent energy (details on latent energy correction is detailed in Fluxnet, 2017). Parameters were separately optimized for each forest type by selecting four years of one randomly selected site from each forest type (DBF:DE-Hai, ENF:DE-Tha and MF:BE-Bra). Optimization was carried out with the R package FME (Soetaert et al., 2016).

4.3.4 Model evaluation

We evaluated the model results with soil moisture and corrected evapotranspiration data from the 12 fluxnet sites, excluding the data used to estimate the parameters discussed in section 4.3.3. For evapotranspiration comparison, we used only the days with more than 80 % non-filled half-hourly observed evapotranspiration data.

4.4 Results and discussions

4.4.1 Field capacity (FC) and wilting point (WP)

Using FC from field soil moisture measurements instead of approximating it with a pedotransfer function improved the model performance in all sites except in BE-Bra (Figure 4.1). The highest improvement was observed in US-Me2 (38 % increase in R^2). R^2 of deciduous forests increased in average ca. 9 %. Different studies have used different soil water potential to estimate FC (e.g. Kätterer et al., 2006; Le Bas et al., 1997; White, 2006, etc.). Here we used a soil water potential of -33 Kpa and pedotransfer functions developed by Saxton et al. (2006) for approximating FC from soil texture (Richards, 1944). Nemes et al. (2011) showed that FC estimated from -33 kPa can differ from the field measured FC.

Similarly, optimizing the texture (clay and sand %) improved the model performance significantly in DBF sites (lower panels of Fig. 4.1). Texture vary spatially within a forest. In Figure 4.16, we show the texture reported in three different papers at DE-Hai (Bittner et al., 2010; Guckland et al., 2009; Kutsch et al., 2010). Even though Kutsch et al. (2010) measured the soil texture in plots approximately three kilometers west of plots measured by Bittner et al. (2010) and Guckland et al. (2009), the values of clay content vary considerably over short distances.

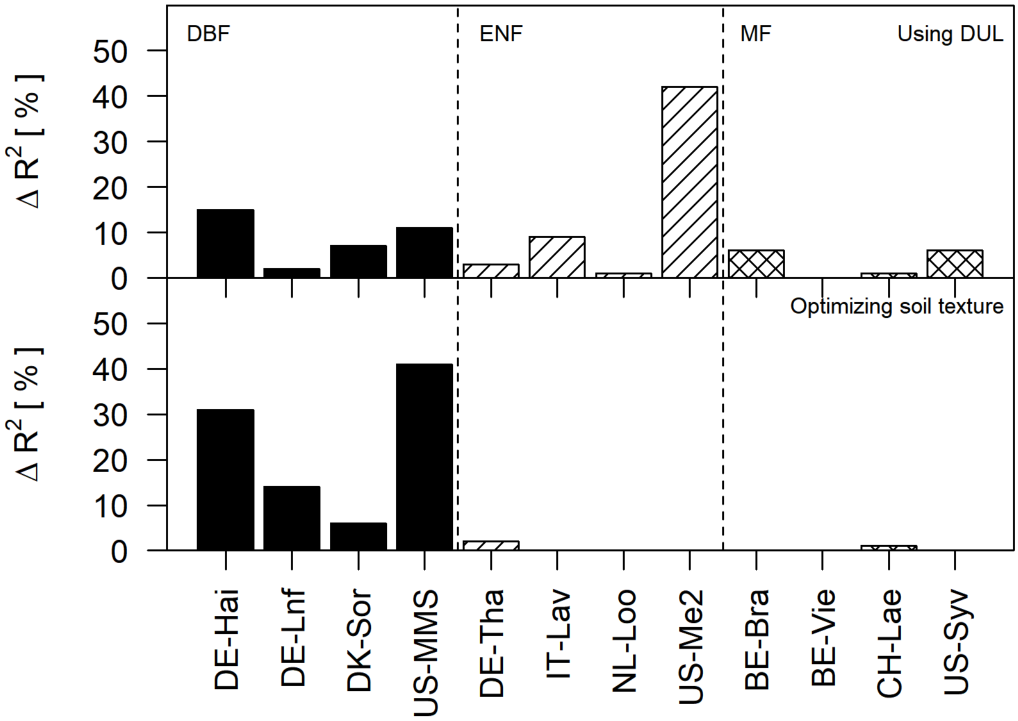


Figure 4.1: Improvement in performance by using FC from field measurements (top row) and by optimizing soil texture (bottom row).

4.4.2 Model parameterizations

Optimized values of parameters β, CSC, ER and g are presented in Table 4.5. β for DBF and ENF are lower than suggested by Jackson et al. (1996). However, the β values are similar to estimates by Bittner et al. (2010) based on fine roots measurement.

CSC values were within the range estimated by different studies. Bittner et al. (2010) estimated CSC between 0.06 to 0.21 mm LAI^{-1} during the foliated period and 0.08 to 0.13 mm LAI^{-1} during the non-foliated period for a beech forest. Link et al. (2004) reviewed values of CSC and found them to lie between 0.1 to 0.22 for needle-leaved forests. However, estimated CSC values are lower than estimated by Cáceres et al. (2015) for all forest types.

Our estimates for ER (0.1 for all forest types) were similar to Cáceres et al. (2015). They estimated ER equal to 0.2 in winter and 0.05 in summer. The parameters CSC and ER are highly correlated in all forest types (Table 4.9).

The desoptivity coefficients (g) values were within the range of other studies. Kustas (2016) reports the value of g between 2.11 to 8 for different soil types. Here, we did not parameterize the value of g for different seasons although a seasonal dependency has been reported (Jackson et al., 1976).

Table 4.5: Optimized values of root distribution parameter (β), canopy water storage capacity (CSC,mm LAI^{-1}), the ratio of the evaporation rate to rainfall rate during the rainfall event (ER), and desorptivity values (g, mm day$^{-1/2}$).

Parameter	Estimate	Std. Error	t value	Pr($>\|t\|$)
DBF				
β	0.93	0.11	8.85	0.00
CSC [mm LAI^{-1}]	0.11	0.01	8.19	0.00
ER	0.10	0.02	6.54	0.00
g [mm day$^{-1/2}$]	3.05	0.14	21.76	0.00
ENF				
β	0.94	0.13	7.06	0.00
CSC [mm LAI^{-1}]	0.25	0.02	11.19	0.00
ER	0.10	0.02	5.63	0.00
g [mm day$^{-1/2}$]	3.32	0.24	13.87	0.00
MF				
β	0.97	0.06	17.01	0.00
CSC [mm LAI^{-1}]	0.10	0.02	4.81	0.00
ER	0.10	0.02	4.54	0.00
g [mm day$^{-1/2}$]	2.79	0.59	4.70	0.00

4.4.3 Model evaluation

Table 4.6 shows the model performance against measured soil water for all sites. The timeseries of modelled and observed soil moisture data for all sites are presented in Appendix 4.6.1.

For DBF sites, the average R^2 was 0.69 with the highest R^2 in the managed beech forest site DE-Lnf and the lowest in DK-Sor after optimizing soil texture. The observed soil moisture time series for DK-Sor (Figure 4.5) shows numerous erratic periods (for e.g. 2007-2010 and 2016-2018). In the case of US-MMS, the new model performed better than for DK-Sor based on the top soil moisture data only (Figure 4.6).

Model performance was average for evergreen needle-leaved forests, with a mean R^2 of 0.45, with the lowest values for NL-Loo. The timeseries of observed data for NL-Loo (Figure 4.9), a sandy site, shows unrealistic constant values (ca. 0.06) from mid 2000 to mid 2002 (flat lines in top layer) and mid 2004 to 2007. Model performance in IT-Lav, though slightly better compared to NL-Loo, was poor. The observed and modelled data better matched for deeper depth than the top depth (Figure 4.8) and observed top soil data differed strongly between 2004-2008 and 2009-2015. In the case of DE-Tha, only data for top soil is available with high inter-annual variation (Figure 4.7).

In the case of mixed forests, model performance was good for two sites (BE-Bra and CH-Lae) and poor for US-Syv. Soil moisture for only the top 10 cm is reported for US-Syv and shows unrealistic constant values from 2009 to 2011. Additionally, the observed soil moisture is higher from 2012 to 2015. There were also errors in the soil moisture data in BE-Vie starting from 2007 (Figure 4.12).

We have found data issues in numerous sites making our evaluation results poor. On top of that if data is only available for top soil, the results are poor. Measurement by soil moisture sensors are more prone to errors in upper soil layer than bottom layers (Mittelbach et al., 2012). Similarly, the soil measurements become more uncertain with time.

Table 4.6: Performance of FSWM tested against measured soil moisture.

Site	FT	R^2	RMSE	Slope	Intercept	Count
DE-Hai	DBF	0.75	0.04	1.05	-0.03	5104
DE-Lnf	DBF	0.84	0.03	0.92	0.03	5344
DK-Sor	DBF	0.54	0.04	0.82	0.04	2557
US-MMS	DBF	0.64	0.06	0.96	0.03	5844
DE-Tha	ENF	0.43	0.08	0.69	0.12	7978
IT-Lav	ENF	0.37	0.03	0.53	0.20	3944
NL-Loo	ENF	0.29	0.05	3.26	-0.13	2557
US-Me2	ENF	0.72	0.07	1.14	0.00	4748
BE-Bra	MF	0.82	0.04	0.83	0.06	1461
BE-Vie	MF	0.52	0.02	1.16	-0.04	2723
CH-Lae	MF	0.60	0.04	1.13	0.00	2192
US-Syv	MF	0.33	0.06	1.46	-0.05	2616

The model performed better when evaluated against measured evapotranspiration data than soil moisture data (Table 4.7). We observed R^2 values between 0.52 to 0.87 with the highest values in DBF sites followed by MF and ENF. The slope between modelled and observed evapotranspiration for two DBF sites (DE-Hai and DE-Lnf) was close to one but lower for the other two sites (DK-Sor and US-MMS). The slope was around one for most ENF sites. For MF, the slope was lower with an average of 0.80.

Underestimation of evapotranspiration, reflected in a slope that is lower than one, can be due to an underestimation of PET, low values of LAI or REW, as in our model transpiration is a function of PET, LAI and REW. Here, we have used the FAO-56 Penman-Monteith equation to evaluate potential evapotranspiration. An earlier version of BILJOU used the Penman equation (Granier et al., 1999), and Cáceres et al. (2015) used a formulation given by Prentice et al. (1992). The choice of the equation makes large differences in potential evapotranspiration (XU et al., 2002). We used the Priestly-Taylor formulation (Priestley et al., 1972) to see if the evapotranspiration data for four sites with low predicted values improved (Figure 4.15). The slope improved by about 10 % (0.76 to 0.90 in DK-Sor, 0.74 to 0.88 in US-MMS, 0.83 to 0.94 in BE-Bra and 0.79 to 0.85 in BE-Vie) with small changes in RMSE.

In Figure 4.2, we compared the FWSM model results for DE-Hai with results from the online BILJOU Model (UMR EEF, 1999). BILJOU model was run using the same parameter values for soil as used in FWSM. It was only possible to check the results of

Table 4.7: Evaluating the model against measured evapotranspiration data.

Site	FT	R^2	RMSE	Slope	Intercept	Count
DE-Hai	DBF	0.87	0.48	0.95	0.05	4193
DE-Lnf	DBF	0.88	0.45	0.94	0.06	2777
DK-Sor	DBF	0.82	0.67	0.76	0.16	5032
US-MMS	DBF	0.87	0.81	0.74	0.31	5633
DE-Tha	ENF	0.76	0.56	0.87	0.19	8033
IT-Lav	ENF	0.61	0.76	1.09	-0.45	3905
NL-Loo	ENF	0.52	1.00	0.91	-0.24	6392
US-Me2	ENF	0.67	0.70	1.02	-0.13	4246
BE-Bra	MF	0.76	0.55	0.83	0.22	5995
BE-Vie	MF	0.83	0.56	0.79	0.18	6027
CH-Lae	MF	0.72	1.06	0.77	-0.13	5479
US-Syv	MF	0.80	0.61	0.79	0.16	1843

the BILJOU Model against evapotranspiration as this model does not return results for individual soil layers. The performance of both models was very similar. Our model, however, had a slightly higher R^2 and lower RMSE. Major differences in two models were the interception (Gash model instead of Rutter model), soil evaporation (Ritchie model instead of simple dependence on topsoil REW) and root water movement (used Richards equation instead of simply distributing the infiltration to different soil layers).

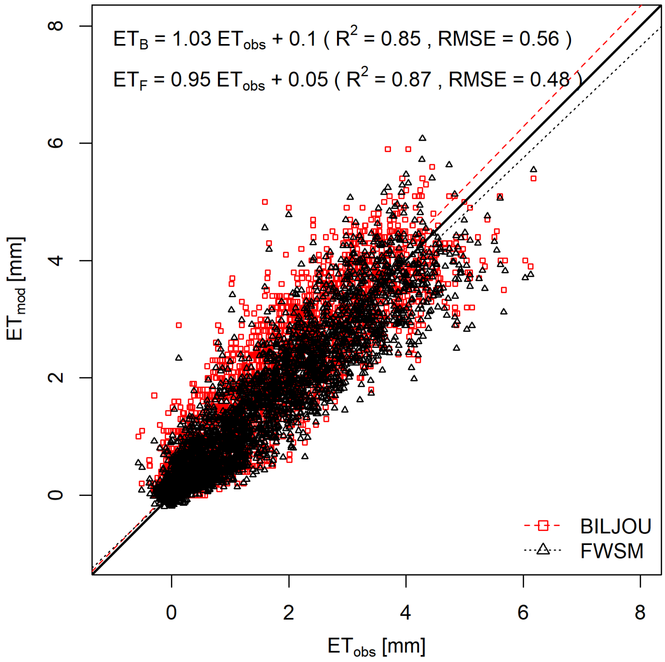


Figure 4.2: Evaluating the results of FWSM against BILJOU Model. ET_B (black triangles) and ET_F (red squares) represent values of evapotranspiration values from FWSM and BILJOU model respectively.

4.4.4 Average annual values of different ET components

Here, we report the average annual ET components namely transpiration, interception, and soil evapotranspiration (Table 4.8). Transpiration was about 40 %, 45 % and 36 % of the total gross rainfall in DBF, ENF and MF, respectively. Interception was about 9 %, 15 % and 11 % of the gross rainfall in DBF, ENF and MF, respectively. Soil evaporation was very similar to interception with 10 %, 8 % and 9 % of total gross rainfall in DBF, ENF and MF. The interception for DE-Hai in our case is much lower than that reported by Bittner et al. (2010) for the same site, where they reported interception values of 21 to 41 % for different plots during 2005-2007. However, they did not include the canopy interception as part of evapotranspiration while comparing it with eddy flux tower data from the same site. Since interception is evaporated back to the atmosphere, their total sum of evapotranspiration is much larger than the evapotranspiration measurement. Our results for DE-Hai was closer to the results from the online BILJOU model (Table 4.10).

Table 4.8: Annual rainfall (mean ± sd) and different evapotranspiration components (mean ± sd) namely transpiration (TR), interception (In), soil evaporation (Esoil) for all study sites.

Site (–)	FT (–)	Rain ± sd (mm)	TR ± sd (mm)	In ± sd (mm)	Esoil ± sd (mm)
DE-Hai	DBF	689 ± 170	292 ± 23	62 ± 13	71 ± 9
DE-Lnf	DBF	614 ± 157	296 ± 15	69 ± 12	62 ± 3
DK-Sor	DBF	837 ± 299	260 ± 24	63 ± 12	74 ± 9
US-MMS	DBF	1083 ± 194	427 ± 31	69 ± 8	119 ± 11
DE-Tha	ENF	820 ± 137	284 ± 32	130 ± 16	67 ± 5
IT-Lav	ENF	1283 ± 300	238 ± 13	130 ± 26	122 ± 3
NL-Loo	ENF	829 ± 214	329 ± 49	147 ± 29	26 ± 2
US-Me2	ENF	486 ± 158	416 ± 23	84 ± 18	47 ± 4
BE-Bra	MF	819 ± 134	249 ± 30	88 ± 12	74 ± 9
BE-Vie	MF	952 ± 201	263 ± 22	89 ± 11	64 ± 4
CH-Lae	MF	832 ± 120	388 ± 22	93 ± 10	60 ± 3
US-Syv	MF	665 ± 174	265 ± 26	78 ± 14	88 ± 11

4.5 Conclusions

Soil water availability is one of the most important determinants of vegetation characteristics. To estimate soil water dynamics in forest soils, the forest soil water model or FSWM, suitable for a wide range of forest soils, was developed in R. This new open-source model improves over similar models (such as the BILJOU model) by incorporating the Gash model for interception, the Ritchie model for soil evaporation and the Richards equation for soil water movement. Model users can directly input texture data to the model instead of providing available soil water in each layer. We have included pedotransfer functions given by Saxton et al. (2006). Model performance was variable, being better in deciduous broad-leaved forests and worse in needle-leaved forests. It is likely that some of this poor fit is the result of poorly constrained soil moisture data at some of the Fluxnet sites. However, we are also not confident about the soil data available in the fluxnet site as there are straight lines or very low soil water content.

