Key ecological research questions for Central European forests

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Abstract

Forests are under pressure from accelerating global change. To cope with the multiple challenges related to global change but also to further improve forest management we need a better understanding of (1) the linkages between drivers of ecosystem change and the state and management of forest ecosystems as well as their capacity to adapt to ongoing global environmental changes, and (2) the interrelationships within and between the components of forest ecosystems. To address the resulting challenges for the state of forest ecosystems in Central Europe, we suggest 45 questions for future ecological research. We define forest ecology as studies on the abiotic and biotic components of forest ecosystems and their interactions on varying spatial and temporal scales. Our questions cover five thematic fields and correspond to the criteria selected for describing the state of Europe's forests by policy makers, i.e. biogeochemical cycling, mortality and disturbances, productivity, biodiversity and biotic interactions, and regulation and protection. We conclude that an improved mechanistic understanding of forest ecosystems is essential for the further development of ecosystem-oriented multifunctional forest management in the face of accelerating global change.

Keywords: Forest Ecology, productivity, mortality, protection, biodiversity, management, conservation

Introduction

Globally, forests are of crucial importance for climate, biodiversity, and human well-being (Costanza, d'Arge, De Groot, Farber, Grasso et al. 1997). However, forests are under pressure from accelerating global change, including climate change, land-use change and land-use intensification, which affect forest structure, forest functioning, and biodiversity (Bonan, 2008; Sala, Chapin, Armesto, Berlow, Bloomfield et al. 2000). In particular, a further increase in temperature and disturbance probability (Rahmstorf & Coumou 2011, Thom & Seidl 2016), a projected decrease in summer precipitation, a possible reduction of areas used for food production and a corresponding increase in area used for biomass production are expected for the coming decades (Schröter, Cramer, Leemans, Prentice, Araújo et al. 2005). It is widely accepted that most goods and services provided by Europe's forests will be impacted by these changes, but not much is known to what extent this will happen and how to quantitatively assess the impact of global change (Lindner, Maroschek, Netherer, Kremer, Barbati, et al. 2010). An improved knowledge of the linkages between the drivers of ecosystem change and the state of nature, the delivery of ecosystem services, and human well-being is of vital importance when managing ecosystems for future generations (Balmford & Bond, 2005). Revealing these linkages, however, is a difficult task: The high variety of forest ecosystems, the heterogeneity in site conditions even within a specific forest type, and the mutual interactions between the different species in a specific ecosystem require consideration. Consequently, regional to local ecological knowledge is needed in order to "influence land-use decisions on a scale at which they are typically made" (Kremen, 2005). This is all the more important when ecosystem services come into play.

Here we are focusing on the temperate nemoral forests of Central Europe, which are particular in many ways. First, under the current climatic conditions one single tree species (*Fagus sylvatica*) would most likely achieve dominance on a wide range of sites across Central Europe (Bohn, Gollub & Hettwer 2000; Giesecke, Hickler, Kunkel, Sykes & Bradshaw 2007; Leuschner & Ellenberg, 2017).

Second, in Central Europe humans have started to influence the distribution, structure and composition of forests more than 5000 years ago (Schulze, Aas, Grimm, Gossner, Walentowski et al. 2016). This has led to a regionally and temporally fluctuating degree of deforestation particularly during medieval times, with forest cover declining until the early 19th century in many regions (Wedekind 1844; Williams 2000; Kaplan, Krumhardt & Zimmermann 2009; Radkau 2012). In the last 250 years, Central European temperate forests have been restored but also managed intensively. They are, with very few exceptions, still under management today and affected by the legacies of postglacial recolonization, forest management history, and/or agricultural aftereffects in the case of afforestations (Glatzel, 1991; Dupouey, Dambrine, Laffite & Moares, 2002; Oheimb, Härdtle, Naumann, Westphal, Assmann et al. 2008; Bebi, Seidl, Motta, Fuhr, Firm et al. 2017; Jiménez-Alfaro, Girardello, Chytrý, Svenning, Willner et al. 2018).

Third, due to the long history of land use, old-growth forests are largely absent in Central Europe. Additionally, the proportion of fast growing conifers has been strongly increased by modern forestry since the 19th century. However, high-intensity industrial plantation forests (i.e. even-aged stands composed of fast growing and often non-native tree species in which trees are harvested in rotation cycles < 50 years) remain widely absent in Central Europe. After 150 years of favouring conifers at the expense of broadleaves and applying an even-aged management system (partly adopted from agriculture), forest management has shifted during recent decades: In large parts of Central Europe forestry today aims at promoting mixed and structured stands composed of several age/ size cohorts, and the dominating regeneration method has changed from planting to natural regeneration in many places (Bürgi & Schuler, 2003; Knoke, Ammer, Stimm & Mosandl, 2008).

Fourth, forest research including long-term monitoring has a long tradition in Central Europe. For example, growth and yield plots still under observation date back to 1870 (Pretzsch, Biber, Schütze, Uhl & Rötzer 2014). Another example is the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), which was launched more than 30 years ago and assesses a broad range of environmental conditions (Sanders, Michel & Ferretti al. 2016). Due to an extensive history of studying different taxa by naturalists, taxonomists, amateur botanists and zoologists, knowledge on the ecology of forest-dwelling plant and animal species may be among the best in the world (Ogilvie, 2008).

Finally, the majority of Central European forests are managed for multiple ecosystem services, addressing the diverging interests and societal demands of the large human population in the area. This does neither mean that all ecosystem services (e.g. timber production, soil protection, provision of drinking water and habitat, recreation, biodiversity conservation, etc.) are provided by each stand at the same time (Ammer & Puettmann, 2009), nor that ecosystem functions are necessarily positively correlated (Byrnes, Lefcheck, Gamfeldt, Griffin, Isbell et al. 2014), but management in Central European forests usually goes beyond maximising a single ecosystem service.

Management for multifunctionality is not straightforward due to many trade-offs between different goals (e. g. Sing, Metzger, Paterson & Ray 2018). It is further challenged by the impacts of global change, such as climate change, N-deposition, invasive species, changing biotic and abiotic disturbances, homogenization and/or intensification of management practices to name just a few. These challenges affect the state of Central European forests, and subsequently the sustainable provisioning of ecosystem goods and services (Wagner, Nocentini, Huth, & Hoogstra-Klein, 2014). In order to regularly assess the state of European forests and the development towards Sustainable Forest Management (SFM), the Ministerial Conference for the Protection of Forests in Europe (Forest Europe) has developed a set of criteria and indicators (Forest Europe, 2015). These criteria and the related indicators include (i) the maintenance and appropriate enhancement of forest resources and their contribution to global carbon cycles, (ii) the maintenance of forest ecosystem health and vitality, (iii) the maintenance and encouragement of productive functions of forests, (iv) the maintenance, conservation and appropriate enhancement of biological diversity in forest ecosystems, (v) the maintenance and appropriate enhancement of protective functions in forest management (notably soil and water), and (vi) the maintenance of other socio-economic functions and conditions (Forest Europe 2015). While these criteria help to characterize the state of European forests and its development over time, they cannot answer underlying questions of forest ecosystem functioning, nor can they identify the causes for changes in forest ecosystem properties. Addressing these questions is the realm of forest ecological research, which we here define as studies on the abiotic and biotic components of forest ecosystems and their interactions on varying spatial and temporal scales. Via improving the knowledge on ecosystem processes and functions, forest ecological research provides the fundamental basis for ecosystem-oriented forest management and nature conservation. Thereby forest history and, hence, legacy effects need to be taken into account.