4.6 Supplementary materials

4.6.1 Model evaluation other sites

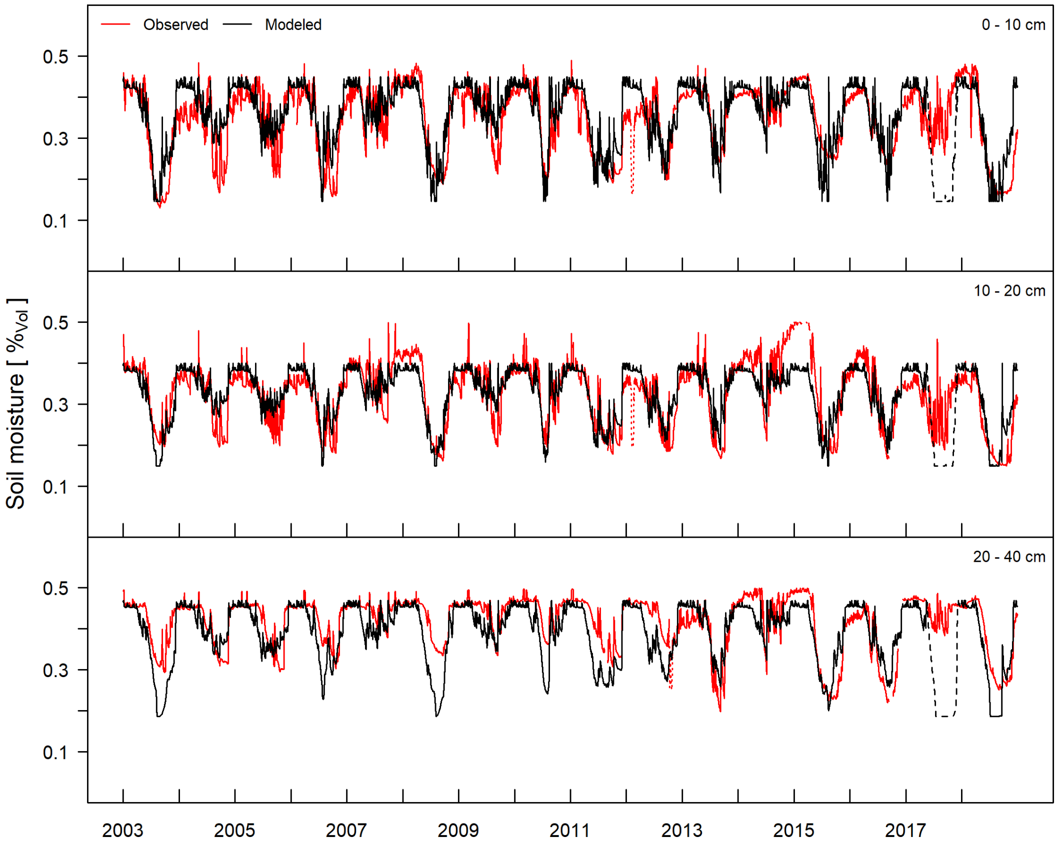


Figure 4.3: The observed and modelled soil moisture data for three layers at DE-Hai site. In 2017, the precipitation data was unrealistic with numerous zero values this led to very low soil moisture prediction.

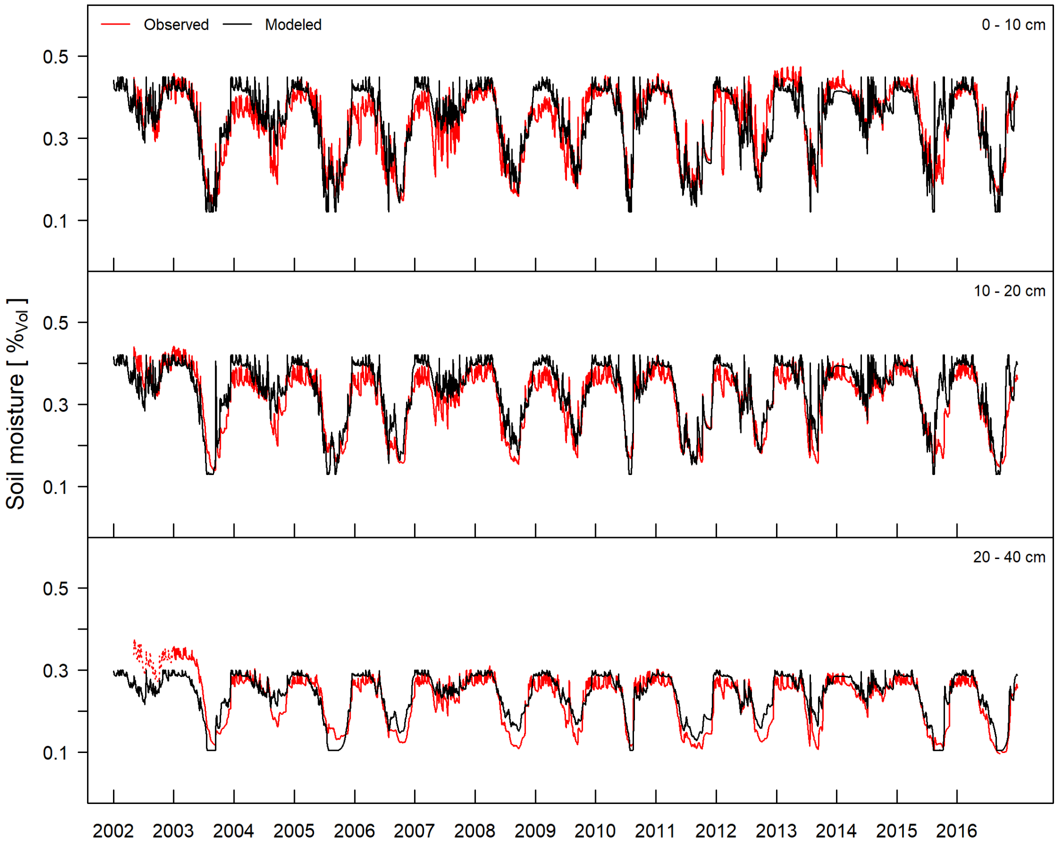


Figure 4.4: The observed and modelled soil moisture data for three layers at DE-Lnf site. The observation and modelled values fit quite well for this site.

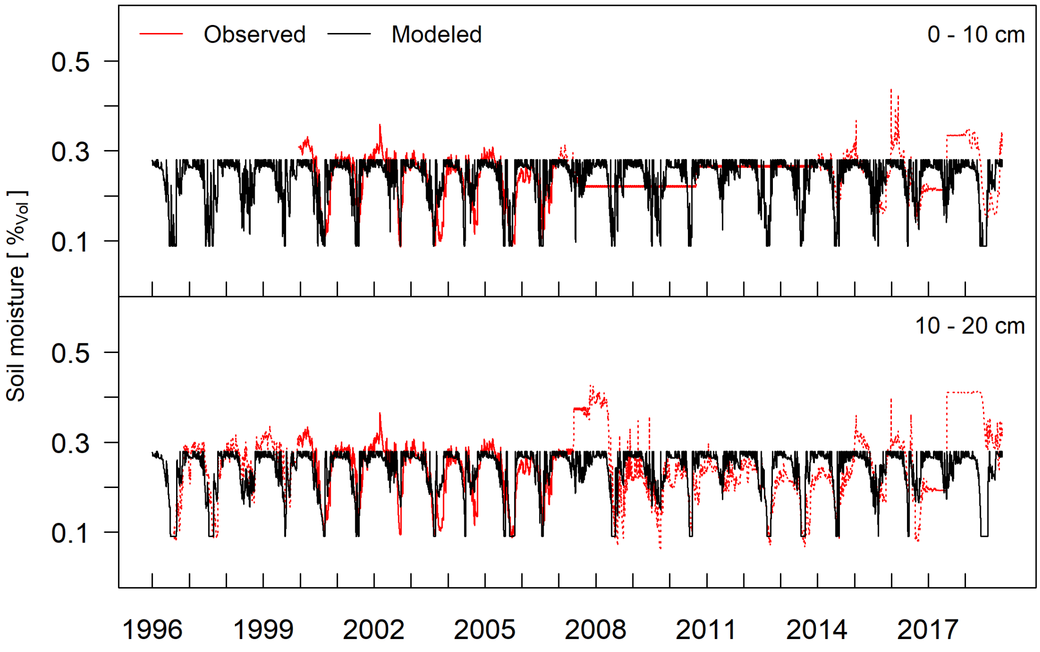


Figure 4.5: The observed and modelled soil moisture data for two layers at DK-Sor site. We observed some unrealistic values for this site in both layers (for example the flat line from mid 2007 to end of 2010 in 0-10 cm layer).

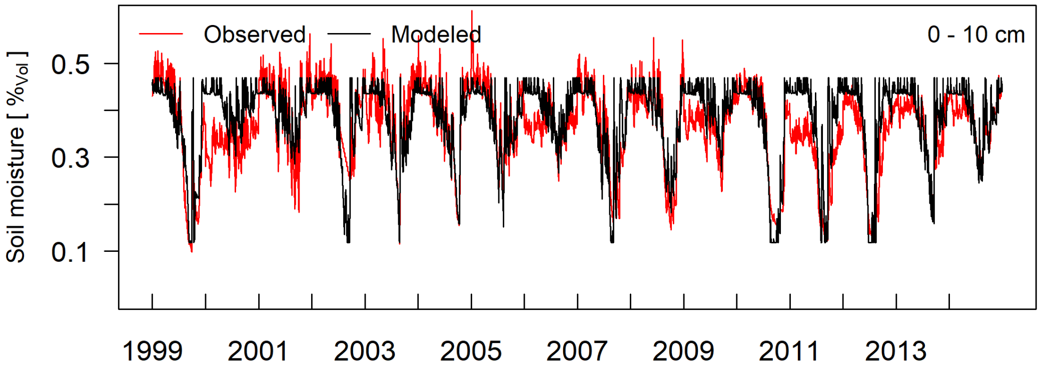


Figure 4.6: The observed and modelled soil moisture data for top layer at US-MMS site. The site reported the data only for top layer.

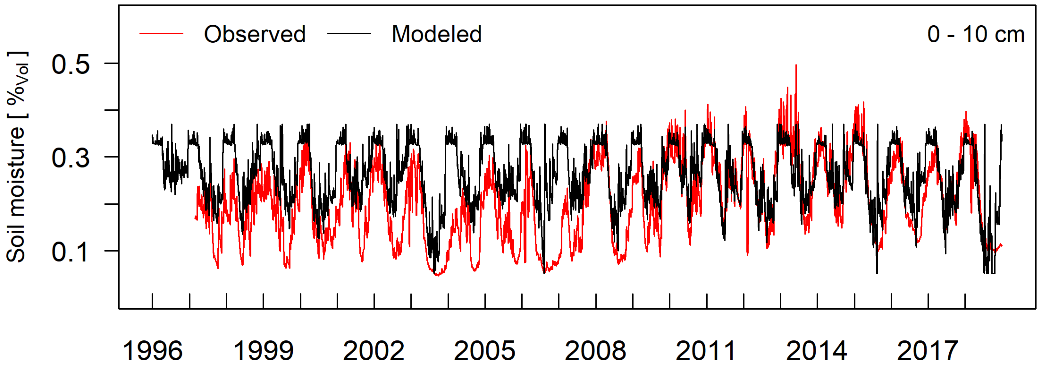


Figure 4.7: The observed and modelled soil moisture data for top layer at DE-Tha site. The site reported the data only for top layer.

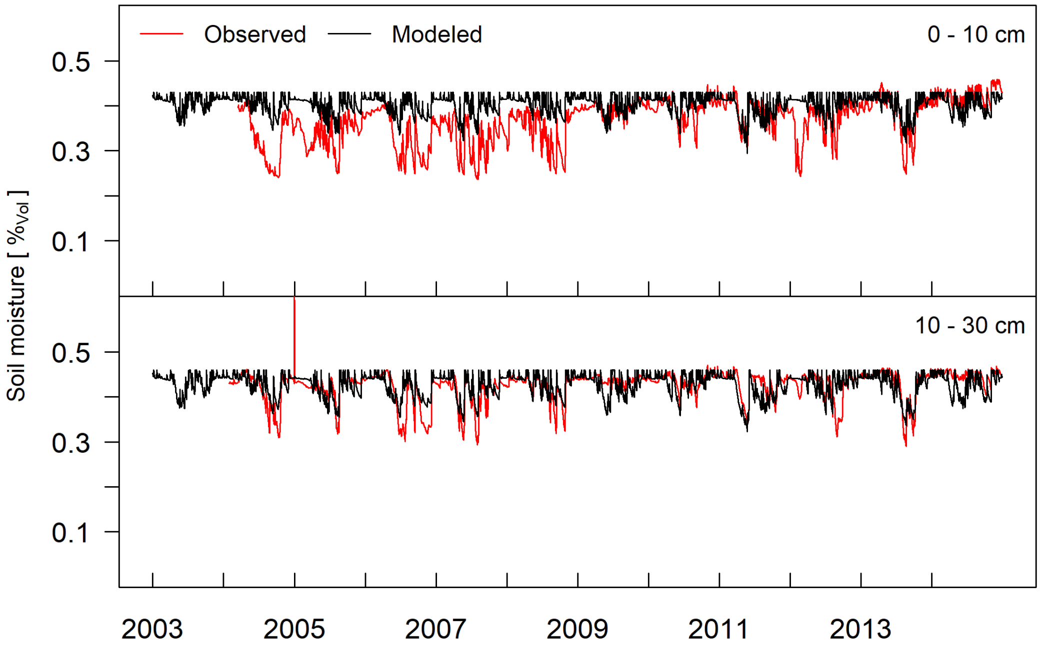


Figure 4.8: The observed and modelled soil moisture data for two layers at IT-Lav site.

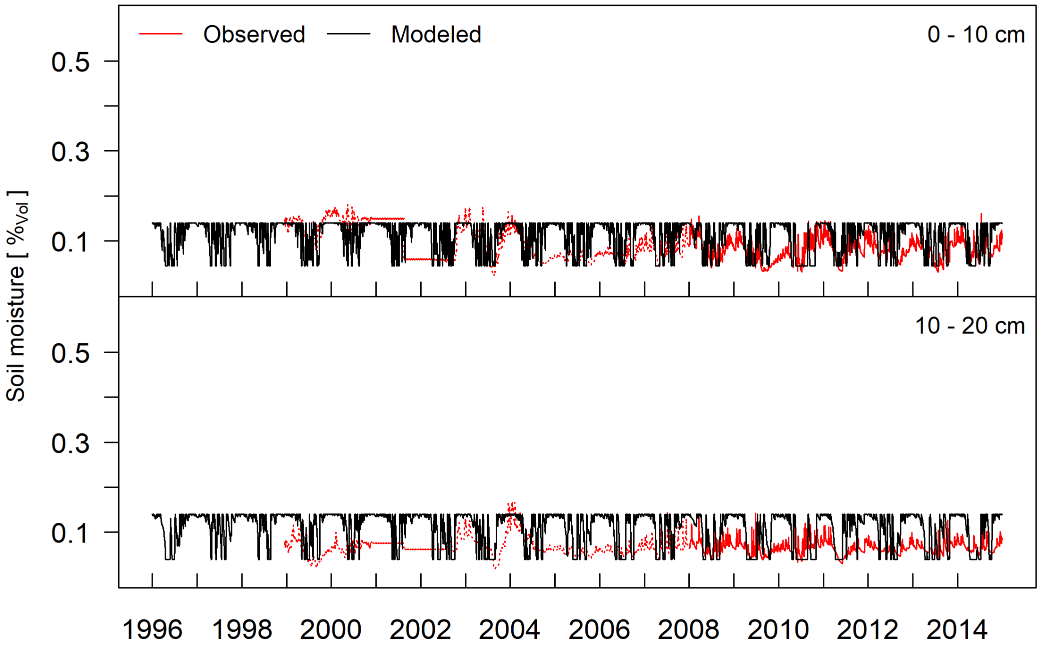


Figure 4.9: The observed and modelled soil moisture data for two layers at NL-Loo site. The values are unrealistic for some periods for this site (for example the values from mid 2000 to end of 2002.

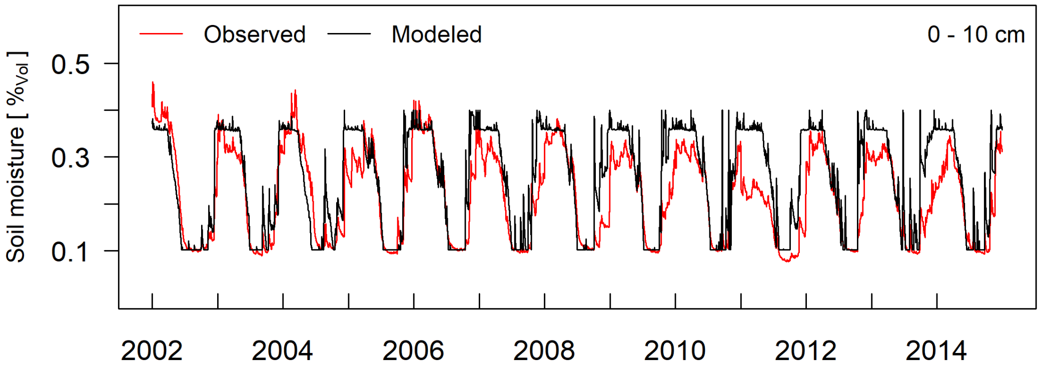


Figure 4.10: The observed and modelled soil moisture data US-Me2 site.