In a recent review, Mori, Lertzman, Gustafsson & Cadotte (2017) have outlined a forest research agenda focusing on the relationships between biodiversity, ecosystem functioning and ecosystem services. Here we extend the scope of this agenda beyond biodiversity relationships, addressing important attributes of five out of the six criteria describing the state of Europe's forests as the fundamental basis for forest policy in Europe. The criteria "maintenance of other socio-economic functions and conditions" does not fall within our definition of forest ecological research and is thus not addressed here. The objective of this opinion paper is to present important questions related to the ecology of Central European forests. We aim to stimulate further research and highlight questions which, once answered, will improve our knowledge of the functioning of Central European forest ecosystems. Based on such an improved mechanistic understanding, ecosystem-oriented forest management and nature conservation strategies may be developed. Although focusing on Central European forests, we believe that the utility of addressing these questions goes considerably beyond our focal systems and will also contribute to our understanding of many other forest types and forest landscapes. Like previous similar papers (Sutherland, Freckleton, Godfray, Beissinger, Benton et al. 2013) we make no claim of completeness. Also, the selection of questions was not generated by majority vote of all Central European forest ecologists, and other consortia certainly would have come up with different questions. Here, our search for important research questions was based on a two-step approach (Fig. 1). First, researchers of the working group "Forest ecology" of the Ecological Society of Germany, Austria and Switzerland (GfÖ) met for a two-day workshop to identify key questions in forest ecological science. During this workshop around 75 questions of varying levels of abstraction were identified, and subsequently condensed to around 40 questions. Second, during the revision process a smaller group of forest ecologists amended, restructured, refocused and harmonised the questions. Through this two-stage process, 45 research questions were identified and grouped along the main criteria selected to describe the state of Europe's forests by policy makers (Forest Europe 2015). The questions are listed at the end of each respective chapter.

Biogeochemical cycling

Biochemical cycles and their dependency on tree species composition, site conditions and forest developmental stage have been a major subject of forest ecology for many years (Schulze 2000, Galloway, Dentener, Capone, Boyer, Howarth et al. 2004, Bredemeier, Cohen, Godbold, Lode, Pichler et al. 2011). However, as in many other parts of the world, water, nutrient, and carbon cycles of European forests have been strongly influenced by anthropogenic activities in the past (e.g. forest grazing, litter raking, large-scale clear cutting, acidic deposition or conversion of species composition towards conifers, nitrogen deposition, etc.; Leuschner & Ellenberg 2017). Consequently, understanding the current situation of Central European forests and modelling the future development of their biogeochemical cycles has to consider strong land-use legacies (Bebi, Seidl, Motta, Fuhr, Firm et al. 2017). In addition, climate change in combination with various other man-made modifications of the environment, e. g. changes in nitrogen cycling (Erisman, Galloway, Seitzinger, Bleeker, Dise et al. 2013) or the introduction of exotic species, require basic and applied research concerning their consequences for forest functioning **(Question 1)**. Yet, challenges for research on forest functioning in general and on biochemical cycling in particular do not only result from the speed and uncertainty of climate change or the multitude of potential interactions across temporal and spatial scales, but also from our incomplete understanding of basic, ecophysiological processes and how they affect ecosystem properties. Thus, we need a better understanding of the importance of intraspecific variation in ecophysiological and anatomic tree traits. Such an improved knowledge base is particularly relevant in the contexts of adaptation to climate change and the forest carbon cycle **(Q 2)**. It was, for example, shown that genetic differences in drought resistance exist and that tree species known as drought-sensitive have developed strategies to adapt their hydraulic system (Meier & Leuschner 2008; Schuldt, Knutzen, Delzon, Jansen, Muller-Haubold et al. 2016; Bolte, Czajkowski, Cocozza, Tognetti, de Miguel et al. 2016; Stojnić, Suchocka, Benito-Garzón, Torres-Ruiz, Cochard et al. 2018; Heer, Behringer, Piermattei, Bässler, Brandl et al. 2018). Such knowledge is urgently needed to further develop adaptive management strategies to counter destabilizing effects on forest ecosystems (Ammer 2017; Bolte, Ammer, Löf, Madsen, Nabuurs et al*.,* 2009; Keenan, 2015).

We have gained important insights into univariate impacts of many global change drivers on ecosystem processes in forests (e.g. warming, drought, N deposition, ozone, exotic tree species, pests and pathogens, and management), but we still know little about how they act collectively (Seidl, Thom, Kautz, Martin-Nenito, Peltoniemi et al. 2017; Yue, Fornara, Yang, Peng, Li et al. 2017). The interaction of combined effects could be buffering (Leuzinger, Luo, Beier, Dieleman, Vicca et al. 2011), additive (Yue, Fornara, Yang, Peng, Li et al. 2017) or multiplicative (Dieleman, Vicca, Dijkstra, Hagedorn, Hovenden et al. 2012). Interactions of the various environmental factors need to be investigated across spatio-temporal scales to reveal non-linear system behaviour and to identify tipping points leading to drastic changes of a system, including the loss of resilience (Reyer, Brouwers, Rammig, Brook, Epila et al. 2015; Scheffer, Carpenter, Foley, Folke & Walker 2001; van Nes, Arani, Staal, van der Bolt, Flores et al. 2016; ; Heer, Behringer, Piermattei, Bässler, Brandl et al. 2018) **(Q 3)**.

Stands dominated by one or two tree species are characteristic for large forested areas in Central Europe. Forests consisting of several tree species might generally be more resistant and resilient to disturbances (Pedro, Rammer, & Seidl 2015; Brockerhoff, Barbaro, Castagneyrol, Forrester, Gardiner et al. 2017). However, mixing tree species also has numerous consequences for biogeochemistry (Pretzsch, Forrester & Bauhus 2017; Scherer-Lorenzen 2014) via several potential mechanisms. These include spatial (e.g. Meißner, Köhler, Schwendenmann & Hölscher 2012) and temporal (Jacob, Leuschner & Thomas 2010, Silvertown, Araya & Gowing 2015) differences in the resource exploitation of tree species, redistribution of nutrients and carbon compounds via leaf litter (e.g., Guckland, Jacob, Flessa, Thomas & Leuschner 2009) or mycorrhiza (Klein, Siegwolf & Körner 2016) and decomposition of organic matter (e.g. Jacob, Viedenz, Polle & Thomas 2010).

However, effects of interspecific tree competition on important functional traits such as rooting patterns and water uptake, remain insufficiently understood (Lei, Scherer-Lorenzen & Bauhus 2012; Meinzer, Warren & Brooks 2007; Meißner, Köhler, Schwendenmann & Hölscher 2012; Thomas, Bögelein & Werner 2015). For example, differentiation of rooting systems may foster complementary water use via phenomena such as hydraulic lift and hydraulic redistribution (Zapater, Hossann, Bréda, Bréchet, Bonal et al. 2011; Pretzsch, Schütze & Uhl 2013), improving water availability to shallow-rooting species. However, increased belowground competition could also increase drought stress for shallow-rooted species, or may diminish ground water recharge (Grossiord, Granier, Ratcliffe, Bouriaud, Bruelheide et al. 2014). Furthermore, it remains unclear whether responses to climatic conditions differ in native and introduced tree species populations (Chakraborty, Wang, Andre, Konnert, Lexer et al., 2016) **(Q 4)**. In addition, plant-plant and plant-animal interactions and their effects on the carbon and nitrogen cycling of forest ecosystems have recently received increasing attention (Klein, Siegwolf & Körner 2016; Zieger, Holczinger, Sommer, Rath, Kuzyakov et al. 2017), but are still insufficiently understood **(Q 5)**.

The functioning of forest ecosystems is strongly related to the decomposition and mineralisation of organic matter during biogeochemical cycling. While the principal factors involved in the decomposition of organic matter and their effects on decomposition rates are well known (Prescott 2010), large knowledge gaps still exist regarding the direct and indirect effects of climate change on the decay of organic matter (Suseela & Tharayil 2018), on the complex interactions between bacteria and fungi in the decomposition process (Bani, Pioli, Ventura, Panzacchi, Borruso et al. 2018), on the role of arthropods for nutrient cycling and forest productivity (Ulyshen 2015; Ulyshen 2016), the interaction of parasites, leaf chemistry, herbivory and decomposition (Künkler, Brandl & Brändle 2013), and on the effects of the ongoing nitrogen deposition on the mineralisation and storage of carbon compounds in the soil (Averill & Waring 2018) **(Q 6)**. In this context, it is also of interest to know what role harvest residuals play for the carbon dynamics of mineral soils. Furthermore, there are large areas of forests on organic soils in Europe, many of which have been drained and now emit large amounts of greenhouse gases (>144,000 km² of peatland drained and currently used in production forestry across Europe; Joosten & Tanneberger 2017). Strategies for managing these forests require basic understanding of the processes that can restore carbon accumulation. Simply rewetting is not enough as it can cause a complete die-back of trees and create shallow lakes which emit high amounts of methane, rather than resulting in productive forests that sequester carbon **(Q 7)**.

Many forest stands in Central-Europe are situated on hillslopes or in mountainous terrain. However, in the past most studies on biogeochemical processes have been conducted at homogeneous and flat sites. Matter and energy fluxes between soil, vegetation and the atmosphere may well differ on slopes (Matyssek, Wieser, Patzner, Blaschke & Häberle 2009). The differentiation of forest stands in heterogeneous landscapes is thus important, and can be addressed through a combination of terrestrial and air-born approaches (Stoffels, Hill, Sachtleber, Mader, Buddenbaum et al. 2015). Remote sensing, monitoring of C-flow between atmosphere and ecosystem (Lyssaert, Ciais, Piao, Schulze, Jung et al. 2010) and ecosystem modelling were successfully used to study terrestrial carbon cycling. These approaches combine spatially continuous information (remote sensing) and model carbon cycling over various temporal scales (Turner, Ollinger, & Kimball 2004). The integration of structural data with ecosystem process models and climate data may pave the way towards a regional assessment of carbon fluxes and the analysis of the underlying processes (Seidl, Spies, Rammer, Steel, Pabst et al. 2012; Turner, Ollinger, & Kimball 2004) **(Q 8)**. At a smaller scale, the importance of heterogeneity within forest stands for biochemical processes (e.g. McLaughlin, Ackerly, Klos, Natali, Dawson et al. 2017) needs to be more thoroughly addressed in forest ecosystem research **(Q 9)**.

Questions

Q 1 In which direction and how rapidly will biogeochemical cycling change under the current and future rates of climate change and eutrophication?

Q 2 How large is the morphological and physiological plasticity of tree species and provenances in the face of climate change, eutrophication and their interaction?

Q 3 How large is the combined effect of climatic stressors on the biogeochemical cycling in forest ecosystems?

Q 4 Are biogeochemical cycles in diverse forests more resistant and resilient towards climatic changes and eutrophication?

Q 5 How do plant-plant and plant-animal interactions influence biogeochemical cycling in forest ecosystems?

Q 6 How do climate change and eutrophication influence the interaction of microorganisms and soil arthropods and their role in biogeochemical cycling?

Q 7 What are the main drivers of the forest soil carbon balance, what is the role of harvest residuals in managed forests on organic soils, and which role do soil organisms play for storing and stabilizing carbon in soils?

Q 8 How can we reliably determine fluxes of matter and energy in spatially heterogeneous forested landscapes?

Q 9 To what extent does small-scale spatial heterogeneity impact biogeochemical cycling in forest ecosystems?

Mortality and disturbances

Due to their complex architecture both above- and belowground, the physical structures in forests are unique among terrestrial ecosystems. Consequently, forest structure is an important focus of research, not least because of the strong relationship of forest structures to the functions and services forests provide (e.g. Lindbladh, Lindström, Hedwall & Felton 2017; Lindenmayer & Franklin 1997). As forest structure can be actively modified through management interventions, it is also a central element of forest management (Motta & Lingua 2005; Bauhus, van der Meer & Kanninen 2010; Parviainen, Bücking, Vandekerkhove, Schuck, & Päivinen 2000; Messier, Puettmann, Chazdon, Andersson, Angers et al., 2015; Schall, Schulze, Fischer, Ayasse, & Ammer 2018). A key process affecting the structure and demography of forests apart from forest management is natural tree mortality. Tree mortality is a complex process and the factors leading to the death of a tree can either come in sudden events, called disturbances, or can unfold over decades, e.g., by fungal infestation (Holzwarth, Kahl, Bauhus & Wirth 2013; Hartmann, Schuldt, Sanders, Macinnis-Ng, Boehmer et al. 2018).

The ultimate reason for death of individual trees – besides mechanical damage – remains unclear (Schweingruber & Wirth, 2009) **(Q 10)**. For example, there is no consensus as to whether cavitation and conductivity loss of the xylem or carbon starvation (or both) cause tree mortality under drought conditions (Sevanto, McDowell, Dickman, Pangle & Pockman 2014). Furthermore, ageing in plants differs from animals especially due to their high degree of meristem integrity (Thomas, 2013; Sarkar, Schmid-Siegert, Iseli, Calderon, Gouhier-Darimont et al., 2017). An improved mechanistic understanding of the maximum attainable age of trees is needed, as it also has implications for the provisioning of ecosystem services. Old-growth forests constitute important carbon stores and continue to take up carbon (Stephenson, Das, Condit, Russo, Baker et al., 2014), but the longevity of trees and their maximum growth rates are inversely related (Bugmann & Bigler, 2011). In addition, the carbon allocation within trees and their response to external drivers change with tree age (Genet, Bréda, & Dufrêne 2010) (**Q 11**). A better understanding of these processes is of high importance for making robust projections of future forest ecosystem dynamics (Bircher, Cailleret, & Bugmann, 2015).

As tree mortality is a natural process in forests, dead trees are a typical element of healthy ecosystems. However, mortality is also highly sensitive to many drivers of global change (e.g., changes in climate, changes in forest structure and composition), making it an important topic of research for current forest ecology, also in ecosystems strongly altered by humans (Hartmann, Adams, Anderegg, Jansen, & Zeppel 2015; Neumann, Mues, Moreno, Hasenauer & Seidl, 2017). The signal of climate change, for instance, differs among seasons. It also influences the length of the growing season (Menzel & Fabian 1999). Plant responses to the environmental conditions of a specific season, however, can have implications for other seasons such as insufficient frost hardening triggered by warm autumn temperatures, potentially reducing winter frost tolerance (Malyshev, Henry, Bolte, Arfin Khan &

Kreyling, 2017). Paradoxically, this can lead to increased mortality from frost despite the general warming trend (Augspurger 2013; Fisichelli, Vor, & Ammer, 2014) **(Q 12)**.

Disturbance can be defined as any discrete event through which live plant biomass is lost (Begon, Harper & Townsend, 1996). This includes both abiotic (especially important in the temperate forests of Europe are windstorm, fire, snow avalanches) and biotic events (such as pests including insect outbreaks and diseases). The temporal duration of these events is short in relation to the length of the processes involved (i.e., the life-span of a tree) and they are clearly spatially differentiated from undisturbed areas (Fischer, Marshall, & Camp, 2013). Disturbances can vary from small-scale events resulting in the loss of patches of trees up to landscape-scale events. Although much is known about stand properties and environmental conditions that increase the susceptibility to disturbances, we still lack an understanding of the natural sizes and frequencies of these events in Central Europe and their impact on forest structure and composition (Seymour, White & deMaynadier 2002; Nagel, Svoboda & Kobal 2014; Svoboda, Janda, Bače, Fraver, Nagel et al. 2014¸ Janda, Trotsiuk, Mikoláš, Bače, Nagel et al. 2017) **(Q 13)**.

Currently, harvesting is the most important and pervasive disturbance in Europe's temperate forests. Because of the forest history of the region (Parviainen, 2005) we largely lack areas which can serve as reference for forest structures and natural disturbance dynamics without human impact. Remaining old-growth forests, such as those of the mountain regions of Central and Eastern Europe, are important sources for studying the natural disturbance regimes of the past (Svoboda, Janda, Bače, Fraver, Nagel et al. 2014; Čada, Morrissey, Michalová, Bače, Janda, et. al. 2016; Schurman, Trotsiuk, Bače, Čada, Fraver et al. 2018). Recent findings suggest, for instance, that intermediate wind disturbances occurred at time intervals similar to or less than the life expectancy of most canopy tree species in Central Europe, and may play a more important role in forest dynamics than previously thought (Nagel & Diaci, 2006; see also Jaloviar, Saniga, Kucbel, Pittner, Vencurik et al., 2017; Petritan, Bouriaud, Frank, & Petritan 2017). How the historic range of variability compares to the current (and future) disturbance regime is an important remaining question for the temperate forest ecosystems of Europe (Kulakowski, Seidl, Holeksa, Kuuluvainen, Nagel et al. 2017) **(Q 14)**. This question is particularly important in the context of climate-mediated changes in disturbance regimes (Seidl, Thom, Kautz, Martin-Nenito, Peltoniemi et al. 2017), as the assessment of any change process requires a robust baseline.