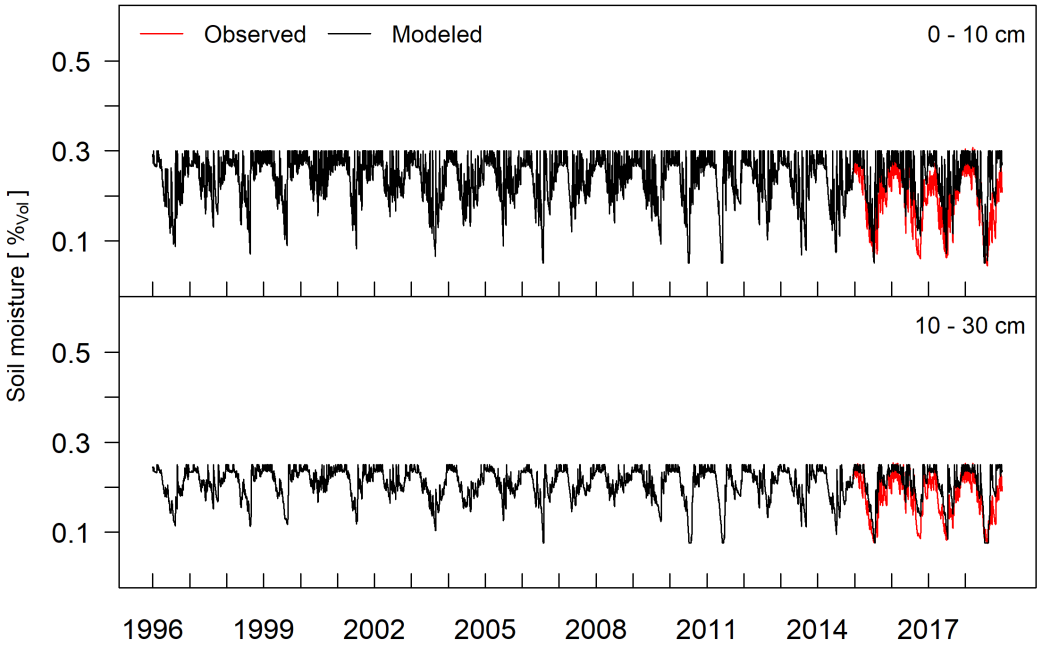


Figure 4.11: The observed and modelled soil moisture data for two layers at BE-Bra site. The measurement data were available only from 2015.

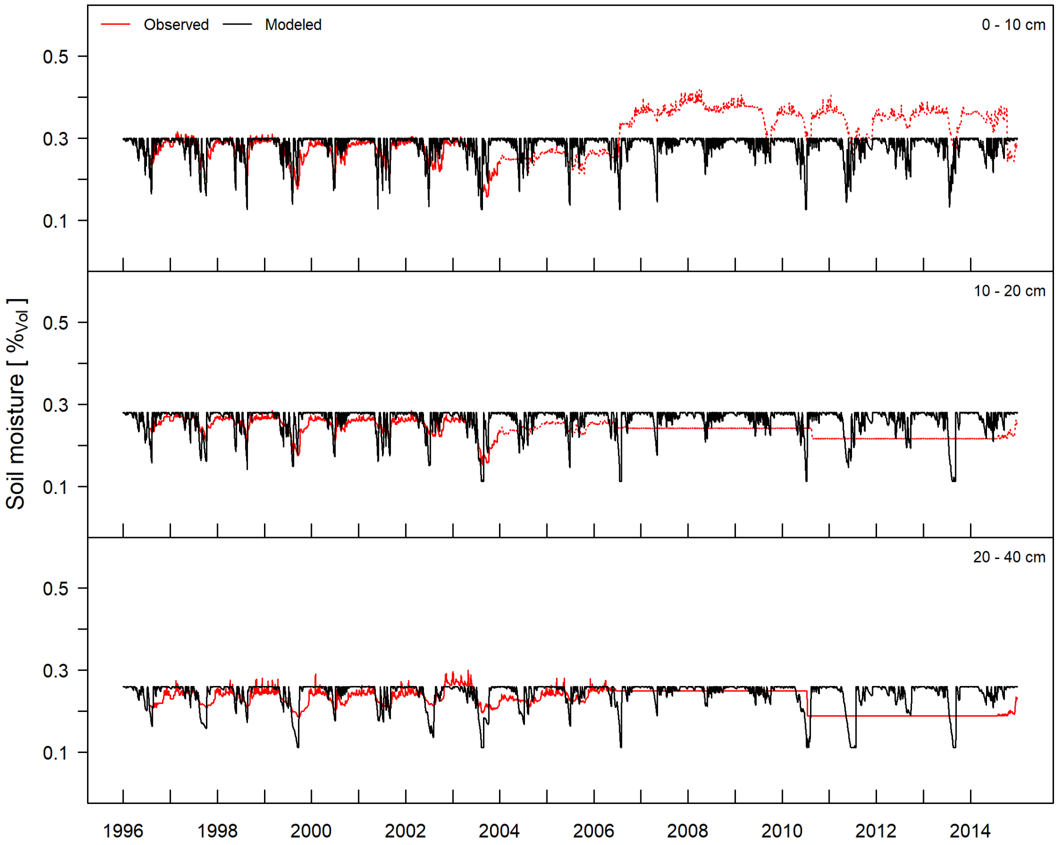


Figure 4.12: The observed and modelled soil moisture data for three layers at BE-Vie site. The reported data were unrealistic for this site from 2006 to 2014.

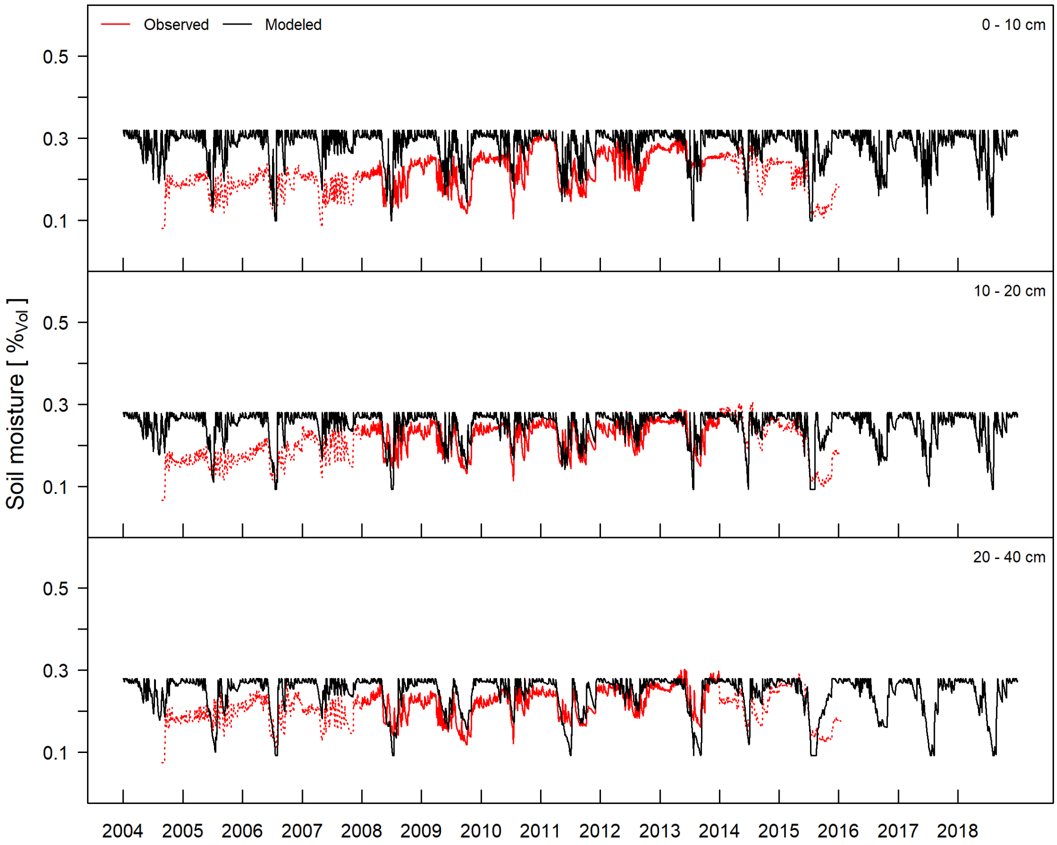


Figure 4.13: The observed and modelled soil moisture data for three layers at CH-Lae site.

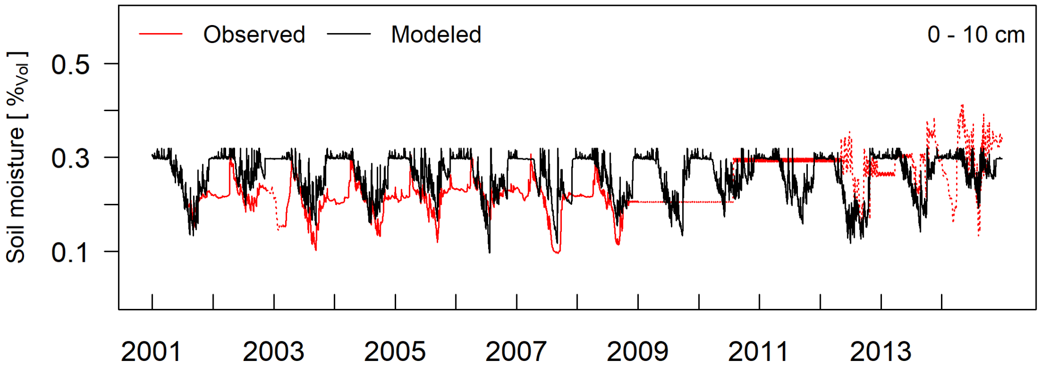


Figure 4.14: The observed and modelled soil moisture data for a layer at US-Syv site.

4.6.2 Model Parameter correlation

Table 4.9: Model parameter correlation

DBF				
	RDb	CSC	ER	gamma
RDb	1.00	0.06	-0.02	-0.25
CSC	0.06	1.00	-0.73	-0.01
ER	-0.02	-0.73	1.00	-0.00
gamma	-0.25	-0.01	-0.00	1.00
MF				
RDb	1.00	0.07	-0.10	-0.72
CSC	0.07	1.00	-0.65	-0.02
ER	-0.10	-0.65	1.00	0.05
gamma	-0.72	-0.02	0.05	1.00
ENF				
RDb	1.00	-0.01	-0.04	-0.69
CSC	-0.01	1.00	-0.66	-0.07
ER	-0.04	-0.66	1.00	-0.01
gamma	-0.69	-0.07	-0.10	1.00

4.6.3 Using Priestley Taylor formulation of evapotranspiration

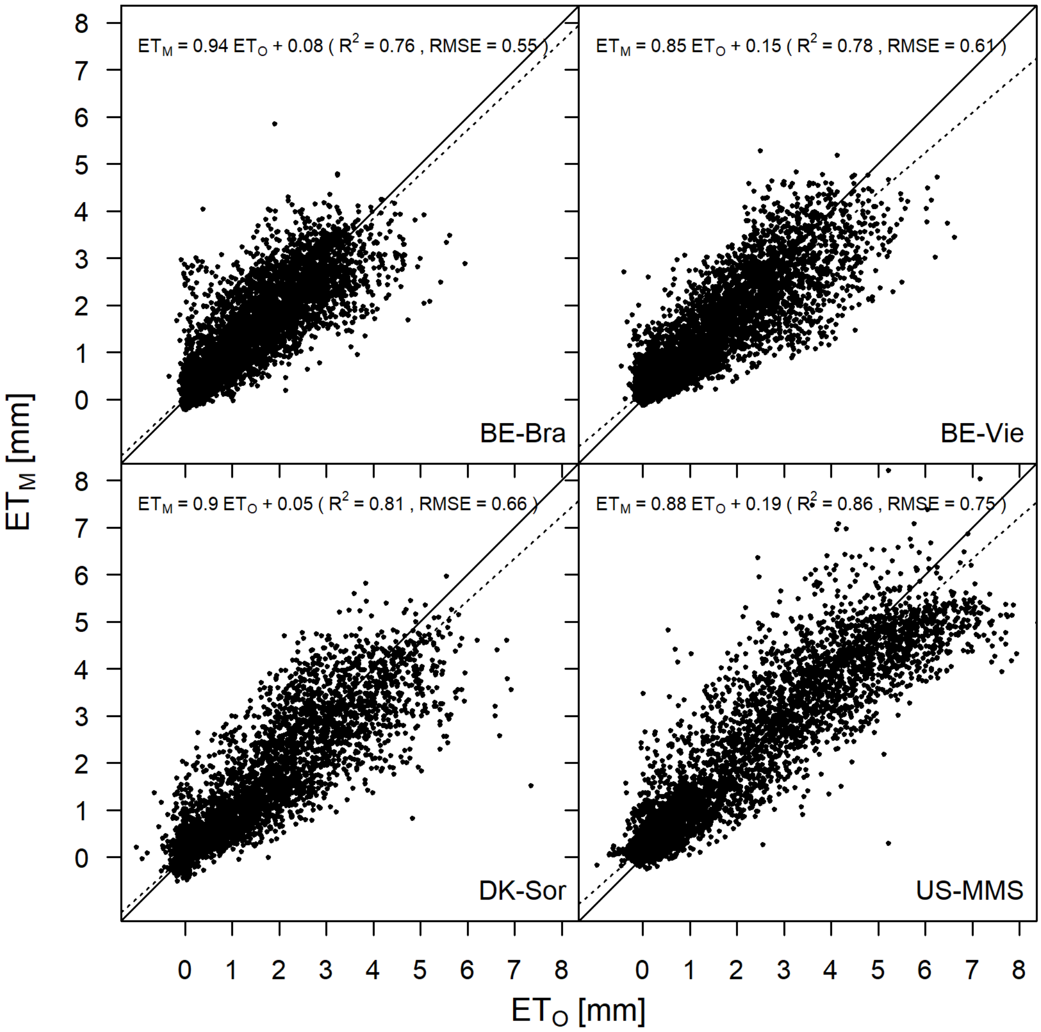


Figure 4.15: Modelled evapotranspiration (ET_M) versus observed evapotranspiration (ET_O) for randomly selected four sites using Priestley Taylor formulation of evapotranspiration. The solid line represent 1:1 line and the dotted line represent the linear regresssion line between ET_M and ET_O.

4.6.4 Evapotranspiration component for DE-Hai from BILJOU model

Table 4.10: Average evapotranspiration components namely transpiration (TR), interception (IN) and soil evaporation (Esoil) from BILJOU for 2003 - 2018.

Site (–)	Year (–)	TR (mm)	IN (mm)	Esoil (mm)
DE-Hai	2003	370	78	35
DE-Hai	2004	313	111	36
DE-Hai	2005	330	104	42
DE-Hai	2006	355	102	34
DE-Hai	2007	310	119	45
DE-Hai	2008	330	95	33
DE-Hai	2009	298	120	43
DE-Hai	2010	352	102	37
DE-Hai	2011	374	101	42
DE-Hai	2012	374	112	35
DE-Hai	2013	346	106	36
DE-Hai	2014	300	122	39
DE-Hai	2015	355	94	39
DE-Hai	2016	370	84	38
DE-Hai	2017	291	55	32
DE-Hai	2018	343	59	37

4.6.5 Variation of texture in DE-Hai

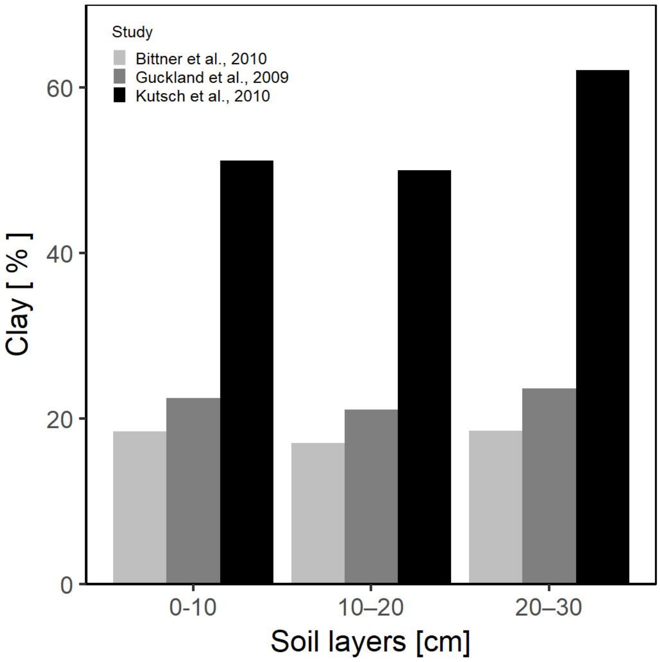


Figure 4.16: Soil clay data for DE-Hai from three different studies (Bittner et al., 2010; Guckland et al., 2009; Kutsch et al., 2010). The results from Kutsch et al. (2010) is different from other two studies.

CHAPTER 5

Synopsis

Climate change poses a threat to many forest ecosystems (Seidl et al., 2017; Stevens-Rumann et al., 2018). Warmer and drier conditions may increase fire, drought and insect disturbances, while warmer and wetter conditions may intensify disturbances from wind and pathogens (Seidl et al., 2017). It has been suggested (Felton et al., 2016; Hardiman et al., 2011; Puettmann et al., 2015; Pukkala, 2016; Yousefpour et al., 2016) that creating heterogeneous forest stand structures through different management approaches can enhance forest stability, adaptability and resilience. Forest structure can be diversified either by mixing different tree species and/or increasing horizontal and vertical heterogeneity. It is important to understand how such changes in forest structure might impact forest ecosystem functions during both normal and stressful conditions. Many studies have focused on the effect of tree species diversity on forest stand productivity (Jactel et al., 2018; Liang et al., 2016; Pretzsch et al., 2015; Zhang et al., 2012, etc), ecosystem services (tree biomass production, soil carbon storage, berry production and game production potential – Gamfeldt et al., 2013; Ruiz-Benito et al., 2014), and forest resistance to natural disturbances (Grossiord et al., 2014c; Jactel et al., 2017; Jactel et al., 2007; Lebourgeois et al., 2013; Merlin et al., 2015; Silva Pedro et al., 2015, etc). Few studies, however, have examined the effect of other forest structural characteristics such as stem size heterogeneity, crown structure, age-related diversity, tree height diversity, etc. Some of the studies that have looked at the effect of forest structural characteristics (other than tree species diversity) on different ecosystem functions (e.g. timber volume, timber volume growth, basal area increment, above-ground carbon storage, etc) are listed in Table 1.1. Apart from a study by Musavi et al. (2017), none of the studies used widely available eddy covariance tower data from Fluxnet (`https://fluxnet.fluxdata.org/data/fluxnet2015-dataset/`). Of all of these studies, only two have looked at the implication of structural attribute on ecosystem functions during drought (Bello et al., 2019b; Merlin et al., 2015).

We took the opportunity to capitalise on the data available from fluxnet and amalgamate these with forest inventory data. With this rich dataset, we aimed to understand how forest structure influences annual and seasonal carbon dioxide fluxes, temporal variability of carbon dioxide fluxes and resistance of carbon dioxide fluxes during drought. This thesis attempts to fulfill these objectives through three major scientific studies and two co-authored papers. The first study (Tamrakar et al., 2018) investigates the abiotic and biotic factors controlling annual and seasonal carbon dioxide fluxes of two forests in Germany that are structurally different due to differing management regimes. This chapter builds on the first co-author chapter (Herbst et al., 2015) where we compared the annual carbon dioxide and water fluxes between these forests and discussed the limitations of the methods. The second study (chapter 3) examined the effect of structure on the temporal variability of ecosystem-level photosynthetic capacity and its resistance to drought across 21 Fluxnet sites. This chapter expanded the analysis of the second co-author paper (Musavi et al., 2017) – which focused on the temporal variability of ecosystem-level photosynthetic capacity but used only species number, tree height, and age – by including basal area, management, DBH, DBH variation (Shannon size index and Simpson size index) and evenness. The third study (chapter 4) was developed in response to the need to derive a consistent soil moisture dataset in order to examine the effect of drought on forest CO_2

fluxes at shorter timescales (i.e. at a daily scale in our case). We have presented a robust and flexible new soil water model, which we believe has a high potential to be used in further research.

In the following sections, we will discuss the major outcome of the objectives listed in section 1.5 with its limitations and wider implications.

5.1 Higher average long-term net ecosystem productivity (NEP) in a structurally homogeneous forest.

Our results suggest that managed forests with homogenous structure with single species (*Fagus sylvatica*) have a significantly higher mean annual NEP than the unmanaged heterogenous forests (Tamrakar et al., 2018). This is in contrast to the assumption that forest with complex stand structure and/or higher tree species diversity are more productive (Dănescu et al., 2016; Hardiman et al., 2011; Jactel et al., 2018; Liang et al., 2016; Pretzsch et al., 2015; Zhang et al., 2012) and in particular, that mixing complementary tree species improves productivity (Pretzsch et al., 2015; Pretzsch et al., 2010). The effect of tree species biodiversity on productivity, however, varies spatially (Jucker et al., 2014; Liang et al., 2016; Ratcliffe et al., 2016) and depends on environmental conditions (Jucker et al., 2016; Ratcliffe et al., 2017). The forests in our case are located very close to each other with similar environmental conditions (Figure 2.2). The difference in NEP was not significant with a shorter dataset of 7 years (Herbst et al., 2015) but differed when we included 4 more years of data. The heterogeneous forest, an old-growth forest, is unmanaged (Mund et al., 2010) whereas thinning activities have been carried out in the homogeneous forest (Tamrakar et al., 2018). Thinning is a silvicultural operation managing inter-tree competition to the benefit of retained trees (Boncina et al., 2007). Thinning periods were followed by periods with a steady increase in carbon uptake, presumably due to a greater availability of resources per tree. For example, soil water availability improved in the thinned plot compared to unthinned plot enhancing the tree growth in the thinned plot (Breda et al., 1995). Thinning, however, did not impact the carbon uptake of a Sitka spruce forest (Saunders et al., 2012) and a boreal forest (Vesala et al., 2005). Both the studies looked at the impact immediately after the year of thinning. Canopy photosynthesis was reduced due to a decrease in leaf area index (LAI) but at the same time ground-vegetation photosynthesis may have increased as a result increasing light penetration to overcast situation. Soil respiration did not differ between pre and post-thinning (Vesala et al., 2005). In our study, we investigated three years after the major thinning and the final year of the study was nine years after thinning. The areas previously thinned may have been colonised by new plants improving the carbon uptake.

Differences in carbon uptake between the forests were strongly driven by higher winter respiration rates and lower spring and summer carbon uptake rates in the heterogeneous forest. The heterogeneous forest, an old-growth forest, is characterized by large amounts of standing dead trees and woody debris in the forest floor (Kutsch et al., 2010) which may have led to the higher winter heterotrophic respiration. However, an important thing to note is that carbon uptake capacity of this heterogeneous old-growth forest was similar to other temperate deciduous forests (Shao et al., 2014; Wilkinson et al., 2012; Wilson et al., 2001), and it still continued to sequester carbon in line with the finding that ageing forests continue to accumulate carbon (Luyssaert et al., 2008). In addition to carbon uptake, this forest also provided the biodiversity conservation benefit associated with high plant diversity (Mölder et al., 2006), addressing two major of the pressing issues of our generation: biodiversity conservation and climate change (MEA, 2005). The managed forest provided greater climate-mitigation benefits but a heterogeneous forest with trees of different ages, standing and fallen dead wood and multiple species provides the additional benefit of biodiversity conservation. Achieving both the targets of biodiversity conservation and climate change mitigation harmoniously in a single forest is challenging (Ferreira et al., 2018; Sabatini et al., 2019). Particularly in a temperate forest, attempting to pursue both biodiversity conservation and climate change mitigation goals simultaneously requires comprimise (Sabatini et al., 2019).

Management rather than tree species diversity positively affected forest productivity (Tamrakar et al., 2018). However, this result was based on two sites only, thus it might be context specific and might not be generally applicable. We suggest using more eddy covariance sites to confirm the hypothesis that the effect of management on carbon uptake is stronger than tree species diversity. Combining the results from eddy covariance measurement with biometric data will generate a more precise quantification of this result, therefore we recommend forest sites in the Fluxnet network conduct regular inventories and record details of the management (e.g. thinning) for future research activities.

5.2 Lower interannual variability of net ecosystem productivity (NEP) in a heterogeneous forest.

In addition to comparing average values of ecosystem functions of forest (section 5.1), stability of the ecosystem function over the period of time (Ives et al., 2007) is important. We have used the interannual variability, specifically the ratio of standard deviation and mean of ecosystem function (i.e. the coefficient of variation of NEP), as a measure of ecosystem stability (Tilman, 1999). Our study suggests that the NEP of heterogeneous forests is more stable than that of homogeneous forests (Tamrakar et al., 2018). An ecosystem is considered to be stable when it is able to preserve its functioning and structure over time (Holling, 1973), i.e. low interannual variability of ecosystem functions or, in our case, a low coefficient of variation. Mechanistically, three processes – overyielding, species asynchrony, and niche complementarity have been suggested to stabilise forest ecosystem functions in mixed forests (Jucker et al., 2014; Río et al., 2017). Overyielding (i.e. higher productivity but similar standard deviation among the compared sites, Río et al., 2017; Tilman, 1999) was not the cause of the higher stability in the heterogeneous forest because the heterogeneous forest had lower productivity compared to the homogeneous forest (section 5.1). We did not observe asynchrony in species responses to environmental fluctuation in our sites but to masting. The higher standard deviation of NEP of homogeneous forest, caused by the time-related growth and the masting, increased the coefficient of variation. As a result of the similar size and age of the trees in the homogenous forest, all the trees had the same and simultaneous reaction during masting whereas in the case of the heterogeneous forest, not all trees (not even all beech trees because of their young age) showed masting (Herbst et al., 2015). That is the structural synchrony or lack of structural heterogeneity in the homogeneous forest led all the trees of the forests to react similarly when masting.

5.3 Lower interannual variability of ecosystem-level photosynthetic capacity in unmanaged forests.

When comparing sites from different climates, it is best to use normalized functional parameters (such as light-saturated ecosystem-level photosynthetic capacity) – which take into account variations in local environment. The interannual variation of such normalized functional parameters is thus caused by management activities, site or climatic-response characteristics. Here, we have identified the factors affecting the interannual variation of light-saturated ecosystem-level photosynthetic capacity ($CV_{GPP1000}$) in Musavi et al. 2017 and chapter 3) using data from multiple Fluxnet sites. Forest stand age explained most of the inter-site variation of $CV_{GPP1000}$ (Musavi et al., 2017). Forest stand age itself does not offer a mechanistic explanation for the difference in $CV_{GPP1000}$. In chapter 3 we went further and calculated structural parameters using the forest inventory data. The forests with higher structural diversity (higher Simpson and Shannon size diversity index) had lower interannual variability. The forests with higher Simpson and Shannon size diversity index were also older. Structural heterogeneity typically results from management activities (Pommerening et al., 2013; Schall et al., 2018). Unmanaged forests had a lower interannual variability of $CV_{GPP1000}$ but were not significantly different from the managed high forest. The managed high forests are mostly managed to resemble old-growth forests (Messier et al., 2013; Puettmann et al., 2015) and none of the managed high forests in our case had been clear cut recently. Thus, managed forests that resemble natural forests are able to dampen their physiological response to environmental conditions. In our case, one of the limitations comparing the interannual variability of an ecosystem function from different sites is the difference in dataset duration, time frame and coverage of drought events. Three sites did not experience drought at all during the data measurement period and one site experienced three drought years. Comparing the interannual variability of site with and without drought years (there was no drought during measurement period and not that site have not experienced drought) biases our reults. Thus, this analysis should be repeated again when longer time series data become available, ideally when all sites have experienced at least one drought event.

5.4 The impact of drought on the ecosystem-level light-saturated photosynthetic capacity of forests.

The interannual variation of ecosystem-level light saturated photosynthetic capacity GPP_{1000} of forests informs us about the response of forests to the interannual variation of environmental drivers and plant physiology. It does not tell us directly about the response of forests to drought events. In the face of changing climate with increasing probability of droughts (Spinoni et al., 2019), it is critical to understand the effects of droughts alongside the effects of interannual variation in other of environmental parameters.

Ciais et al. (2005) reported a 30 % reduction in GPP in Europe during the 2003 European heatwave and drought, but other studies estimated a lower reduction (Vetter et al., 2008; Von Buttlar et al., 2018). We observed a maximum of 27 % reduction of GPP_{1000} in Mediterranean forests and much less in other forests (Chapter 3). The two

Mediterranean forests in our study are coppice forests. The repeated vegetative propagation in coppice forests may cause genetic stagnation reducing the adaptive capacity to the climate change(Marko Stojanović, 2017). Another interesting point to note is that GPP_{1000} of managed high forests were not affected by droughts (Chapter 3 - Figure 3.10). In our two-site study, we found that NEP and GPP of managed forest (composed of *Fagus*) was less affected by 2003 drought than the unmanaged forest (mostly composed of *Fraxinus* and *Fagus*, Herbst et al., 2015). The leaf-out and leaf fall in *Fraxinus* occurs later than in *Fagus*. The drought in 2003 occurred in later summer affecting the GPP of *Fraxinus* which alone still had leaves. The managed forest is thinned regularly, the thining can reduce the transpiration and increase the water availability during droughts (Sohn et al., 2013; Sohn et al., 2016). One of the strategies to improve the resistance of forest to drought could be to plant the appropriate mix of trees (for example mixing beech, spruce and oak in Central Europe, Pretzsch et al. 2013 and manage (thin) them.

Three of the sites did not experience any drought events during the period analyzed and 14 sites experienced only one drought. European sites experienced strong droughts in 2018 (Buras et al., 2019) and 2019, years that were not part of this analysis. Adding data for these years may improve our understanding of the impact of droughts on forests.

In some cases, the effect of drought was not captured at the annual scale because of compensation by higher productivity in non-drought periods within a year. For example in DE-Lnf during the 2003 drought, higher net ecosystem productivity was observed in the warm spring and summer, compensating the reduction of net ecosystem productivity in the late growing season period (Herbst et al., 2015). We lose important information by only conducting analysis using annual ecosystem productivity or annual tree ring data. The Fluxnet data allows us to conduct analysis down to half-hourly timescales. A full understanding of the effects of droughts on ecosystem productivity requires analysis at with at multiple timescales.

We limited ourselves to look at direct effects of the droughts on GPP_{1000}, i.e. the response of GPP_{1000} during drought years. Any lagged effects of the droughts (Bréda et al., 2006; Thabeet et al., 2009; Vennetier et al., 2007) were not captured in our study. A further analysis would include looking at tree mortality or insect infestation in the years following drought in order to identify any carryover effect of previous droughts.

5.5 Development of an open-source soil water model.

The development of an open-source, flexible, forest soil water model-FSWM in R offers a new freely available tool to estimate soil water dynamics in forest soils. Open-source models help in improving the chances of collaboration among scientists, increasing productivity through collaborative burden-sharing, and making them available for public scrunity (Pfenninger et al., 2017).

The model can be applied to a range of forest soils and offers flexibility to simulate different numbers of soil layers, and is thus adaptable to the available soil data. The model performance varied across forest types, being best in deciduous broad-leaved forests and less good in needle-leaved forests. We noted sometimes significant deviations between modelled and measured data, and we suggest that this is not always because the model predictins are poor, but that sometimes the practical difficulties of measureing soil moisture are significant. We suggest regular and spatially comprehensive monitoring of soil moisture.

5.6 Outlook

This thesis has resulted in a useful database of structural stand parameters not currently included in the Fluxnet database, and a practical approach to quantify the effect of forest structure on ecosystem function during droughts. Significant questions are raised in this thesis and should be addressed in future research.

- **Extending the structural indices database:** As a large repository of data, the Fluxnet database provides a unique opportunity for exploring and understanding numerous different ecosystems. Currently, data for many ecosystem fluxes (carbon dioxide, water and heat fluxes) and meteorology are available in the Fluxnet database with some general site characteristics and biological data. However typical forest inventory data e.g. on DBH distribution is not included. Forest inventory data can be integrated with Fluxnet data to further understand these ecosystems. In the case of forestry, inventory of stands has been an important tool to understand forest dynamics. In our work, we have combined the inventory data and ecosystem fluxes and calculated numerous structural indices. This work can be extended to more sites creating an increasingly useful dataset for understanding the effect of forest structure on forest ecosystem processes.
- **The use of the forest soil water model (FWSM).** Here, we looked at the effect of forest structure on the annual responses of forests to climate variation and drought. The effect of drought is often not detectable at annual scales, therefore, it is important to assess the effects on shorter timescales. The FWSM is able to simulate soil moisture at daily time scales, yet it can also easily be used for multiple sites and years. This provides a unique tool to understand soil moisture dynamics within and between years and during droughts. Additionally, FWSM is open-source and can also be used and improved by other scientists.
- **Extending the analysis with more data:** Our findings, particularly those on the effect of forest structure on ecosystem functioning during drought, are inconclusive. To reach more robust results, the analysis should be extended with more sites that include forest structural indices. Increasing the number of sites will increase the statistical power and confidence in the results. The summer of 2018 was unusually dry in Europe (BURAS et al., 2019). Including the data from this year might provide more insight into the modulation of drought effects by forest structure.
- **Looking at the response of other forest functions:** The Fluxnet database offers a unique opportunity tfor studying forest functions beyond those analysed in this thesis, e.g. water use efficiency (WUE) and microclimate. WUE is the rate of carbon uptake per unit water loss (KEENAN et al., 2013), and is affected by tree size and stand density (FORRESTER, 2015). More research can be done on how the WUE is modified by forest structure. Another research direction involves looking for vegetation effects on local climate. For example TANG et al. (2018) reported that forests generally cool the land surface and lower air temperatures. By assessing this,

we could investigate if differences in land surface temperatures (also during droughts) vary across forests of varying structural complexity.

Finally, we conclude that this thesis presents a complete analysis of the available data, focusing on understanding the effect of forest structure on ecosystem functions. Next to our results and conclusions, the new model tool and dataset provide significant support for further investigations into the role of forest structure in modifying ecosystem function during drought.

A Difference in carbon uptake and water use between a managed and an unmanaged beech forest in central Germany

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I supported in the preparation, analysis and discussions of figures A.2 and A.4 (section A.5.2). Further, I read and reviewed the manuscript.

A.1 Abstract

Net atmospheric carbon dioxide exchange, total evapotranspiration and net primary production of two neighbouring beech(*Fagus sylvatica L.*)forests in central Germany differing in site management were measured using the eddy covariance technique and biometric methods. The unmanaged site was an old-growth forest with admixtures of ash (*Fraxinus excelsior L.*) and sycamore (*Acer pseudoplatanus L.*)trees whereas the managed site was a regularly thinned, even-aged (about 130 years old), pure beech stand. Average carbon fluxes measured over seven years did not differ significantly between the two forests. Evapotranspiration was slightly higher (and consequently water use efficiency lower) at the unmanaged site. The maximum rates as well as the interannual variability of both net ecosystem exchange and net primary production were considerably larger at the managed, even-aged stand. The lowest annual carbon sequestration rates were observed in years with high fruit production in beech combined with cold and dry spells during leaf development which affected the carbon balance of the managed forest more than that of the unmanaged forest. In contrast, an extraordinarily dry period in late summer 2003 caused a stronger reduction in net carbon uptake in the old-growth forest which can probably be attributed to the contribution of ash to the ecosystem fluxes. Ash has a different phenology which madeit more susceptible to the late summer drought. The relative importance of tree and structural (age, size) diversity, leaf area index and regenerative growth as well as the temporal frame and extent of single weather extremes for the forest–atmosphere exchange is discussed and it is concluded that site management and forest structure needs to be included in soil–vegetation–atmosphere-transfer models as it can often override effects of land use or plant functional type.