In addition to putting disturbance regimes in their historical context, it is of high relevance to better understand the impacts of disturbances. Remote sensing allows the assessment of variability in forest structure (size differentiation) or the estimation of other biophysical structures such as canopy rugosity (Bolton, Coops, Hermosilla, Wulder, & White, 2017; Clark & Clark, 2000; Simard, Pinto, Fisher & Baccini,

2011) and their effects on forest functioning (e.g. Coops, Hermosilla, Hilker & Black, 2017) in response to different disturbances (e.g. White, Wulder, Hermosilla, Coops & Hobart, 2017) **(Q 15)**.

Tree mortality in the future will differ from the past; many studies suggest a potential increase in tree mortality for the coming decades (Trumbore, Brando & Hartmann, 2016; Seidl, Thom, Kautz, Martin-Nenito, Peltoniemi et al. 2017). Climate change is, for instance, expected to amplify drought in many forest ecosystems (Allen, Breshears & McDowell, 2015). In addition disturbances from wind, wildfire, and insects are expected to increase in the temperate forest ecosystems of Europe (Seidl, Schelhaas, Rammer & Verkerk, 2014). Thus, climate change will strongly alter tree mortality regimes. Improved simulation models are needed to make more robust projections on potential future trajectories of ecosystems under emerging future disturbance regimes. In addition to changes in native disturbance agents novel agents of tree death, such as invasive alien pests and pathogens, are increasingly introduced by global trade. In temperate North-America exotic insect pests and pathogens are estimated to be the most serious threat to forest health and ecosystem processes (Lovett et al. 2006). For Europe's temperate forests, comparable estimates are widely lacking, yet examples such as Dutch elm disease (Karnosky 1979) and the dieback of European ash (Pautasso, Aas,Queloz, & Holdenrieder, 2013) illustrate the severity of the threat. In addition to alien pests and pathogens, also alien plant species can be a threat to the health and integrity of forest ecosystems. In North-America, for instance, Ehrenfeld, Kourtev and Huang (2001) have shown that invasive plant species are able to change soil functions. In this particular case invasive plant species seem to be driven by invasive earthworms (Nuzzo, Maerz, & Blossey, 2009). Furthermore, the interaction between invasive species and global warming is likely to further aggravate the issue (Seidl, Klonner, Rammer, Essl, Moreno et al. 2018) and impact abiotic and biotic ecosystem properties (Eisenhauer, Fisichelli, Frelich, & Reich 2012). A better understanding of the emerging future forest mortality regimes (consisting of both, native and alien agents) is needed to assess potential consequences on ecosystem structure and functioning **(Q 16).**

Questions

Q 10 Why does a tree die?

Q 11 Which traits are conferring longevity, and how is longevity modulated by environmental factors?

Q 12 How do trees respond to changes in seasonality?

Q 13 At which intervals do small and large-scale disturbances occur naturally in the forest ecosystems of Central Europe, and which pattern of forest succession do they create at the landscape scale?

Q 14 How do the current and projected future disturbance regimes (and the ecosystem structures emerging from them) compare to the historical range of variability?

Q 15 What is the effect of different mortality patterns and processes on ecosystem functioning?

Q 16 What future mortality regimes are emerging from climate change and the introduction of alien species?

Productivity

Forests play an important role in providing ecosystem services such as wood production. Although forest productivity increased during the last century in Central European forests (Pretzsch, Biber, Schütze, Uhl & Rötzer, 2014), ongoing global environmental changes (e.g. climate change and anthropogenic nitrogen deposition) can impose significant variation in wood production (Lindner, Maroschek, Netherer, Kremer, Barbati et al., 2010). Numerous studies have demonstrated that increasing temperatures and altered precipitation regimes can lead to growth decline or forest dieback across the globe (e.g. Allen, Macalady, Chenchouni, Bachelet, McDowell et al., 2010; O'Brien, Engelbrecht, Joswig, Pereyra, Schuldt et al., 2017). However, the co-occurring effects between climate extremes and nitrogen deposition remain poorly understood (Lindenmayer, Likensa, Krebs, & Hobbs, 2010; Greaver, Clark, Compton, Vallano, Talhelm et al., 2016). For example, recent work showed that climate-induced growth decline is amplified by nitrogen fertilization (Dziedek, Härdtle, von Oheimb, & Fichtner, 2016; Braun, Schindler & Rihm, 2017; Hess, Niemeyer, Fichtner, Jansen, Kunz et al. 2018). According to the 'Optimal Partitioning Theory', plants should allocate carbon to the organ acquiring the most limiting resource (Shipley & Meziane, 2002; McCarthy & Enquist, 2007). Thus, an improved understanding of processes including drought-induced shifts in above- and belowground allocation patterns and nutrient cycling will improve our ability to predict changes in forest productivity **(Q 17, Q 18)**.

In addition to the physiological response of trees (see also **Q 2**), forest structure and tree species composition have been identified as important factors in determining how forest productivity will respond to climate change (Coomes, Flores, Holdaway, Jucker, Lines et al., 2014; Ruiz-Benito, Madrigal-González, Ratcliffe, Coomes, Kändler et al., 2014). The structural characteristics of a forest depend on a variety of factors such as natural disturbances, climate, stand development stage, species composition and forest management (e.g. Messier, Puettmann, Chazdon, Andersson, Angers et al., 2015; Bebi, Seidl, Motta, Fuhr, Firm et al., 2017). For example, structural attributes such as stand basal area, leaf area index (LAI) or canopy space filling are important attributes of forest productivity (Reich 2012; Juchheim, Ammer, Schall, & Seidel, 2017) and closely linked to resource availability (e.g. soil moisture; Gebhardt, Häberle, Matyssek, Schulz & Ammer, 2014). It may be conceivable that belowground complementarity leads to higher aboveground biomass, which in turn could improve light interception (Niklaus, Baruffol, He, Ma, & Schmid 2017; Ammer 2018). However, it remains unclear to what extent structurally diverse forests shape resource availability and forest functions under changing climatic conditions **(Q 19)**.

There is increasing evidence that productivity is often positively related to diversity in tree morphology, species or functional traits (e.g. Paquette & Messier 2011; Zhang, Chen, & Reich, 2012; Dănescu, Albrecht & Bauhus, 2016; Liang, Crowther, Picard, Wiser, Zhou et al. 2016). Several mechanisms have been proposed for the observed diversity-productivity relationships (for reviews see Scherer-Lorenzen 2014, Forrester & Bauhus 2016, Grossman, Vanhellemont, Barsoum, Bauhus, Bruelheide et al. 2018; Ammer 2018), and positive net diversity effects are often summarized as 'complementarity effects' (Forrester & Bauhus 2016). Such effects can be attributed to niche partitioning, which can lead to competitive reduction, and facilitation (Grossman, Vanhellemont, Barsoum, Bauhus, Bruelheide et al. 2018). For example, by disentangling tree-tree interactions recent work provided evidence that competitive reduction and facilitation are critically determined by the functional traits of the target tree (Fichtner, Härdtle, Li, Bruelheide, Kunz, & von Oheimb 2017). However, it remains largely unclear whether positive diversity effects are mainly driven by competitive reduction or facilitation, what role functional diversity plays **(Q 20)**, and how productivity patterns change with stand development **(Q 21)**. Maintaining structurally complex and functionally diverse forests also seems to be a promising approach to mitigate the impact of climate change on forest productivity. Although tree species richness has been shown to positively affect forest productivity at the global scale (Liang, Crowther, Picard, Wiser, Zhou et al., 2016), we still largely lack an integrated understanding of how tree diversity effects on productivity will vary with climate (but see Jucker, Avăcăriței, Bărnoaiea, Duduman, Bouriaud et al., 2016; Paquette, Vayreda, Coll, Messier, & Retana, 2017; Ruiz-Benito, Ratcliffe, Jump, Gómez-Aparicio, Madrigal-González et al., 2017). For example, we do not know under which conditions climate change will shift the existing species interactions in forest ecosystems from complementarity effects *sensu* Loreau (2000) towards systems where the selection effect prevails, or vice versa (Ammer 2018) **(Q 22)**. As both the diversity of forest structure and composition critically depend on forest management, mixing tree species and promoting structurally diverse stands are important measures for mitigating climate change effects on forest productivity (Ammer, 2017). Moreover, 'active adaptation measures' include the introduction of highly productive and drought-tolerant non-native tree species such as Douglas-fir (*Pseudotsuga menziesii*; Spellmann, Weller, Brang, Michiels, & Bolte, 2015) but it remains unclear whether climate responses differ in native and introduced populations (Chakraborty, Wang, Andre, Konnert, Lexer et al., 2016).