A.2 Introduction

Changes in land cover and their biophysical and biogeochemical effects have been investigated much more thoroughly so far than differences in land management within a single land cover type (Luyssaert, 2014). Forest management can alter species and structural diversity as well as ecophysiological traits. Their influence on the carbon cycle and the water use efficiency of forest ecosystems and their interannual variability are as yet not well understood. This hampers any robust assessment of the impact of management practices on the greenhouse gas balance. Many recent studies about the effect of land cover type on the ecosystem carbon budget and the water use efficiency are based on the increasing number of canopy gas exchange measurements by means of the eddy covariance technique (Keenan et al., 2013; Luyssaert et al., 2007). However, it has also been noted that a large variability in gas exchange is caused by species-specific traits within one land use type (Groenendijk et al., 2011; Law, 2014) which can make it difficult to transfer general trends to specific sites. Inhomogeneous instrumentation and data analysis often amplifies the problem.

Therefore we present a case study of paired measurements of ecosystem carbon and water fluxes in two neighbouring forests that are characterised by the same site conditions and are dominated by European beech (*Fagus sylvatica*), and where identical instrumentation and data analysis were used, to investigate the effect of structural diversity and the admixture of other tree species, caused by different historical and recent forest management, on canopy gas exchange. In terms of recent trends in forest management, beech is considered as “pillar of close-to-nature forestry in the central European lowland” (Pretzsch, 2014). Understanding its responses to natural and anthropogenic changes and disturbances is thus of high relevance and significance. With this study, which combines eddy covariance measurements with more traditional biometric methods to assess the forests’ primary production, we try to test the following two hypotheses:

(1) Forest management in terms of establishing and maintaining an even-aged, monospecific stand improves the carbon gain and the water use efficiency compared to an unmanaged forest. (2) Structural diversity as encountered in the unmanaged forest decreases the interannual variability of growth and water use as well as the susceptibility to disturbances.

A.3 Material and methods

A.3.1 Sites

The two forests sites are located in Thuringia in centralGermany, ca. 30 km apart from each other. Both stands grow at an altitude of 450 m a.s.l. and face similar soil conditions (Triassic limestone covered with variable Pleistocene loess deposits) and climatic conditions (suboceanic–submontane climate with long-term means of about 8 °C for annual air temperature and 750 mm precipitation). Annual air temperature and precipitation sums during the study period are given in Table A.1.

Table A.1: Mean annual air temperature (t_a) and annual precipitation (P) during the study period.

Year	t_a (°C)	P(mm)
2003	8.50	544
2004	7.83	763
2005	8.13	736
2006	8.66	660
2010	6.71	756
2011	8.85	544
2012	8.27	701

The Hainich site is an unmanaged stand in the central part of Hainich National Park. The area was never clear-cut but used as a coppice-with-standards system until the end of the 19th century and then for selective cutting by the local population until 1965. From 1965 to 1997 it was part of a military training area and only single, very valuable trees were cut. Since December 1997 no management activities at all have taken place. Regarding to its highly diverse horizontal and vertical structure the forest can be characterised as an old-growth forest with tree ages varying between 0 and 250 years (Figure A.1, Knohl et al., 2003; Mund, 2004). Beech (*F. sylvatica L.*) is the dominating tree species, accounting for ca. 64% of tree biomass, and ash (*Fraxinus excelsior L.*) and sycamore (*Acer pseudoplatanus L.*) make up most of the remaining biomass with a share of 28% and 7%, respectively (Table A.2). Single trees of *Carpinus betulus (L.)*, *Ulmus glabra (L.)*, *Acer platanoides (L.)* and *A. campestre (L.)* are admixed as remnants of the historical forest management regime (Mund et al., 2010).

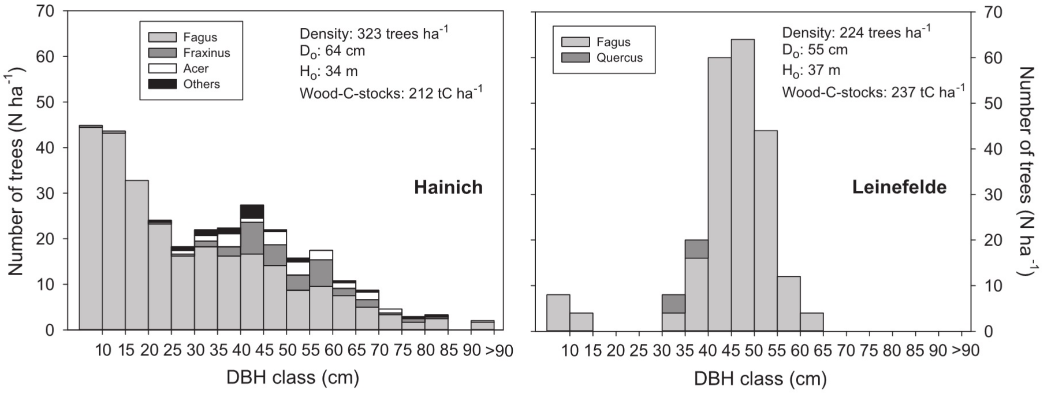

Figure A.1: Frequency distribution of stem diameter (DBH, diameter at breast height) and key stand characteristics of the study sites Hainich and Leinefelde. Do: quadratic mean of DBH of the 20% largest trees per study plot; Ho: tree height predicted for Do (dominant stand height).

Table A.2: Some stand characteristics of the two forests.

	Hainich (unmanaged)	Leinefelde (managed)
Soil	Pleistocene loess deposits with dominance of Cambisols	Pleistocene loess deposits with dominance of Luvisols
Most abundant tree species (%biomass)	*Fagus sylvatica* (64%) *Fraxinus excelsior* (28%) *Acer pseudoplatanus* (7 %)	*Fagus sylvatica* (99%)
Tree age (years)	0–250	130
Mean canopy height (m)	35	35
Stand density (stems ha^{-1})	323	224
Leaf area index (–)	5.1	4.2

The Leinefelde site is an even-aged, pure beech stand managed as a shelterwood system for maximum wood production. Thinning was carried out regularly every 10–20 years (Anthoni et al., 2004). The measurement site consists of a 130 year-old stand which is surrounded by other even-aged beech stands. The site at Leinefelde is characterised by a slightly thicker loess cover, associated with a dominance of Luvisols, than the Hainich site where Cambisols are the dominant soil type (Mund, 2004). The herbaceous ground vegetation differs in species composition between the two forests (Anthoni et al., 2004).

The maximum annual effective leaf area index as measured with an LAI-2000 plant canopy analyser (LI-COR Inc., Lincoln, NE, USA) was on average 5.1 at the unmanaged site and 4.2 at the managed site (Table A.2). The latter had a lower stand density (224 m^{-2} vs. 323 m^{-2}) but a higher wood biomass (above- and belowground; 237 t C ha^{-1} vs. 212 t C ha^{-1}). The leaf area was concentrated more towards the canopy top than it was the case at the unmanaged site. The maximum canopy height as determined by visual inspection from the respective tower was about 35 m at both sites.

A.3.2 Eddy covariance data

The eddy covariance measurements at the two sites were carried out at 44 m above the ground with identical instrumentation and data acquisition techniques. Each measurement system consisted of a three-dimensional sonic anemometer (Solent R3, Gill Instruments Ltd., Lymington, UK) and a closed-path CO_2/H_2O infrared gas analyser (LI-6262, LI-COR Inc., Lincoln, NE, USA) placed at the bottom of the instrument tower and connected to the gas inlet close to the anemometer by a 50 m long tube. Technical details about the installation can be found in Knohl et al. (2003). Data were synchronised and stored on a field computer using the "EddySoft" data acquisition software by O. Kolle (Max-Planck-Institute for Biogeochemistry, Jena, Germany). The turbulent fluxes were recalculated in 2013 with version 4.1 of the "EddyPro" software (LI-COR Inc., Lincoln, NE, USA).

The data collection and quality control followed the methodology of Aubinet et al. (2000) and Foken et al. (2004). The gap filling and the partitioning of the net ecosystem CO2 exchange (NEE) into gross primary production (GPP) and ecosystem respiration (Reco) was carried out using the 'Fluxnet' online-tool based on Reichstein et al. (2005). Evapotranspiration was calculated as the residual of net radiation and sensible heat flux (Gash et al., 1999) in terms of the annual totals. Direct eddy covariance measurements of ET based on the water vapour concentrations recorded by the LI-6262 were rejected because of a large underestimation of the flux caused by attenuation of the water vapour fluctuations in the long tubing. For details about standard meteorological variables recorded at the sites we refer once again to earlier descriptions of the two measurements stations (Anthoni et al., 2004; Knohl et al., 2003). Due to a lack of funding, no flux data could be obtained at the managed site from 2007 to 2009.

A.3.3 Biometric data

The estimates for annual wood NPP of the study sites resulted from continuous measurements of stem diameter at breast height (1.3 m above ground level) in combination with stand inventories. At the tree scale stem diameter increment was measured with dendrometers distributed over different diameter size classes and at Hainich also over different tree species. At the homogenous stand Leinefelde up to 22 trees were equipped with a dendrometer and at the unmanaged stand Hainich up to 96 trees. The exact number of measurement trees in each year of the study period varied because of damages to single dendrometers, and at Hainich also because of the natural dieback of individual trees that had to be replaced with new trees. For 2003 and 2004 also data from stem increment cores taken at the Hainich site were available (Kahl et al., 2012, M. Bryukhanova, Institute of Forest SB RAS, Akademgorodok, Krasnoyarsk, Russia, unpublished) and included in this study.

To scale up stem growth from the tree level to the stand level site- and species-specific regression functions describing the annual relationship between initial basal area (cross-sectional area of a stem at breast height) and basal area increment were developed and applied to stand inventories of the study sites. The extent of the stand inventories represent the different stand structure of the study sites. At the homogenous, pure beech stand Leinefelde stem diameter and tree height of all trees P7 cm in diameter of one plot (25 / 25 m) located within the main footprint of the eddy-covariance-tower (Anthoni et al.,

2004) was measured. At the diverse Hainich site the regression functions were applied to repeated stand inventories. The first inventory (2000) comprised 14 plots (radius of each plot: 15 m) that were located along a transect within the centre of the main footprint. The second inventory included 20 additional plots distributed over the entire footprint. The distribution of these plots was based on an "importance sampling design" (Anderson, 1999). This means that a predefined number of locations for the plots were randomly chosen according to a probability distribution that defines the probabilities of the source areas of the carbon fluxes detected by the eddy-covariance-measurements (Göckede et al., 2008; Göckede et al., 2004; Rebmann et al., 2005). At each plot stem diameter of all trees P7 cm in diameter and in 2005 also tree height was measured. Above- and belowground woody biomass per tree and year were calculated via biomass regression functions (F. sylvatica: Wutzler et al. (2008); all other species: Fehrmann (2006) (aboveground woody biomass) and Wutzler et al. (2008) (coarse roots)). For the conversion of woody biomass into carbon stocks a mean carbon concentration of 50% was assumed.

The annual net primary production (NPP) of leaves, buds and fruits was derived from litter sampling within the main footprint. The samples were separated, dried and weighed. Growth, ripening and dropping of the fruits occur during one year. Thus, fruit NPP can be estimated directly from annual fruit fall, similar to leaf NPP. However, in mast years we observed a substantial premature as well as delayed dropping of beech fruits. Thus, in mast years all fruits sampled between early summer of the current year and spring of the following year were summed up to fruit NPP of the respective mast year. Mean carbon concentration of beech leaves was 48%, of leaves from the other species 46%, and that of fruits 54% (nuts and shells).

For the comparison between the inter-annual variability of NEP and wood NPP it is assumed that by far the largest proportion of annual NEP results from carbon accumulation in living, aboveand belowground woody biomass. This assumption is based on the following features of the study sites: (1) the natural mortality of trees was close to zero at Leinefelde and very low (<1%vol.) at Hainich, (2) because of the low mortality rates and the lack of any major disturbances at Hainich, more or less constant rates of dead wood decomposition can be expected at the stand scale, (3) during the study period no tree harvesting occurred within the main footprint of the managed site Leinefelde, and (4) the largest proportion of carbon allocated to leaves, fine roots, fruits and the ground vegetation is respired within 1–2 years, and, except for the fruits, the inter-annual variability of their production is low compared to that of wood NPP (Mund, 2004; Mund et al., 2010). The largest source of uncertainty results from the net uptake or release of carbon by the soil. Schrumpf et al. (2014) showed that at the Hainich site and during the period 2004–2009 on average 65 ± 29 g C m^{-2} a^{-1}) were accumulated in the soil. The accumulation rates of single years most likely differ from this mean value, but because of the high spatial heterogeneity of soil carbon stocks it is extremely difficult to detect their changes in single years (Schrumpf et al., 2011). For Leinefelde, only one soil inventory was available (Mund, 2004). Consequently, for the present study we assumed that the inter-annual variability of soil carbon accumulation can be neglected.

A.4 Results

Over the seven year period of simultaneous eddy covariance measurements the annual net carbon exchange, i.e. net ecosystem productivity (NEP), with the atmosphere varied less from year to year at the unmanaged forest stand (standard deviation (SD) = 70 g C m^{-2} a^{-1}) than it did at the managed site (SD = 119 g C m^{-2} a^{-1}; Figure A.2). The lowest annual NEP was observed in 2004 and the second lowest in 2011 in both forests. The largest net uptake occurred in 2012 at the managed site and in 2005 at the unmanaged site. Most of the interannual variation in NEP resulted from changes in GPP by up to 400 g carbon per square metre ground area between different years indicating a surprisingly constant ecosystem respiration ($R_e$co), which indeed varied only by less than 200 g carbon per square metre at both sites. The lowest Reco was calculated for 2010 which was on average the coldest year of the studied seven years (Figure A.2). The only, weak exception of the close relationship between GPP and NEP was observed at the Hainich site in 2004, where GPP was less reduced compared to the other years than NEP.

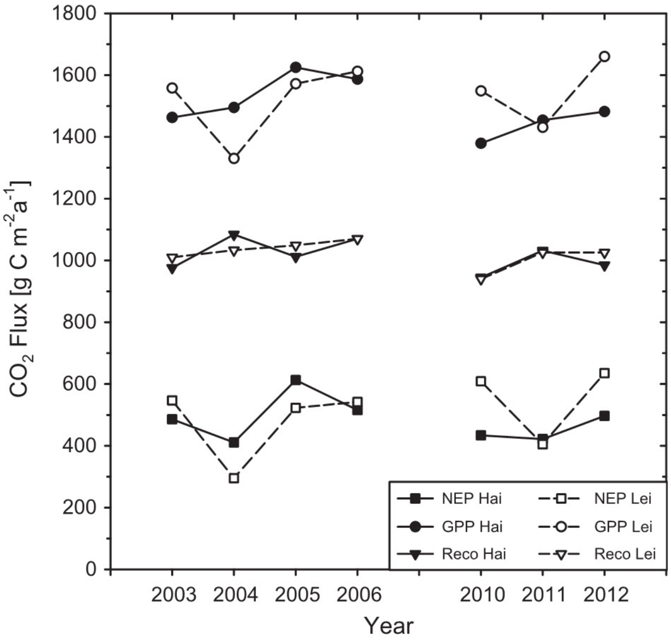

Figure A.2: Annual totals of net ecosystem production (NEP), gross primary production (GPP) and ecosystem respiration ($R_e$co) for a managed and an unmanaged beech forest over seven years.

Particularly low GPP and NEP rates were observed in 2004 and 2011 for the managed beech forest. At least in 2011 this result from the eddy covariance measurements corresponded well with the measurements of relative stem diameter increment (Figure A.3). Both 2004 and 2011, but also 2006 and 2009, were so-called masting years which were characterised by a high fruit production of the beech trees (Figure A.3). In 2004 and 2011, but not in 2006 or 2009, the period of leaf unfolding in beech was accompanied by unusually low temperatures, which, in combination with the masting, may have caused the low net CO2 exchange (Mund et al., in prep.). The mean NEP values obtained at the two sites over the seven years period did not differ significantly from each other (Figure A.2, Table A.3).

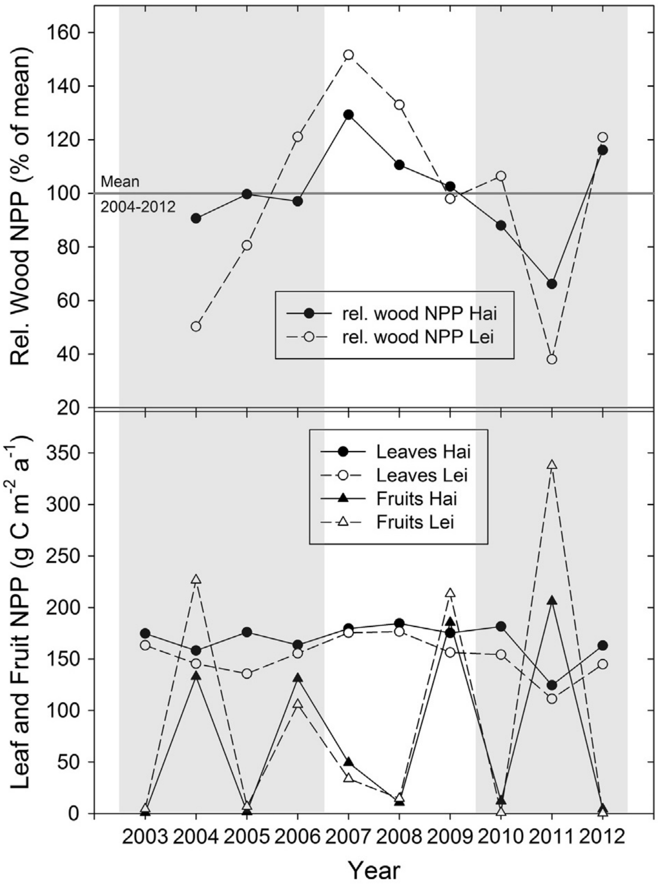

Figure A.3: Relative wood NPP (annual wood NPP in percent of mean wood NPP 2004–2012 per study site) (above) and leaf and fruit NPP (below) of the study sites Hainich and Leinefelde. The grey bands mark the time frame of the eddy covariance data.

Table A.3: Statistical assessment of the observed differences in mean fluxes between the sites, using a t-test for correlated samples with observation years as replicates. P values in bold type indicate a significant difference between sites.

Flux	Net radiation	Sensible heat	Latent heat	NEP	R_eco	GPP	WUE	Bowen ratio
P-value	0.28	0.004	0.003	0.56	0.59	0.52	0.11	0.003

The deviations between the two forests did not occur evenly throughout the seasons. If GPP during the first three years of the observation period is taken as an example (Figure A.4)then it can be seen that GPP in the managed stand always increased more rapidly in the spring than it did at the other site, but started earlier to decline in late summer, especially so in the masting year of 2004. The year 2003 was characterised by an unusually warm and dry period in late summer which affected large parts of central Europe (Granier et al., 2007), and interestingly this was detected more strongly in GPP of the unmanaged stand than in the managed, pure beech stand where GPP was affected less (Figure A.4).

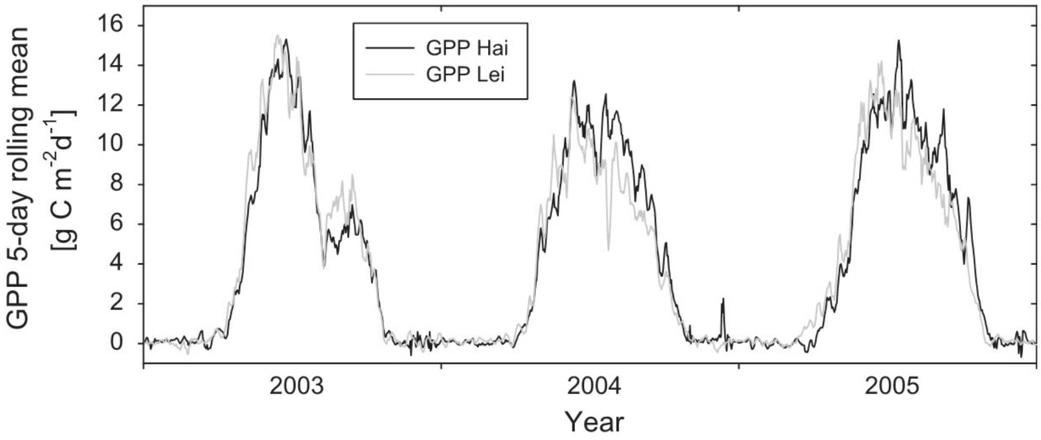

Figure A.4: Five-day running mean of GPP of the two beech forest stands over the first three years of the measurement period as calculated from gap-filled eddy covariance data.

Total annual evapotranspiration varied between 461 and 559 mm at the managed site and between 476 and 604 mm at the unmanaged sites (Figure A.5) and was lowest in 2003, the year with the drought period in late summer, at both forests. The corresponding mean values for the two stands were 503 and 549 mm, respectively. This means that the amplitude of the interannual variability was fairly similar but the mean rate was higher at the unmanaged forest. Conversely, the Bowen ratio, i.e. the ratio between sensible and latent heat flux, was consistently higher at the managed forest and peaked at both sites in 2003 (Figure A.5). This observation resulted mainly from differences in sensible heat flux rather than available energy which did not differ significantly between the two sites (Table A.3). As a result of the nearly similar net carbon uptake and the differing water loss, the water use efficiency was higher at the managed beech forest, however this tendency was not significant (Table A.3).

In conclusion, forest management in terms of regular thinning and the establishment of even-aged, homogenous stands thus appears to have reduced the unproductive components of evapotranspiration, in particular interception evaporation, but have increased the interannual variability of carbon fluxes.

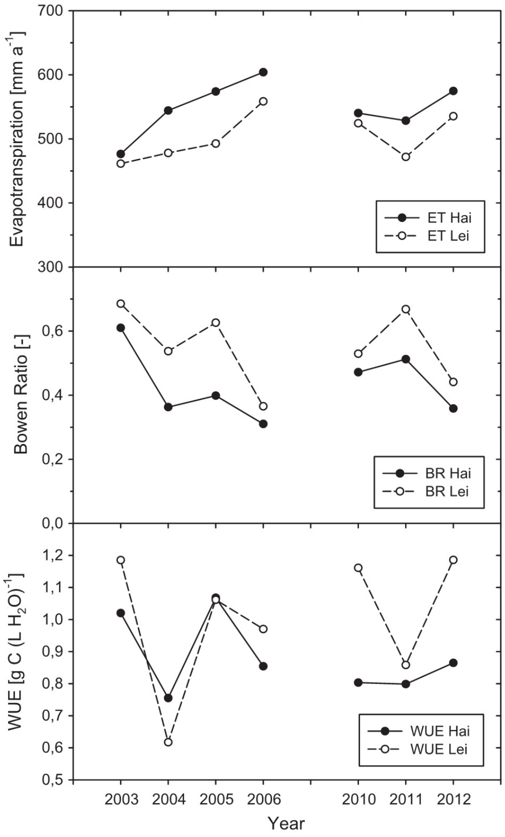

Figure A.5: Total annual evapotranspiration (ET, upper panel) and water use efficiency (WUE, lower panel) as measured over seven years in two beech forests differing in management only.

A.5 Discussion

A.5.1 Methodological uncertainties

Some uncertainty in our eddy flux data may have been induced through the method chosen to gap-fill NEE and to partition NEE into GPP and Reco. The common REICHSTEIN et al. (2005) technique based on night-time data faced the problem that night-time data at the two research sites were scarce because of the relatively high u_* threshold of 0.5 used for this data set. The threshold was chosen following KUTSCH et al. (2008) who compared the eddy covariance night-time CO_2 fluxes with soil chamber measurements. Although the high threshold should not have biased Reco in the long-term, it cannot be excluded that it may have suppressed its apparent interannual variability. The fact that the eddy covariance tower at the Hainich site is located on a gentle slope downwind of a hill (with respect to the main wind direction) and that the measurements had to be carried out 44 m above the ground, due to the large canopy height, causes considerable advection of CO_2 and thus some further uncertainty in the eddy fluxes obtained at this site (FINNIGAN, 2008; KUTSCH et al., 2008; KUTSCH et al., 2010). The topography at the other site is not flat either and could theoretically also have induced some advective carbon fluxes that would have contributed to the ecosystem carbon exchange. The uncertainties in annual carbon budgets resulting from the choice of the u_* threshold (within a reasonable range) and the gap filling of missing night-time respiration data using temperature as a driving factor were quantified as 30 g C m^{-2} a^{-1} and 50 g C m^{-2} a^{-1}, respectively, according to the sensitivity analysis carried out by Knohl et al. (2003) for the Hainich site. Although all the potential errors mentioned above are unlikely to occur in the same direction, an overall uncertainty of about 100 g C m^{-2} a^{-1} for NEP, $R_e$co and GPP should nevertheless be assumed, if possible sensor inaccuracies are also taken into account. As long as this uncertainty remains unsolved we focus more on the observed interannual variability than on long-term average fluxes in our further discussion. Furthermore we use only relative numbers (in relation to the mean of 2004–2012) when comparing the micrometeorological data with the biometric data which were calculated as in Mund et al. (2010). Nevertheless we believe that a possible bias in the eddy fluxes is only small since the annual fluxes in this study correspond well with those from other forest sites in similar regions and of similar age (Luyssaert et al., 2007; Luyssaert et al., 2008).

As far as evaporation is concerned, we did not use the water vapour measurements by the closed-path gas analyser to calculate eddy fluxes of latent heat because of a large uncertainty and likely bias caused by the very long tubes between the air intake and the gas analyser (Ibrom et al., 2007). In fact, the systems at our sites were never intended to measure the water vapour flux accurately, but optimised to obtain accurate CO_2 fluxes (E.-D. Schulze, pers. comm.). Therefore we used a well established alternative method in terms of the eddy covariance energy balance (ECEB) technique which relies on accurate measurements of net radiation and sensible heat flux and assumes a closed energy balance. However, for eddy flux sites it is well known that a complete closure is hardly achievable, even at sites where every component is measured accurately (Foken et al., 2011; Stoy et al., 2013). Horizontal advection and/or transport by low-frequency air motions have been identified as the most important reasons for the missing energy in the total budget. These processes would affect all turbulent fluxes in the same way and could therefore bias the calculation of latent heat as residual of the energy balance if the sensible heat flux is underestimated for the above named reasons. The global average of the energy balance closure, based on 173 sites, is 84% (Stoy et al., 2013). If we assume a similar number for our two sites and a Bowen ratio of about 0.5, then we might have underestimated sensible heat by 16% and overestimated latent heat (if calculated as residual) by 8%. This uncertainty does not yet include potential errors in the radiation measurements. However, the described uncertainty would likely affect both sites in a similar way and thus not eliminate the observed differences in forest water use. It is also worth mentioning that, in practice, often only a fraction of the energy balance gap can be explained by processes affecting all fluxes, and that the sensible heat flux is often less underestimated than other turbulent fluxes (Barr et al., 2012) which would mean that the error in ET as determined by the ECEB method is even smaller than 8%.

A.5.2 Interannual variability in carbon fluxes

When distinguishing between the effects of plant functional type and land use type on the one hand and site management on the other on CO_2 exchange (Luyssaert, 2014), it needs to be considered which NEE components are particularly sensitive to management activities. It seems likely that GPP and NPP will often be more strongly affected by site management than Reco which is dominated by soil respiration, with autotrophic and heterotrophic respiration having a similar order of magnitude (Kutsch et al., 2010). Above-ground management activities will therefore not be reflected to the same extent in below-ground biological activity as in canopy processes. Whilst it is unsurprising that GPP was more variable than $R_e$co, just as in other beech forests (Pilegaard et al., 2011), it is somehow unexpected that no difference at all in the average ecosystem respiration rates were found between the two sites despite a much higher proportion of dead wood at the unmanaged site. However, the total above- and belowground wood biomass was about 10% lower at the unmanaged site (Figure A.1) and the observation of similar respiration rates corresponds to the results of soil organic carbon inventories that observed an ongoing net carbon accumulation in forest soils (Kutsch et al., 2010; Osterburg et al., 2013; Schrumpf et al., 2014; Tefs et al., 2012) but no significant differences in C stocks of the mineral soil among differently managed forests – provided that the forests are sustainably managed without soil disturbances (e.g. Grüneberg et al., 2013; Jandl et al., 2007; Mund, 2004; Schöning et al., 2013; Wäldchen et al., 2013).

The most obvious ecosystem properties related to management activities that may play a role when comparing the gas exchange of the two forests with each other are the structural and physiological traits of the respective canopies. The homogeneity at the managed site caused a higher variability in NEP and GPP due to the same and simultaneous reaction of all trees to weather conditions (incl. masting), whereas at the unmanaged site the opposite was the case since beech and ash had a different climate sensitivity and not all trees (not even all beech trees because of their young age) showed masting. None of the sites showed any consistent trend in annual NEP over the seven years of investigations as observed e.g. in younger forests. A continuous increase in net carbon uptake of a Danish beech forest over 14 years was reported by Pilegaard et al. (2011) and could possibly result from the relatively young age of their forest, compared to the two sites considered here where no such trend was found.

A.5.3 Evapotranspiration

The difference in ET between the two sites could possibly result from higher rates of interception evaporation at the unmanaged site, having a denser canopy with a higher storage capacity for intercepted rain (Carlyle-Moses et al., 2011), if transpiration is considered as a conservative parameter, independent of forest structure or species composition (Herbst et al., 2008; Roberts, 1983). Other authors, in contrast, have found that canopy conductance and hence canopy transpiration scale with LAI (Granier et al., 2000), which could just as well explain the difference in ET between the two forests investigated in this study since the unmanaged stand had indeed a higher LAI. However, the similarity of GPP between the sites would rather suggest similar transpiration rates, too, since these two processes share the same pathway of gas exchange through the stomata.

New measurements of individual ET components at the two sites will hopefully shed more light on this question. The overall effect of management on ET remains controversial anyway (Komatsu et al., 2010). It has been suspected that reduced forest management activities would result in less percolation and runoff (due to higher evapotranspiration in denser forests), but this could not always be verified.

A.5.4 Diversity and resilience

Tree diversity in beech dominated forests is amenable to management, for example through close-to-nature forestry or through establishing mosaic-like plantations with admixtures of different species instead of maintaining even-aged monocultures. It affects growth at species level through changes in competition and/or small scale soil properties and nutrient stocks but not necessarily at stand scale (e.g. Holzwarth et al., 2011; Ratcliffe et al., 2015; Schmidt et al., 2015), although some studies found a positive correlation between species number and productivity in temperate forests (Morin et al., 2011). In case of the two investigated beech forests it seems that species and structural diversity effects on carbon exchange at the tree level were balanced at the stand level where similar average NEP rates were observed.

More relevant at stand scale is the resilience to disturbance which is generally higher in mixed forests (Pretzsch, 2014). An example for this phenomenon is the response to drought in beech/ oak mixtures where it has been reported that beech benefits from the mixture and is more resilient than in mono-specific stands (Pretzsch et al., 2013). However, our study shows that the timing of a disturbance such as a drought period is important, too, and may in some cases even cause an opposite effect due to the variability of tree phenology in mixed stands. *Fraxinus*, for example, is more flexible than *Fagus* with respect to the time of leaf unfolding in spring (Vitasse et al., 2009a) and can thus more easily avoid damage by late frosts. At Hainich there were years when these two species came into leaf practically simultaneously at the end of April or start of May, whereas in the relatively cold spring of 2011 leaf unfolding in *Fraxinus* showed a time lag of about four weeks compared to *Fagus*. The fact that, vice-versa, the flexibility of *Fraxinus* is lower in autumn (Vitasse et al., 2009b) is not that relevant for NEP due to the much lower irradiance at this time of the year. Whilst maximum incoming shortwave radiation at our sites reached about 850W m^{-2} in late April (time of leaf out), corresponding to maximum daily totals of about 25 J m^{-2} d^{-1}, the respective values for late October (time of leaf fall) were 450W m^{-2} for the maximum irradiance and 9.5W m^{-2} d^{-1} for the daily totals.

GPPmax is reached later in *Fraxinus* than in *Fagus* (W.L. Kutsch, pers. comm.) which is also mirrored in the green fraction of the leaves (Ahrends et al., 2009) and could probably explain why Hainich, in contrast to the aforementioned observation of Pretzsch et al. (2013), had a stronger GPP reduction than the monospecific Leinefelde stand in the dry year 2003 with the drought only occurring in late summer and thus affecting GPP in *Fraxinus* more strongly than in *Fagus*. When looking at the bigger picture regarding drought resilience and tree diversity, the recent paper by Grossiord et al. (2014c) produced incongruent results with drought stress increasing with species number in boreal forests but decreasing in some temperateand thermophile forests. The two forests investigated here do not fall into this pattern though, as the monospecific stand appeared to be less affected by the 2003 drought than the unmanaged stand containing other, more sensitive species, too. However, the discussion of this observation should not be restricted to soil water uptake as in Grossiord et al. (2014c). Instead, it seems plausible that interception evaporation, which can amount to 50% of ET in humid temperate climates (Ringgaard et al., 2014) may have caused this incongruent behaviour, since interception evaporation depends on forest structure (Ringgaard et al., 2014) which often depends on species number (Pretzsch, 2014).

The key finding of our study may be summed up as follows. If different species with different traits and phenology and trees of different age are present in a forest due to reduced (or ceased) management activity it becomes more unlikely that weather extremes or rare biological processes such as fruiting would affect the forest ecosystem as a whole in terms of its annual matter and energy exchange with the atmosphere. The hypothesis that species richness and/or structural diversity leads to more stability and less variation in carbon fluxes (Loreau, 2001) is confirmed by our study if the years 2004 and 2011 (with cold spring plus high fruit biomass) are considered that showed a more moderate response at the unmanaged site, but not if the late summer drought of 2003 is considered.

A.6 Conclusions

Defining the plant functional type is not sufficient to describe and predict the interaction between forests and the atmosphere (Groenendijk et al., 2011). Species and size specific traits (Law, 2014), including forest structure (Pretzsch, 2014), as well as management activities (Luyssaert, 2014) need to be represented in reliable and transferable prediction schemes as well. Looking back at the two hypotheses put forward in the Introduction section of this study we can conclude that hypothesis number two (regarding the enhanced interannual variability of gas exchange in the managed forest) could be confirmed, whereas hypothesis number one(regarding differences in the average exchange rates) was only true for water vapour but not for carbon dioxide if both fluxes are considered at ecosystem scale. Paired tower approaches at neighbouring forest sites can help disentangle control factors of forest–atmosphere exchange as affected by management activities, especially so if they are accompanied by independent biometric measurements.

A.7 Acknowledgements

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B Stand age and species richness dampen interannual variation of ecosystem-level photosynthetic capacity

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In this paper, I provided data from the Hainich site and edits to the manuscript.

B.1 Abstract

The total uptake of carbon dioxide by ecosystems via photosynthesis (gross primary productivity, GPP) is the largest flux in the global carbon cycle. A key ecosystem functional property determining GPP is the photosynthetic capacity at light saturation GPP_{sat}, and its interannual variability (IAV) is propagated to the net land-atmosphere exchange of CO_2. Given the importance of understanding the IAV in CO_2 fluxes for improving the predictability of the global carbon cycle, we have tested a range of alternative hypotheses to identify potential drivers of the magnitude of IAV in GPP_{sat} in forest ecosystems. Our results show that while the IAV in GPP_{sat} within sites is closely related to air temperature and soil water availability fluctuations, the magnitude of IAV in GPP_{sat} is related to stand age and biodiversity ($R^2 = 0.55$, $P < 0.0001$). We find that the IAV of GPP_{sat} is greatly reduced in older and more diverse forests, and is higher in younger forests with few dominant species. Older and more diverse forests seem to dampen the effect of climate variability on the carbon cycle irrespective of forest type. Preserving old forests and their diversity would therefore be beneficial in reducing the effect of climate variability on Earth's forest ecosystems.