Legacy effects of land-use have been shown to determine nutrient cycling in forests due to altered soil microbial communities (Fraterrigo, Balser & Turner, 2006; Fichtner, von Oheimb, Härdtle, Wilken & Gutknecht, 2014). Accordingly, recent studies have stressed the importance of land-use legacies on the response of forests to global environmental change (Johnstone, Allen, Franklin, Frelich, Harvey et al., 2016; Perring, De Frenne, Baeten, Maes, Depauw et al., 2016), but empirical evidence remains limited (but see Mausolf, Härdtle, Jansen, Delory, Hertel et al. 2018) **(Q 23)**. Improving our understanding of how tree diversity affects forest productivity and of how drivers of global environmental change interact with forest structure, tree diversity and legacy effects are therefore vital for assessing the future trajectories of forest productivity.

Questions

Q 17 How important are weather patterns and climatic extremes for the productivity of trees?

Q 18 To what extend do climatic changes affect above- and belowground biomass allocation patterns in forest stands?

Q 19 How is structural diversity linked to resource availability and forest productivity?

Q 20 Which functional traits are key to the diversity-productivity relationship?

Q 21 How does the diversity-productivity relationship vary with stand development and tree ontogeny?

Q 22 Can climate change shift diversity-productivity relationships from being dominated by complementarity effects to selection effects or vice versa?

Q 23 How do drivers of global change interact with land-use legacies to shape forest productivity?

Biodiversity and biotic interactions

Forests comprise a large proportion of Central Europe's biodiversity and its protection is an important objective in forest policy and management (Forest Europe 2015). However, it needs to be considered that the current state of forest biodiversity in Central Europe is a result of interacting intrinsic dynamics and human land-use (Kirby & Watkins, 1998; Bengtsson, Nilsson, Franc & Menozzi, 2000). Thus, we need to understand the natural processes driving forest biodiversity as well as the relationships between different components of management, forest structure and biodiversity. Biodiversity comprises different facets including species richness, diversity, identity, and composition as well as genetic, functional, structural, ecosystem, and landscape diversity. These facets might be differently affected by environmental drivers. Moreover, the diversity and functional composition of communities and the biotic interactions within and across trophic levels are considered a fundamental element of forest ecosystem functionality (Hooper, Adair, Cardinale, Byrnes, Hungate et al., 2012; Soliveres, van der Plas, Manning, Prati, Gossner et al., 2016), as they mediate ecosystem processes and services (Scherer-Lorenzen, Körner, & Schulze, 2005; Mori, Lertzman, Gustafsson & Cadotte, 2017), such as water and nutrient cycling (Scherer-Lorenzen, 2014), or pest control (Jactel, Brockerhoff & Duelli, 2005). For effective conservation a more detailed understanding of the important drivers of biodiversity and biotic interactions at different temporal and spatial scales is crucially needed.

Tree individuals provide habitat for a large number of organisms spanning several orders of magnitude in body size (Brändle & Brandl, 2001; Strätz, Wagner & Müller, 2009; Wagner, Wehnert, Wong & Stoyan, 2016). The driving factors, i.e. the relevant tree traits providing ecological niches as well as the importance of habitat continuity (Ohlson, Söderström, Hörnberg, Zackrisson & Hermansson, 1997; Nordén, Dahlberg, Brandrud, Fritz, Ejrnaes et al., 2014; Janssen, Fuhr, Cateau, Nusillard, & Bouget, 2017) and connectivity (Fahrig, 2013; Seibold, Bässler, Brandl, Fahrig, Förster et al., 2017) remain only partly understood. Moreover, recent studies have stressed the importance of intraspecific trait variability at different trophic levels for the adaptive ability of species to environmental change as well as for their effects on ecosystem processes (Ali, Reineking & Münkemüller, 2017; De Bello, Lavorel, Albert, Thuiller, Grigulis et al., 2011; Hulshof, Violle, Spasojevic, McGill, Damschen et al., 2013; Lepš, de Bello, Šmilauer & Doležal, 2011). For instance our understanding of how inter-individual genetic and physiological variation of trees impact the assemblage of associated organisms is still far from being complete (Gossner, Simons, Achtziger, Blick, Dorow, 2015; Hughes, Inouye, Johnson, Underwood & Vellend, 2008; Whitham, Gehring, Lamit, Wojtowicz, Evans, et al., 2012) **(Q 24)**. This also relates to the fact that intra-specific variability is not systematically reflected in common trait databases for plants (Kattge, Diaz, Lavorel, Prentice, Leadley et al., 2011) and animals (Homburg, Schuldt, Drees & Assmann, 2013; Gossner, Simons, Achtziger, Blick, Dorow, 2015). Future studies should focus on the importance of intraspecific trait variability for species interactions and resulting ecosystem processes **(Q 25)**. Additionally, spatial effects of fragmentation, habitat loss and the surrounding matrix on biodiversity need to be better understood to develop efficient conservation strategies (Huxel & Hastings 1999; Widerberg Koch, Ranius, Drobyshev, Nilsson & Lindbladh, 2012; Müller, Bae, Röder, Chao, & Didham, 2014; Humphrey, Watts, Fuentes-Montemayor, Macgregor, Peace et al., 2015) **(Q 26)**. In the face of climate change the question arises how tree species might adapt to changing conditions at larger spatial scales, and whether forest managers should select for particular genotypes in species in response to these changes (Rose, Leuschner, Köckemann & Buschmann, 2009; Weber, Bugmann, Pluess, Walthert & Rigling, 2013). This could affect tree genetic diversity and associated organisms and their interactions **(Q 27)**.

Biodiversity is strongly influenced by abiotic site conditions (Keddy 2017) as well as resource availability ('More Individuals Hypothesis', Srivastava & Lawton, 1998) and heterogeneity ('Resource Heterogeneity Hypothesis', Hutchinson, 1959). The available evidence on the relative importance of these mechanisms is, however, inconclusive and thus more studies disentangling these mechanisms are needed. Forest structure and hence forest management largely determine the abiotic and biotic conditions that are important for biodiversity. The relevance of forest structure for biodiversity has been demonstrated for various species groups over several decades (MacArthur & MacArthur, 1961; Karr & Roth, 1971; Gerell, 1988; Paillet, Berges, Hjältén, Odor, Avon et al., 2010; Kraus & Krumm, 2013; Schall, Gossner, Heinrichs, Fischer, Boch et al., 2018). Beyond the current state of knowledge, however, we need a better understanding of key structural attributes (from microhabitats to the landscape scale) for biodiversity, their proper quantification (Zenner, & Hibbs, 2000; Neumann & Starlinger, 2001;

Pommerening, 2002; Seidel, 2018; Schall, Schulze, Fischer, Ayasse, & Ammer 2018) and how they should temporally and spatially be arranged to foster biodiversity (Drobyshev, Niklasson, Linderson, Sonesson, Karlsson et al., 2008) **(Q 28, Q 29)**. For example, several approaches have been suggested on how to integrate key features of old-growth forests into managed forests (Aubry, Halpern & Peterson, 2009; Gustafsson, Kouki & Sverdrup-Thygeson, 2010; Gustafsson, Baker, Bauhus, Beese, Brodie et al., 2012). However, not much is known about how fast retention trees develop microhabitats (Vuidot, Paillet, Archaux, & Gosselin, 2011; Larrieu, Cabanettes, Gonin, Lachat, Paillet et al. 2017) and over which distances they might help to promote biodiversity. In this context the role of habitat amount ('Habitat-amount Hypothesis') vs. spatial arrangements ('Habitat-patch Hypothesis') of key structural attributes such as habitat trees and dead wood is important, and strongly relies on the dispersal ability of focal species (Fahrig 2003; Komonen & Müller 2018). So far only a limited number of studies addressed these questions for Central European forests (Schall, Gossner, Heinrichs, Fischer, Boch et al., 2018; Seibold, Bässler, Brandl, Fahrig, Förster et al., 2017). For an evaluation of the most effective conservation strategy, we need well-designed studies aiming at disentangling the relative importance of habitat area, habitat quality, as well as spatial and temporal connectivity for biodiversity. Ultimately this may lead to the question whether or not conservation strategies in nature reserves should consider interventions shaping habitat heterogeneity, e.g. by considering the mixed disturbance severity concept (Mikoláš, Svitok, Bollmann, Reif, Bače et al., 2017), or enhancing the restoration of old-growth attributes (Bauhus, Puettmann & Messier, 2009).

Homogenization of ecosystems by land-use is a main driver of biodiversity loss (Gamez-Virues, Perovic, Gossner, Borschig, Bluthgen et al., 2015; Gossner, Lewinsohn, Kahl, Grassein, Boch et al. 2016; McKinney & Lockwood 1999; van der Plas, Ratcliffe, Ruiz-Benito, Scherer-Lorenzen, Verheyen et al., 2016). Ecosystems may be homogenized by land-use intensification or land-use equalization. Land-use intensification in Central European forests is characterized by decreasing the age, size, and biomass of tree populations through harvests, as well as by altering the tree species composition compared to the natural vegetation (Schall & Ammer 2013). In contrast to other regions of the world, interventions like fertilization, pesticide application and soil preparation are negligible in Central European forests (Ammer, Balandier, Bentsen, Coll, & Löf, 2011), and will most likely remain an exception due to public pressure, at least in the near future. Land-use equalization, in contrast, reduces the diversity of land-use practices irrespective of their intensity, leading to a convergence of the structure and composition of forests at the landscape scale (Beese & Bryant, 1999). Current forest management guidelines and certification criteria (FSC Working Group Germany, 2012) promote land-use equalization by favouring a single management system, in Central Europe a fine-grained continuous cover forestry regime (Messier, Puettmann, Chazdon, Andersson, Angers et al., 2015). In the past the impact of forest management systems on biodiversity was focused on alpha-diversity along a land-use intensity gradient or between different forest management interventions (Paillet, Berges, Hjältén, Odor, Avon et al., 2010). It is, however, necessary to also consider entire silvicultural systems including different developmental stages, tree species identities and mixtures types at different spatial scales **(Q 30)**. Therefore, research should be directed towards a landscape approach by considering different scales of diversity (alpha, beta, gamma), different diversity metrics (species richness, species and functional diversity and composition) as well as species interactions. This will result in a better mechanistic understanding (e.g. biotic and abiotic filtering) of the management-diversity-ecosystem relationships, and can form the basis for improved forest management strategies (e.g. Edwards, Gilroy, Woodcock, Edwards, Larsen et al., 2014, van der Plas, Manning, Allan, Scherer-Lorenzen, Verheyen et al., 2016; Schall, Gossner, Heinrichs, Fischer, Boch et al., 2018).

Disturbance in natural forest systems can vary between small-scale events resulting in the loss of single trees up to landscape-scale disturbances caused by factors such as storm, fire, pests and pathogens (Turner, 2010). The 'Intermediate Disturbance Hypothesis' (Connell, 1978) suggests that overall biodiversity peaks at intermediate disturbance levels (Roxburgh, Shea, & Wilson 2004), as different taxonomic and functional groups respond differently to disturbances. However, this theory has been contested recently (Fox, 2013) and the effects of disturbances on biodiversity across spatial and temporal scales (Belote, Sanders, & Jones, 2009) remain incompletely understood (Winter, Ammer, Baier, Donato, Seibold, et al., 2015; Winter, Bässler, Bernhardt-Römermann, Krah, Schaefer, et al., 2017; Thom, Rammer, Dirnböck, Müller, Kobler et al. 2017) **(Q 31)**. A better understanding of how different organisms react to disturbance is needed to predict how extreme events (Mann, Rahmstorf, Kornhuber, Steinman, Miller et al., 2017) may shape our forests in an uncertain future (Seidl, Thom, Kautz, Martin-Nenito, Peltoniemi et al. 2017). Understanding the importance of successional as well as disturbance-driven natural dynamics for biodiversity can further help to develop effective forest management strategies. Preferentially natural dynamics are studied in primeval forests, but these have virtually been eradicated from Central Europe in the past (Parviainen, 2005). Strict forest reserves allow establishing gradients of forest-use intensity and studying the impact of natural and anthropogenic disturbances on biodiversity (Müller, Hothorn, & Pretzsch, 2007; Paillet, Berges, Hjältén, Odor, Avon et al., 2010; Winter, Flade, Schumacher, Kerstan, & Möller, 2005). As set-aside areas are only an incomplete substitute for primeval forests, we additionally need to more intensively make use of the remaining primeval forest in, e.g. the Carpathians for studying how biodiversity is shaped by varying disturbances at different spatial scales **(Q 31)**. In combination with studying disturbance events such as windthrows and wildfires in managed landscapes, new avenues for forest management might be opened by considering such disturbances as part of a dynamic integrative approach (Bollmann & Braunisch 2013). However, a better mechanistic understanding of the succession of species and the recovery processes following disturbance events is important; here recently developed trait- and phylogenetic based approaches are promising (Cadotte, Albert, & Walker, 2013). Among biotic drivers of forest dynamics, pest outbreaks (e.g. bark beetles) and the introduction of alien pathogens such as *Hymenoscyphus fraxineus* (causing ash dieback) and the emerald ash borer (*Agrilus planipennis*) might become increasingly important, in particular in combination with climate change and the resultant drought stress. In order to support forest adaptation to climate change cultivating non-native drought-tolerant tree species such as Douglas-fir is frequently discussed in Central Europe (Bolte, Ammer, Löf, Madsen, Nabuurs et al. 2009). How such active (including host associated species) and passive introductions will influence biodiversity and biotic interactions and the resulting processes is still debated **(Q 32)**.

To improve the state of Central European forests in the context of biodiversity, the role of past and present forest management needs to be addressed in more detail. Specifically, ownerships and land tenure as well as land-use legacies need to be considered more explicitly **(Q 33, Q 34)**. For systematic conservation planning, e.g. of priority sites for conservation, knowledge on disturbance and management history of potential areas is crucial (Lachat & Bütler, 2009; Hannon, Niklasson, Brunet, Eliasson, & Lindbladh, 2010, Flensted, Bruun, Ejrnæs, Eskildsen, Thomsen et al., 2016). Historical ecology helps to elucidate this dimension and provides guidance for future management (Szabó & Hédl, 2011). Management intensity or traditional management techniques are known to be closely linked to forest ownership type (Flensted, Bruun, Ejrnæs, Eskildsen, Thomsen et al., 2016; Johann & Schaich 2016, Mölder 2016, Cervellini, Fiorini, Cavicchi, Campetella, Simonetti et al., 2017). The long life-span of trees results in lag effects of past management and ongoing climate change on future biodiversity-related processes in forests (Hermy & Verheyen, 2007; Fichtner, von Oheimb, Härdtle, Wilken & Gutknecht, 2014; Thom, Rammer, Dirnböck, Müller, Kobler et al., 2017). Legacy effects of land-use have been shown to determine the diversity and composition of above- (e.g. Flinn & Vellend 2005; Hermy & Verheyen 2007) and belowground communities (e.g. Fraterrigo, Balser & Turner, 2006; Fichtner, von Oheimb, Härdtle, Wilken & Gutknecht, 2014) in forests and, thus, affect ecosystem functioning **(Q 33)**. However, the interactive effects between land-use legacies and drivers of global environmental change and their consequences for forest biodiversity and species interactions remain poorly understood **(Q 34)**.

Questions

Q 24 How do the genetic and physiological differences within and among tree species affect other organisms and species interactions?

Q 25 How does intraspecific variability in tree traits affect intraspecific trait diversity in consumer guilds and ecosystem processes?

Q 26 How do tree species characteristics and traits affect the diversity of organisms living on trees and what is the spatial extent to which single-tree-effects on biodiversity stretch?

Q 27 How is biodiversity affected by tree species adaptations to climate change and by selection of particular genotypes by forest managers?

Q 28 Which are key structural attributes related to biodiversity at different spatial scales (single trees, forest stands, landscapes), and what are their temporal dynamics?

Q 29 How does the spatial and temporal arrangement of microhabitats and habitat patches affect biodiversity and how important is this compared to habitat amount?