B.2 Introduction

Interannual variability (IAV) of the net carbon dioxide exchange over land is globally the main determinant of the variability of atmospheric CO_2 growth rate (Ahlström et al., 2015; Le Quéré et al., 2009). So understanding the factors controlling the IAV in CO_2 fluxes is essential to improve the predictability of the global carbon cycle (Luo et al., 2015). Ecosystem biotic properties – such as soil and canopy nutrient status, rates of change in physiological properties of the vegetation, or the sensitivity of these properties to environmental factors – influence ecosystem CO_2 exchange. Recent studies have shown that the IAV of the carbon budget can be better explained by variation in biotic properties of ecosystems such as photosynthetic capacity (GPP_{sat}) than directly by environmental and climatic drivers (Ma et al., 2011; Reichstein et al., 2014; Richardson et al., 2007). GPP_{sat} is defined as the value of gross primary productivity (GPP) at saturating light under non-stressed conditions, minimizing the influence of anomalous hydrometeorological conditions (for example, droughts and heatwaves), which potentially affect photosynthesis. A robustly retrieved characterization of GPP_{sat} can be regarded as an ecosystem functional property reflecting the physiological response of the ecosystem to the environment. Given that IAV of GPP_{sat} must propagate to observed GPP, this quantity is thought to be a key variable in understanding IAV of carbon fluxes (Musavi et al., 2015). In fact, recent studies demonstrated that GPP_{sat} correlates more strongly than any climatic variable with annual GPP (Xia et al., 2015), but also correlates with net ecosystem CO_2 exchange (Reichstein et al., 2014) . The magnitude of IAV in GPP_{sat} has been shown to exhibit considerable variation across ecosystems (Musavi et al., 2016), yet no obvious explanation for this pattern has been reported in the literature. However, the consequences are important: a low IAV in GPP_{sat} would suggest that ecosystem functioning is not very sensitive to climatic variability, and that it preserves its functionality under the influence of that variability – and, likewise, high IAV is a consequence of high sensitivity. The capability of an ecosystem to preserve its functioning and structure over time (after external disturbances or climate extremes), is often defined as ecosystem stability and is linked to ecosystem resilience (Holling, 1973). Using this terminology, low values of IAV in GPP_{sat} can be understood as a characterization of high ecosystem functional stability.

The relation of ecosystem functionality, structure and stability has been a matter of debate for many decades in the field of ecology. In particular, the diversity of vascular plants has been investigated as a stabilizing factor with respect to variations in productivity, for example by buffering the ecosystem's sensitivity to climate extremes (Jucker et al., 2014). However, it is also well known that plant diversity is co-limited by soil properties (García-Palacios et al., 2010), ecosystem management, and climate conditions. Another variable to consider is stand age (the mean age of the forest stand or the number of years after a major stand replacement after disturbance), which may affect ecosystem stability through adaptation, particularly of trees to their environment – hence increasing ecosystem resilience to climate Variability (Oheimb et al., 2014). Moreover, structural parameters such as canopy cover, rooting depth, canopy height or leaf area index (LAI), which also depend on tree species diversity and stand age (Kutsch, 2009), have an important effect on the ecosystem response to variation in environmental drivers since they define the capacity of trees to access resources such as water and light (Herbst et al., 2015). For instance, a regional study in the Amazon basin has shown that GPP, derived from the remotely sensed enhanced vegetation index, is less sensitive to environmental influences in regions with high canopy cover (Brando et al., 2010).

Despite this growing body of ecological knowledge, it remains largely uncertain which factors stabilize ecosystem functional properties at the global scale. In particular, we do not understand the causes of variability of specific ecosystem functional properties, such as photosynthetic capacity across ecosystem types, which ultimately controls ecosystem productivity. Here we hypothesize that stand age and species diversity play an important role in stabilizing ecosystem photosynthetic capacity. We test this hypothesis while also considering other factors related to climate, water availability, forest structure and soil properties that might have direct or indirect effects on ecosystem photosynthetic capacity.

In this study, we used measurements of ecosystem-level fluxes, and climate variables (temperature, precipitation, and water availability), species richness, stand age, forest structure (canopy cover, height, and LAI), and soil properties (nutrient availability Fernández-Martínez et al. 2014) derived from satellite data, *in situ* observations and the literature (see the Methods).

We used half-hourly ecosystem-level GPP fluxes estimated by the means of the eddy-covariance technique at 50 FLUXNET sites (Baldocchi, 2008) with at least 4 years of measured fluxes, and with different vegetation types across different climatic regions. We included data from evergreen forest (EF) as well as deciduous broadleaved and mixed forest (DBMF) located in temperate, boreal, mediterranean, tropical and dry climate regions (Supplementary Figure 1 and Table B.1). All 50 sites have information on stand age (referred to simply as 'age' in Figure B.1 - B.3) and species richness in addition to the CO_2 flux data. Species richness ('sp. no.' in Figures B.1 - B.3) is the number of dominant plant species (for example tree or herb) that account for a cumulative abundance of 90 percent at a given site. We collected additional information on (i) canopy cover, (ii) canopy height,

(iii) LAI, (iv) temperature and precipitation, and (v) soil water availability index (WAI) for a subset of 44 sites; and (vi) an index of nutrient availability for 36 sites compiled from the literature (Fernández-Martínez et al. 2014- see Methods).

We characterized the response of half-hourly GPP estimates to incoming shortwave radiation by fitting ecosystem-level light response curves yielding daily estimates of $\mathrm{GPP_{sat}}$ (see Methods). The site-level estimates of annual $\mathrm{GPP_{sat}}$ (that is, GPP at saturating light conditions) were then determined by extracting the 90th percentile of the daily estimates of $\mathrm{GPP_{sat}}$. The magnitude of the IAV in $\mathrm{GPP_{sat}}$ was computed as the coefficient of variation of annual estimates of $\mathrm{GPP_{sat}}$ ($\mathrm{cvGPP_{sat}} = \sigma(\mathrm{GPP_{sat}}(t))/\mu(\mathrm{GPP_{sat}}(t))$), where $\mathrm{GPP_{sat}}(t)$ is the annual $\mathrm{GPP_{sat}}$ for year t, and σ and μ are the standard deviation and mean of $\mathrm{GPP_{sat}}(t)$, respectively. Two variable selection methods based on (i) relative importance of regressors (Grömping, 2007), and (ii) multivariate generalized regression models and a stepwise algorithm based on Akaike Information Criteria (stepAIC) were used to select the most relevant predictors of the IAV of $\mathrm{GPP_{sat}}$(see Methods).

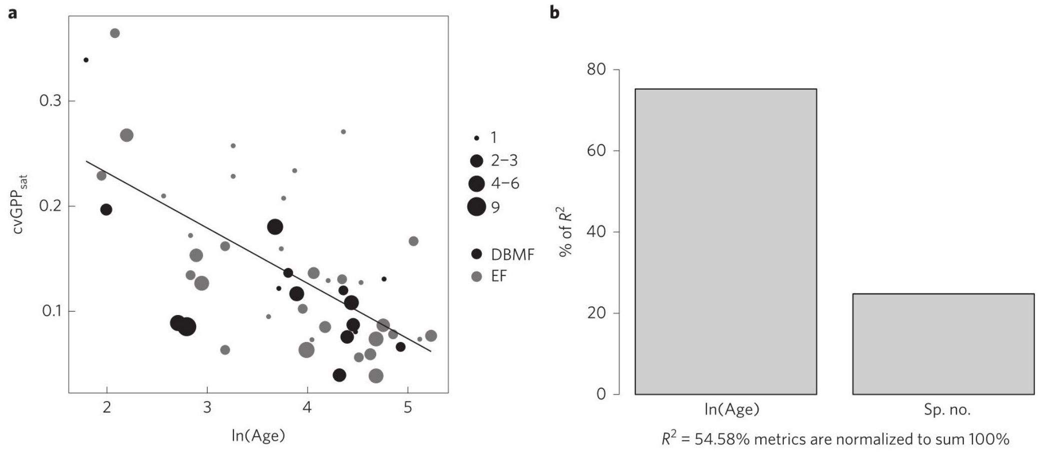

Figure B.1: Relationship of $\mathrm{cvGPP_{sat}}$ with stand age and species richness. (a) The relationship between the interannual variability of ecosystem photosynthetic capacity ($\mathrm{cvGPP_{sat}}$) computed for each FLUXNET site and stand age (which is transformed using the natural logarithm, ln(age)): ($R^2 = 0.39$, $P < 0.0001$, $n = 50$). The number of plant species at the sites that account for 90 % of the total species abundances (sp. no.) is indicated with the size of the points. DBMF, deciduous broad leaf and mixed forests (n = 16; black); EF, evergreen needleleaf and broadleaf forests (n = 34; grey). (b) Relative importance metrics of ln(age) and sp. no. as predictors of $\mathrm{cvGPP_{sat}}$. For a version of this figure using age without logarithm transformation, see Supplementary Fig. 11

B.3 Material and methods

B.3.1 Data

In this study we brought together a wide range of data: ecosystem-atmosphere CO_2 fluxes measured at eddy covariance flux sites, information about climate (temperature, precipitation, and water availability index (WAI)), species richness, stand age, and plant traits, derived from field campaigns, and information about forest structure derived from satellite data for each of the selected sites; finally, data about nutrient availability was derived from the literature (Fernández-Martínez et al., 2014). Sites were selected according to the availability of eddy covariance flux measurements for at least 4 years, information about stand age, canopy cover, canopy height, and species abundance. This led to a global dataset of 50 sites with different vegetation types across different climatic regions. We included data from evergreen forest (EF) and deciduous broadleaved and mixed forest (DBMF) located in temperate, boreal, tropical, Mediterranean and dry climate regions.

CO_2 fluxes and meteorological data. From the global eddy covariance flux database (Baldocchi, 2008) we downloaded half-hourly ecosystem-level gross primary productivity (GPP) fluxes estimated from net ecosystem exchange (NEE) data (Reichstein et al., 2005). Half-hourly shortwave incoming global radiation, temperature, and precipitation were also downloaded. From the dataset WAI was computed according to ref. (Tramontana et al., 2016). Here the WAI is the ratio between soil water storage and plant available water storage capacity at lower layer (100 mm) (Tramontana et al., 2016).

Average stand age. These data were obtained from the Biological, Ancillary, Disturbance and Metadata (BADM) of the FLUXNET database (Law et al., 2008). Stand age (expressed in years) reported in the BADM is the average tree age of the stand or the age of the stand since the last major disturbance that caused stand replacement. Stand age was reported for different years at the sites, and so we normalized the data by using the age of all sites at the year 2007 (which is the year of the release of FLUXNET LaThuile Database used in this study).

Species richness. Species identity and abundances from the BADM data and literature search were collected. Because these data come from diverse sources and are collected with different protocols, they can have variable level of details. Therefore, we developed a strategy to guarantee comparability of the plant species richness computed across sites. For each site we sorted the plant species according to their abundance, from the one with highest abundance to the lowest. Then we considered only the number of species that add up to 90% of the total site abundance.

Canopy structure. For the selected sites we extracted satellite products to characterize canopy structure: canopy cover, plant height and Leaf Area Index (LAI).

Canopy cover was extracted from the Moderate Resolution Imaging Spectroradiometer (MODIS) vegetation products continuous field version 437 `http://glcf.umd.edu/data/vcf/`. Plant height was derived for each site from the estimates reported in ref. (Simard et al., 2011 `http://lidarradar.jpl.nasa.gov/`).

We used estimates of LAI derived at 1 km (0.01°) spatial resolution by the JRC-TIP (Pinty et al., 2007) from the MODIS broadband visible and near-infrared surface albedo products (Schaaf et al., 2002). The processing for the gap filling and the extraction of the time series from MODIS-TIP LAI products is described in ref. (Musavi et al., 2016). Annual maximum LAI values were derived at each site by extracting for each year the 90th percentile of the 16-day LAI time series. Finally for each site the maximum LAI (LAI_{max}) and the coefficient of variation of the annual maximum LAI ($cvLAI_{max}$) were estimated. In this study we did not use site level LAI data reported in the FLUXNET database for the following reasons:

1. LAI data have been collected with a variety of different methods, from direct(that is, harvesting and litter fall) to indirect (for example, hemispherical photography or LAI-2000) methods. Site-level method intercomparisons of various techniques always reveal large and non-systematic differences among LAI methodologies, rendering the LAI information reported in the FLUXNET database not always suited for network synthesis studies. Efforts toward the standardization of the collection of these measurements are ongoing in the context of the Integrated Carbon Observation System (ICOS) and National Ecological Observatory Network (NEON), but these data are not yet available. 2. The availability of data in regular annual measurement is very different among sites. For some sites the LAI is available for each measurement year (and sometimes even seasonally), but for many sites only one estimate during the whole measurement period is available.

Considering the limitations of site-level LAI data, we selected the MODIS-TIP LAI product. MODIS-TIP LAI is recognized as one of the most effective LAI products available and it was successfully evaluated at a FLUXNET site included in this study (Pinty et al., 2011).

Nutrient availability. Part of the dataset (36 sites) was complemented with soil nutrient availability classes derived from literature (Fernández-Martínez et al., 2014). For each site, nutrient availability was computed using site-level specific information about the following variables: carbon, nitrogen and phosphorus concentrations of soil and/or leaves, soil type, soil texture, soil C/N ratio, and soil pH. These data were derived for each site from the literature and in some cases provided by the site principal investigator. The sites were eventually classified in three classes: low, medium and high nutrient availability. Afterwards the classification was approved by the site principal investigators (Fernández-Martínez et al., 2014).

B.3.2 Estimation of photosynthetic capacity and its interannual variability magnitude

Site-level estimates of the annual photosynthetic capacity ($\mathrm{GPP_{sat}}$) were determined from half-hourly GPP estimates and global solar radiation (Rg) (Musavi et al., 2016).

In summary, we fit a non-rectangular hyperbolic light response curve (NHLRC) to GPP and Rg data (Gilmanov et al., 2003). The NHLRC was fit to 5 days of data selected with a moving window approach. The parameters of the NHLRC were estimated and we computed the GPP at 1,000 W $\mathrm{m^{-2}}$ of Rg ($\mathrm{GPP_{1,000}}$), which represents the GPP at saturating light (that is, ecosystem photosynthetic capacity in the selected 5-day window). The estimated parameters and the ($\mathrm{GPP_{1,000}}$ values were assigned to the day in the middle of the 5-day window. Parameters estimated with R^2 of the fitting lower than 0.6 were removed.

To estimate the annual $\mathrm{GPP_{sat}}$, for each year from the daily $\mathrm{GPP_{1,000}}$ time series, we calculated the 90th percentile. The interannual variability (IAV) of the annual estimates of $\mathrm{GPP_{sat}}$ was computed as the coefficient of variation of ($\mathrm{GPP_{sat}}$, that is, $\mathrm{cvGPP_{sat}}$calculated by dividing the standard deviation by the mean.

$$\left(\frac{standard\ deviation}{mean}\right) \tag{B.1}$$

In young stands $\text{cvGPP}_{\text{sat}}$ might depend on the trend in annual growth and GPP that can lead to high $\text{cvGPP}_{\text{sat}}$ values that are not related to interannual variability in photosynthetic capacity. To remove this confounding factor we first tested the presence of a significant trend in GPP_{sat} time series at each site with the Mann-Kendall non-parametric trend test. Finally, for the sites with a significant trend ($P < 0.1$) we recomputed the $\text{cvGPP}_{\text{sat}}$ by detrending the GPP_{sat} time series (that is, the standard deviation of detrended GPP_{sat} divided by the mean of the GPP_{sat} , hereafter referred as detrended $\text{cvGPP}_{\text{sat}}$).

Aggregation of environmental variables: For the estimation of year-to-year variability of climate we used temperature and precipitation measured, and the WAI35 estimated at the flux sites. To aggregate temperature and precipitation we used only daily values with more than 70% of original half-hourly data (gaps in the half-hourly data are filled using ERA-Interim climate data downscaled at the FLUXNET, `http://www.bgc-jena.mpg.de/~MDIwork/meteo/index.php`). Average temperature, WAI, and cumulative precipitation over the active growing season were computed. Active growing season was considered as the days with daily GPP higher than the annual median GPP. From these annual estimates we derived the standard deviation (s.d.) of annual mean temperature, WAI and precipitation during the growing season as a measure of their IAV.

B.3.3 Statistical analysis

We used a variable selection method and relative importance method to select and quantify the contribution of each predictor (for example, average stand age (age), ln(age), species richness (sp. no.), canopy cover, canopy height, and nutrient availability, temperature, WAI) to the $\text{cvGPP}_{\text{sat}}$; precipitation was once used in the calculation instead of WAI.

The stepwise algorithm based on the Akaike Information Criteria (AIC) algorithm with generalized linear regression models was used43. The independent variable was $\text{cvGPP}_{\text{sat}}$, while the predictors were stand age (referred to in the figures simply as 'age'), species abundance (sp. no.), ln(age), s.d. of temperature and of WAI, canopy cover, canopy height, LAI, and so on; interactions of age and sp. no., s.d. of temperature and s.d. of WAI and canopy height and (LAI_{max} were also included (cumulative precipitation was also used in place of WAI with similar results; data not shown). The algorithm was set up with the possibility to account for model pairwise interactions, and imposing a selection only if the model is statistical significant ($P < 0.01$). Although the sites used in this study have at least 4 years of flux data, the number of years (no.years) with available data at each site was different. Therefore, we used

$$\frac{1}{\sqrt{no.years}} \tag{B.2}$$

to weight the model selection, weighting more the sites with higher numbers of years. A stepwise selection without the weighting was used as well. The distribution of the residuals of the best model was tested for normality using the Shapiro and Kolmogorov-Smirnov test. The results showed that the residuals were normally distributed; therefore the weighting was not strictly necessary, but was used for a comprehensive evaluation.