Q 30 To which extend, and how, is regional gamma-diversity of organismic groups controlled by landscape-scale forest structure and composition and what are the relative contributions of different forest types (respectively silvicultural systems, forest developmental phases, etc.) to regional gamma-diversity?

Q 31 How important are varying disturbance size and severity for biodiversity on different spatial scales?

Q 32 Which effect do active introductions of alien tree species (including their associated species) and passive invasion of species have on biodiversity and species interactions? How do these effects interact with land-use and climate change?

Q 33 What is the importance of past management, ownership, and land tenure relative to present management intensity in affecting biodiversity and biotic interactions?

Q 34 How do drivers of global change interact with management and land-use legacies to shape the diversity and composition of forest communities at different scales?

Regulation and protection

The regulation of important ecosystem fluxes such as the water cycle and the protection of humans against natural hazards are important ecosystem services of forests (for climate regulation see the section on biogeochemical cycling). In addition, forests also protect soils from the eroding forces of wind, water, and gravity. As intact soils are a prerequisite for healthy forests (and the sustainable provisioning of ecosystem services), the regulation and protection functions are of integral importance for the future of forests in Europe.

More than 25 million ha of forests are dedicated to soil protection and water regulation in Europe and an additional 3 million ha are protecting humans and their infrastructure from natural hazards (Forest Europe, 2015). The spatial variation in the importance of these forest functions is considerable, with water quality being especially relevant in densely populated areas and protection being particularly important in mountain areas with high relief energy. While the regulation and protection functions of forests have long been a focus of forest ecology and management in mountain areas, they are often only implicitly regarded as co-benefits of other functions in the stewardship of many other forest ecosystems (Forest Europe, 2015). This raises the question of multifunctionality, and under which contexts and conditions regulation and protection are positively correlated with other functions and services **(Q 35)**. Recent analyses indicate a high potential for multifunctionality in Europe's forests (van der Plas, Ratcliffe, Ruiz-Benito, Scherer-Lorenzen, Verheyen et al. 2018) yet ecological context plays an important modifying role (Ratcliffe, Wirth, Jucker, van der Plas, Scherer-Lorenzen, et al. 2017), and trade-offs between functions are frequently reported in local studies (Lafond, Cordonnier, Mao, & Courbaud, 2017; Langner, Irauschek, Perez, Pardos, Zlatanov et al., 2017).

The relationship between many attributes of forest ecosystems and the regulation and protection functions they provide is highly non-linear. Water transpiration and outflow, for instance, change nonlinearly with leaf area (Pötzelsberger, & Hasenauer, 2015), and protection against natural hazards changes disproportionally with gap size and stem density (Rammer, Brauner, Ruprecht, & Lexer, 2015). Many of these relationships have long been known and are phenomenologically well described (e.g. Frehner, Wasser, & Schwitter, 2005). Yet, our process understanding of how forest structure and composition influences regulation and protection remains incomplete **(Q 36)**. A conclusive mechanistic explanation of how diversity in traits and species bolsters regulating functions is still lacking. Furthermore, whether thresholds of forest structure required to provide protection functions (e.g., in terms of minimum stem number and dbh) frequently applied in management (e. g. Frehner, Wasser, & Schwitter, 2005) are generally applicable across systems and contexts remains to be conclusively tested. Understanding the underlying mechanisms of how forest structure and composition are related to regulation and protection is also an important prerequisite of scaling these functions from the stand to the landscape and regional scale.

Addressing spatial scales beyond the stand scale is important, as many regulation and protection functions provide *ex situ* ecosystem services (i.e., services that are not consumed where they are provided; Millennium Ecosystem Assessment, 2005). The full functionality of forests in providing protection and regulation can thus only be considered at spatial scales beyond the stand scale (Laudon, Kuglerová, Sponseller, Futter, Nordin et al. 2016). The efficiency of a given forest structure and composition to protect against snow avalanches, for instance, strongly increases with a stand's proximity to the avalanche's place of origin. Consequently, the configuration of a landscape (i.e., the spatial arrangement of different land-use types) is an important factor contributing to regulation and protection (Lamy, Liss, Gonzalez, & Bennett, 2016). The variable contribution of individual stands to the overall functioning of a forest landscape harbours great potential for improved forest management (Seidl, Albrich, Thom, & Rammer, 2018), yet the effects of landscape configuration and composition on regulation and protection remain incompletely understood **(Q 37)**.

Compared to other forest functions, continuity is an aspect of paramount importance in the context of regulation and protection. If the production function, for instance, is reduced for a few years, the negative effects, e.g., on forest C storage, can be compensated by improved tree growth in the following years. In contrast, losing the functionality to protect against erosion even for a short period of time can result in substantial loss of soil and subsequent regeneration failure. Temporal stability is thus a crucial element for the regulating and protecting functions of forests; it depends on the sensitivity of forest ecosystems to external drivers, but also on their ability to quickly recover their functionality (Wohlgemuth, Schwitter, Bebi, Sutter & Brang, 2017). Stability is increasingly challenged by the growing variability and uncertainty induced by global change. Adaptive management strategies considering the potential future changes in climate, N deposition, and atmospheric CO_2 are thus needed (Bolte, Ammer, Löf, Madsen, Nabuurs et al*.,* 2009; Keenan, 2015) in order to ensure a stable regulation and protection function of forests also in the future **(Q 38)**. Increasing natural disturbances can, for instance, affect the water quality and quantity provided by forest ecosystems (Beudert, Bässler, Thorn, Noss, Schröder et al., 2015; Buma & Livneh, 2017). However, also legacies from past land-uses (e.g. forest grazing, litter raking, large-scale clear-cuttings, acidic deposition, and the conversion towards conifer-dominated forests; Leuschner & Ellenberg, 2017) still influence forests and their functioning in Europe. The temporal prevalence of these legacies remains still poorly quantified to date. Also, these legacies have the potential to modulate the sensitivity of regulation and protection to drivers of global change, e.g., where past developments created disequilibria in stand age and structure, which now result in elevated disturbance risk (Bebi, Seidl, Motta, Fuhr, Firm et al. 2017; Schurman, Trotsiuk, Bače, Čada, Fraver et al. 2018). The effect of legacies on the current and future provisioning of regulation and protection functions thus requires further attention in research **(Q 39)**.

Another factor potentially influencing the regulation and protection functions of forests are ungulates. It is well documented by a large number of studies across the northern hemisphere that high ungulate densities can have drastic effects on tree species composition and stand development, and hence on the regulation and protection functions of forests (Gill 1992; Ammer 1996; Motta 1996; Fuller & Gill 2001; Rooney 2001; Reimoser 2003; Kupferschmid & Bugmann 2005; Pellerin, Saïd, Richard, Hamann, Dubois-Coli, et al. 2010). High ungulate densities can even result in detrimental effects on soil fertility (Prietzel & Ammer 2008), but not much is known about how these different effects of ungulates will be altered by climate change (Didion, Kupferschmid, Wolf & Bugmann 2011; Cailleret, Heurich & Bugmann 2014). Only recently large predators such as wolf and lynx have started to recolonize Central Europe, where they now occur in a habitat characterized by an overabundance of ungulate populations and a strongly fragmented landscape. It remains to be shown if and to what extent the returning large predators will change ungulate densities as well as behaviour, and how such changes will affect tree recruitment and the regulation and protection functions of forests **(Q 40)**.

Questions

Q 35 Under which conditions and contexts are regulation and protection functions generated as co-benefits from other functions (multifunctionality), and where do trade-offs between functions exist?

Q 36 Which structural attributes and tree species traits confer regulation and protection functions, and what are the underlying mechanisms?

Q 37 What is the contribution of individual stands to landscape-level functioning, and how does the configuration and composition of a landscape affect the regulation and protection functions provided by forest ecosystems?

Q 38 How can temporal stability in the regulation and protection functions be achieved in the face of accelerating global change?

Q 39 How strongly are the current regulation and protection functions determined by legacies of past land-use and forest development, and how are legacy effects interacting with drivers of global change?

Q 40 How will the large predators returning to Central Europe affect ungulate densities and behaviour, and will the effect help to restore natural patterns of tree regeneration, fostering regulation and protection functions?