In order to assess the uncertainty introduced by the potential trend in GPP_{sat} in young stands, we repeated the analysis using the detrended $cvGPP_{sat}$ dataset, and the $cvGPP_{sat}$ for the sites without a significant trend in GPP_{sat}.

To disentangle the importance of each predictor in determining $cvGPP_{sat}$ we used the Lindeman-Merenda-Gold (LMG) relative importance method19. This method allows the assessment of the importance of correlated predictors in a multiple linear regression model. Moreover, the pairwise linear regression and correlation between the different predictors and $cvGPP_{sat}$, and between the predictors themselves, was tested.

Both stepwise AIC and the LMG identified ln(age) and sp. no. as the most important variables controlling the $cvGPP_{sat}$. We used a generalized linear model to fit the coefficients of the multiple linear model.

To test differences of $cvGPP_{sat}$ between the age and nutrient availability classes, we used the Kruskal-Wallis rank sum test. Sites were divided by age class (young, middle aged and mature stands) according to the 33rd and 66th percentiles of the distribution of age. Nutrient availability classes were defined according to ref. (Fernández-Martínez et al., 2014)(low, medium and high).

The correlation between GPP_{sat} and climate variables was tested with distance correlation (Székely et al., 2007). Distance correlation is a measure of statistical dependence between random variables and here we tested the dependence between GPP_{sat} and temperature and WAI jointly.

B.4 Results

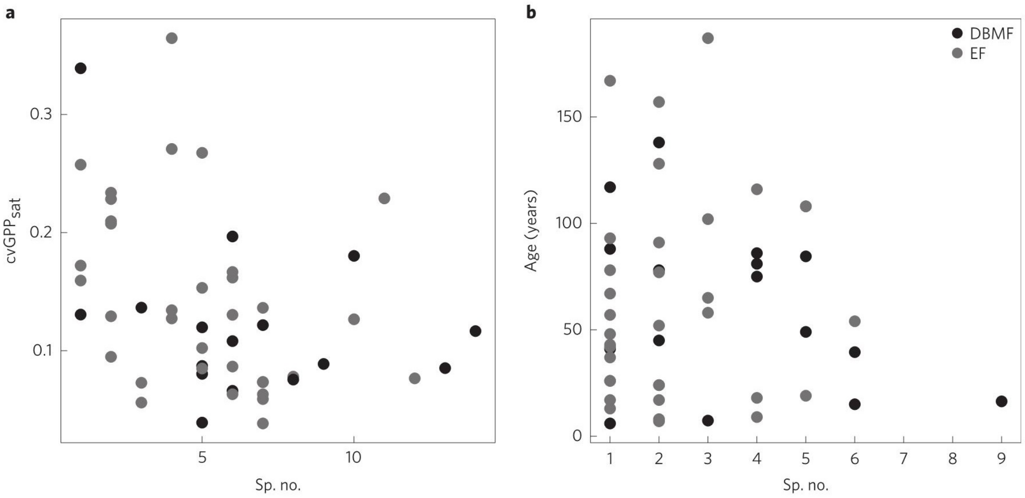

Figure B.2: Relationship of species richness with stand age and $cvGPP_{sat}$. (a) The relationship between $cvGPP_{sat}$ computed for each FLUXNET site and species richness (sp. no.) ($R^2 = 0.12$, $P = 0.01$, $n = 50$). (b) The relationship between species richness and stand age ($R^2 = 0$, $P = 0.68$, $n = 50$). DBMF are deciduous broad leaf and mixed forests ($n = 16$; black) and EF are evergreen needleleaf and broadleaf forests ($n = 34$; grey).

Results from the variable selection and relative importance methods (see Methods) conducted over the 44 sites with all variables are consistent with our hypothesis that stand age and species richness of the sites are the most important predictors of cvGPP$_{\mathrm{sat}}$, with stand age being statistically the dominant factor (Figure B.1a). We further tested the performance of a multiple linear model, where cvGPP$_{\mathrm{sat}}$ is a function of stand age and species richness, using all sites with data available for these two predictors (50 sites). The model suggests a clear relationship between cvGPP$_{\mathrm{sat}}$ and the logarithm of stand age and the species richness (Table B.2, $R^2 = 0.55$, $P < 0.0001$). Stand age, which is negatively correlated with cvGPP$_{\mathrm{sat}}$, is the most important predictor (from the 55% explained variance by both variables, the relative contribution to the explained variance by stand age and species richness is 74.5% and 25.5%, respectively; Figure B.1b and Supplementary Fig. 2). The relationship between cvGPP$_{\mathrm{sat}}$ and stand age also holds across the different forest types (ENF and DBMF) (Figure B.1a and Table B.1). Species richness has a complementary effect: for the same age class, higher values of species richness yield lower IAVs of GPP$_{\mathrm{sat}}$(Table B.2 and Figure B.1a). While species richness has a negative relation with cvGPP$_{\mathrm{sat}}$ (Figure B.2a and Table B.1), it is not correlated with stand age ($R^2 = 0$, Figure B.2b). Furthermore, Figure B.1 shows that the slope of cvGPP$_{\mathrm{sat}}$ versus stand age is similar for the two different forest types, which suggests that the relationship between cvGPP$_{\mathrm{sat}}$ and stand age is independent of forest type (Table 1). The relationship is also independent of (LAI$_{\mathrm{max}}$ of the sites (Supplementary Fig. 3). In young forests, cvGPP$_{\mathrm{sat}}$ might depend also on the expected trend in annual growth and GPP, as young stands are expected to rapidly increase their biomass and LAI in the first years of establishment (Magnani et al., 2007). Thus, young stands could have a higher variability of GPP$_{\mathrm{sat}}$ – but this does not necessarily reflect instability. To remove this potentially confounding factor, we tested whether there is a temporal trend in our data of annual GPP$_{\mathrm{sat}}$ at the sites (Methods). Using a Mann-Kendall test, we found only five sites had a significant trend, two of which were old sites (> 80 years). The results of the model selection and the relationship between cvGPP$_{\mathrm{sat}}$, stand age and species richness remains the same regardless of whether the trend in GPP$_{\mathrm{sat}}$ from these sites is removed (see Supplementary Information).

Table B.1: Summary of the linear models fitted for cvGPP$_{\mathrm{sat}}$ (the interannual variability of ecosystem photosynthetic capacity computed for each FLUXNET site) with the chosen predictors for the different groups of sites classified according to vegetation type.

PFT	R^2	$Adj.R^2$	Predictors	Coefficients	s.e.	d.f.	p
DBMF	0.65	0.60	Intercept	0.38	0.05	13	< 0.0001
			ln(Age)	- 0.06	0.01		0.0004
			Sp. no.	- 0.01	0.00		0.02
DBMF	0.46	0.42	Intercept	0.31	0.05	14	< 0.0001
			ln(Age)	- 0.05	0.01		0.004
EF	0.49	0.46	Intercept	0.38	0.04	31	< 0.0001
			ln(Age)	- 0.05	0.01		< 0.0001
			Sp. no.	- 0.02	0.007		0.02
EF	0.40	0.38	Intercept	0.35	0.05	32	< 0.0001
			ln(Age)	- 0.05	0.01		< 0.0001

PFT, plant functional types; s.e., standard error; d.f., degree of freedom; DBMF, deciduous broad leaf and mixed forests; EF, evergreen forests. ln(Age) is the natural logarithm of the average stand age, and sp. no. is the number of dominant plant species that have a cumulative abundance of 90% at the sites.

While there is a strong relationship between the annual GPP_{sat} and mean growing season temperature and WAI (Figure 3 and Supplementary Figures 4-7) across all sites, the magnitude of the IAV of GPP_{sat} is best explained by stand age differences, and not by the differences in the IAV of climate and environmental factors (that is, standard deviation of annual growing season temperature and WAI). The distance correlation coefficient between GPP_{sat} and climate variables, which can account for nonlinearity in statistical relations, is also not linked to stand age, species richness or $cvGPP_{sat}$ (Supplementary Fig. 8). Pairwise relationships between $cvGPP_{sat}$, environmental variables and ecosystem structural variables were also tested. Soil nutrient availability has no effect on the $cvGPP_{sat}$ (Supplementary Fig. 9), and neither do the other variables (Supplementary Fig. 10).

Table B.2: Comparison of different models computed using the set of predictors chosen by both stepwise model selection according to aIC and relative importance methods.

Model		R^2	Adj. R^2	Coefficients	p
$cvGPP_{sat}$ =	Intercept sp. no.	0.12	0.1	0.18 ± 0.02 -0.01 ± 0	0.01
$cvGPP_{sat}$ =	Intercept Age	0.25	0.24	0.19 ± 0.01 0 ± 0	0.0002
$cvGPP_{sat}$ =	Intercept ln(Age)	0.39	0.38	0.33 ± 0.04 -0.05 ± 0.01	< 0.0001
$cvGPP_{sat}$ =	Intercept ln(Age) sp. no.	0.55	0.53	0.39 ± 0.03 -0.05 ± 0.01 -0.02 ± 0	< 0.0001
$cvGPP_{sat}$ =	Intercept ln(Age) sp. no. ln(Age):sp. No	0.55	0.52	0.42 ± 0.06 -0.06 ± 0.01 -0.03 ± 0.02 0 ± 0	< 0.0001

$cvGPP_{sat}$ is the IAV magnitude of ecosystem photosynthetic capacity, and sp. no. is the number of dominant plant species that have a cumulative abundance of 90 % at the sites. ln(Age) is the natural logarithm of the average stand age. The number of sites is n = 50.

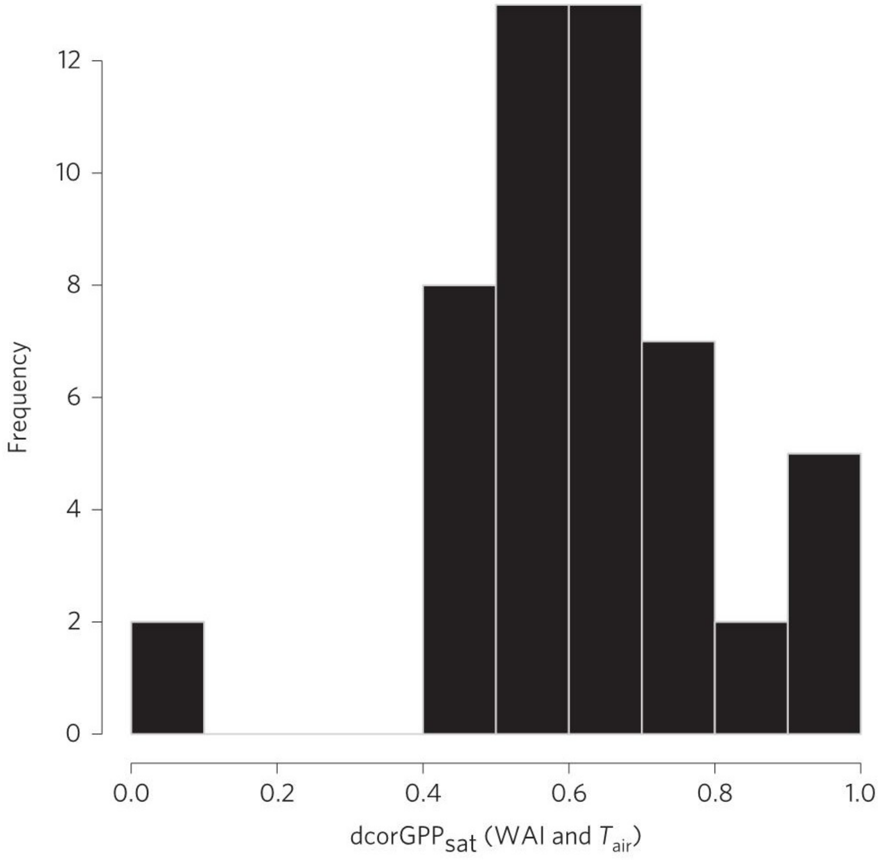

Figure B.3: Frequency distribution of the distance correlation coefficients computed between the annual ecosystem photosynthetic capacity (GPP$_{sat}$) and the environmental variables WAI and Tair ($n = 50$). WAI, average water availability index; and Tair, temperature (both during the growing season). Using the distance correlation coefficient (dcor) (Luyssaert et al., 2008), we show the strength of the correlation of GPP$_{sat}$ with WAI and Tair jointly (see the Methods).

B.5 Discussion and conclusion

Previous studies have shown that vegetation responses to climate variability can explain the IAV of ecosystem fluxes better than climate variables themselves on longer timescales (Ma et al., 2011; Richardson et al., 2007; Urbanski et al., 2007). Here we show further that the magnitude of IAV in GPP$_{sat}$ (ecosystem photosynthetic capacity) is best explained by vegetation properties of the sites. We identify a joint control of stand age and biodiversity on the magnitude of the IAV of ecosystem photosynthetic capacity (that is, cvGPP$_{sat}$). Part of the unexplained variance in cvGPP$_{sat}$ by stand age and species richness could be also associated with management and disturbances that were not included in the ancillary database of the sites, and can therefore not be formally investigated. Accurately simulating GPP in terrestrial biosphere models depends crucially on parameters related to GPP$_{sat}$ (Bonan et al., 2012). These parameters are typically assumed to be constant over time, but may vary spatially according to forest types (MEDVIGY et al., 2013). Our findings suggest that stand age and species richness should be accounted for to dynamically adjust parameters related to photosynthetic capacity.

Stand age can influence GPP_{sat} stability in different ways by enhancing soil conditions over time (for example, a thicker humus layer with favourable microbial communities, increased water storage capacity, and access to deeper water with a tap root system OHEIMB et al. 2014). Also, a forest may develop a more diverse canopy and rooting structure, allowing for more complementary use of nutrients and water. In addition, older forests are more resilient to environmental changes because with time species selection leads to a better adaptation to the environment. Site fertility can also improve with stand age, following the nutrient losses occurring during major disturbances (such as fire or harvest). In fact, the ecosystem internal cycle of macronutrients is particularly relevant (BUTTERBACH-BAHL et al., 2011; SUTTON et al., 2011) and leads to a progressive accumulation of nutrients in the living biomass with age (YANG et al., 2011).

Although species diversity is generally assumed to increase ecosystem resilience, exceptions have been reported (GROSSIORD et al., 2014c). For example, species diversity can enhance forest resistance to drought only if the system is prone to drought (GROSSIORD et al., 2014c). This is considering the gradual adaptation of the ecosystem to its environment by changing species composition to track environmental changes. Facilitation (species interactions that results in the species benefitting from each other) and complementary functioning of plant species can explain why species richness is important for ecosystem stability and how the interaction of species modulates the climate effect on ecosystem functioning (DEL RÍO et al., 2014). In addition, mixed forests are able to buffer the effect of climate IAV through competition and facilitation in normal and stressful years, respectively (DEL RÍO et al., 2014). Facilitation and complementary effects are clearly related to the functional richness of the species pool (that is, species with different functional traits), which is linked to stand age as shown by a regional study in the tropics (BECKNELL et al., 2014). Diverse ecosystems with a higher number of plant species respond less dramatically in their functioning (compared to ecosystems with single or few species) to climate and environmental stresses.

The Earth's forest cover is essential to remove CO_2 from the atmosphere, and afforestation is important to compensate for forest loss due to land use changes (such as agriculture). While young forests established on former agricultural lands, or burned and harvested forests for several years cannot compensate for the initial carbon loss nor contribute to CO_2 sequestration from the atmosphere, old forest stands retain their capacity to sequester CO_2 for long periods (COURSOLLE et al., 2012; LUYSSAERT et al., 2008). We show that the photosynthetic capacity and therefore the gross primary production of old growth forests are more resilient to climate variability than young forests. In addition, our study suggests that species-rich forest stands offer a larger potential for maintaining a stable photosynthetic capacity across time than species-poorer stands. Therefore, preserving our current forest (with old forests covering 15% of Earth's surface (LUYSSAERT et al., 2008)) and their species diversity may attenuate the annual fluctuations of global forest-atmosphere CO_2 exchange.

B.6 Acknowledgements

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B.7 Author contributions

T.M. wrote the manuscript and performed the analysis. T.M., M.M., M.D.M. and M.R. designed the study. M.M., M.D.M., M.R., J.K., I.J., A.K., A.C., C.W., T.A.B. and A.V. discussed the interpretation of the results. M.M., M.D.M., M.R., J.K., C.W., T.A.B., A.C.,A.K., D.L. and O.R. contributed significantly to editing the paper. S.R., R.T. and D.G.contributed to editing the paper. T.A.B., I.J., A.K., D.L., O.R., A.V., S.R., A.C., H.K. and T.F. contributed data.

B.8 Additional information

B.8.1 Code availability

The analysis was conducted in R version 3.2.4 and the script of the analysis is available within the supplementary files of the paper.

B.8.2 Data availability

The authors declare that the data supporting the findings of this study are available within the Supplementary Information.

B.8.3 Supplementary information

is available for this paper `https://www.nature.com/articles/s41559-016-0048`.

B.8.4 Reprints and permissions information

is available at www.nature.com/reprints.

B.8.5 Correspondence and requests for materials

should be addressed to T.M.

B.8.6 How to cite this article

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B.9 Competing interests

The authors declare no competing financial interests.

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Publications

2019	Mund, M., Herbst, M., Knohl, A., Matthäus, B., Schumacher, J., Schall, P., Siebicke, L., **Tamrakar, R.**, and Ammer, C. (2019): 'It is not just a 'trade-off' – indications for sink- and source-limitation to vegetative and regenerative growth in an old-growth beech forest'. *New Phytologist*
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