Outlook

The research questions of the five domains described above are connected in many ways. For example, the effects of mixing tree species is not only of interest with regard to productivity but also with regard to the regulation and protection functions of forests, the diversity of associated organisms in forests and their biochemical cycling **(Q 4, Q 20, Q 21, Q 36)**. Actually, it was shown that multifunctionality may be best achieved through diverse stands (van der Plas, Manning, Allan, Scherer-Lorenzen, Verheyen et al. 2016). This example illustrates that many of the questions listed above are worth being addressed in both managed and unmanaged forests. Another example is related to stand structure. It is not well understood to what extent and how spatial heterogeneity within stands affects biochemical cycles, productivity, biodiversity, resistance towards stressors and regulation functions **(Q 8, Q 19, Q 28, Q 36)**. Even less is known about the importance of spatial heterogeneity at the landscape scale. These two examples highlight that the complexity of forest ecosystems can rarely be adequately addressed by strict disciplinary approaches. In contrast, progress in revealing underlying mechanisms (as opposed to correlative descriptions) will only be achieved by fostering cross-disciplinary exchange.

Another way of linking key questions of ecological research is along ecological concepts, such as the functional trait approach (Violle, Navas, Vile, Kazakou, Fortunel, et al. 2007). There is increasing evidence that functional diversity or the presence, abundance, distribution, and diversity of functional traits is more important for ecosystem functioning than species diversity per se (e.g. Díaz, Fargione, Chapin & Tilman, 2006; Nadrowski, Wirth & Scherer-Lorenzen, 2010; Gagic, Bartomeus, Jonsson, Taylor, Winqvist et al., 2015). Functional traits reflect adaptations to variation in the physical and biotic environment as well as trade-offs (ecophysiological and/or evolutionary) among different functions within an organism (De Bello, Lavorel, Díaz, Harrington, Cornelissen et al., 2010). As species functional traits determine their response to environmental pressures (response traits) and these are linked to traits affecting species interactions and ecosystem processes (effect traits), the consequences of global change depend on the strength of alteration in these interacting functional traits. Therefore, functional traits have received increasing attention in plant and animal ecology recently. However, in forest ecosystems, response and effect traits have rarely been studied together and across trophic levels. Consequently, little is known about the mechanisms, synergisms, and antagonisms that may explain the observed effects on ecosystem functioning (Lavorel & Granier, 2002; Lavorel, Storkey, Bardgett, de Bello, Berg et al., 2013). Functional traits are thus a promising concept for linking disciplines and questions **(Q 20**, **Q 25, Q 26, Q 36)**.

A third element that links different ecological questions is scale. While some questions address the individual tree scale **(Q 11, Q 12, Q 25, Q 26)**, most of the questions highlighted here focus on the stand and/or the landscape scale. Forest management mainly operates at the stand scale. This is why studies carried out at this scale may be directly considered for adjusting silvicultural approaches. A good example is the growing evidence of the importance of deadwood for biodiversity (e. g. Müller & Bütler, 2010; Seibold, Bässler, Brandl, Büche, Szallies et al., 2016), which resulted in clear recommendations for forest practice. As a consequence, public forest administrations in Central Europe have issued instructions how to deal with habitat trees, aiming at minimum amounts of at least 20-30 m^3 ha^{-1} of deadwood.

To improve the linkages between subfields within forest ecology we do need an intensified exchange among the different methodological approaches (monitoring, comparative studies, experiments, models) and scales. This is particularly important in forest research because of the longevity of trees as the main entities of analysis. Without exploring the importance of patterns and processes on small scales for larger entities, and without integrating approaches operating at fine scales and testing to what extent the findings can be scaled up, our mechanistic understanding of forest ecosystem dynamics will hardly improve. In other words, we need to consider different spatial and temporal scales, acknowledging that processes of interest are usually affected by mechanisms acting at scales above and below the focal scale. For most forests in Central Europe, dynamics and functioning cannot be fully understood and/or mechanistically described without taking their history as well as the current land tenure and management regime into account. In this regard, the forests of Central Europe are the epitome of coupled human and natural systems (Liu, Dietz, Carpenter, Alberti, Folke, et al. 2007) and are very well suited to study ecological processes that are tightly entwined with anthropogenic processes. Consequently, questions addressing legacy effects are pertinent across research areas **(Q 23, Q 33, Q 34, Q 39)**.

Many of the above-mentioned questions and challenges require long-term ecological research, including monitoring approaches and experiments (Dovers, Norton, & Handmer, 1996; Simberloff, 1999). Only long-term research will allow us to detect drivers that may ultimately threaten the integrity of forest ecosystems. The most prominent example in this regards is climate change, which fundamentally affects all aspects of forest ecosystem functioning. The importance of climate change and the related uncertainties for forest ecosystem patterns and processes are reflected by the fact that nearly one third of all research questions highlighted here touch issues related to climate change **(Q 1, Q 2, Q 3, Q 6, Q 14, Q 16, Q 17, Q 18, Q 27, Q 32, Q 38, Q 39)**.

Understanding the response of forest ecosystems to different drivers and the underlying mechanisms is crucial in the context of forest ecosystem services, and points towards the societal importance of forest ecological research beyond mere curiosity and an interest in natural processes. This requires inter- and transdisciplinary research because ecology and society affect each other through various positive and negative feedbacks. Against this background, future research needs to be matched with social demands and findings need to be better communicated with policy makers (Andersson, Feger, Hüttl, Kräuchi, Mattsson et al., 2000; Farwig, Ammer, Annighöfer, Baur, Behringer et al., 2017). Interdisciplinary approaches are, for instance, needed to test how highly productive non-native tree species added to a matrix of native species alter ecosystem functioning and biodiversity. Tackling such a question requires interdisciplinary work on the same sites to elucidate the processes and organisms influenced by such an introduction. Another example is the integration of trees into agricultural systems in order to reduce negative impacts of agricultural land-use (e.g., on biodiversity) and simultaneously increase economic flexibility. Transdisciplinary approaches are needed to address questions frequently asked by forest managers, such as: Which forest management strategies can minimize negative effects on biodiversity or even promote it, and to what extend would society be willing to cover additional costs of management to compensate for income losses? Another question clearly requiring transdisciplinarity is how large predators can be re-integrated in a highly fragmented and intensively used forested landscape (Breitenmoser 1998). Additionally, scientists need to increasingly engage in the science-policy transfer, even if such activities do not increase scientific reputation (Müller & Opgenoorth 2014). In fact, the growing complexity and uncertainty seem to have rather complicated the communication between ecologists and society (Dovers, Norton, & Handmer, 1996). However, policy makers usually only address crucial problems if they know what is at stake and how integrative solutions could look like.

An intensified transfer of findings from forest ecological research to forest management is also urgently needed. Sustainable forest management in a broader sense needs to be flexible enough to address the demands of future generations, which may differ from present needs (Wagner 2004). That is why answering the questions highlighted here is not only of interest from a scientific point of view, but also could promote improved forest management regimes. For example, for protecting biodiversity and the provision of regulation and protection functions it is not known, which size class distribution of areas that were set aside from forest interventions, yields optimal results. To answer such questions appropriate monitoring is needed which may be integrated in existing European forest monitoring networks. This illustrates that in addition to questions of fundamental ecological understanding also various applied questions are of high relevance for future forest ecological research in Central Europe. Five of them are listed in the following:

Q 41 How effective are conservation measures such as habitat tree retention, setting aside small unmanaged patches etc. for species spreading and hence nature conservation?

Q 42 How should key conservation measures be temporally and spatially arranged at the landscape scale to most effectively protect biodiversity?

Q 43 How can the growing demand for wooden biomass be met in a sustainable manner?

Q 44 How can disturbances be positively integrated in forest management systems?

Q 45 How can large predators be integrated into a fragmented and densely populated landscape?

Forest management depends on an improved mechanistic understanding of ecosystem functioning in order to allow future generations to "*respond adaptively to future changes and cope with surprises, potentially providing multiple options*" (Mori, Lertzman, Gustafsson & Cadotte, 2017, page 12). Future research focusing on the concrete questions identified here may enable the development of scientifically sound and flexible forest management and conservation strategies in the face of accelerating global change. In addition, they could deepen our knowledge of forest ecosystems, and could interest a next generation of ecologists for the captivating field of forest ecology.

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Fig. 1. Composition of the group (number of people per discipline in parenthesis) and work-flow.