



Review

Effects of forest management on biodiversity in temperate deciduous forests: An overview based on Central European beech forests



E.D. Schulze

Max-Planck Institute of Biogeochemistry, Box 100164, 07701 Jena, Germany

ARTICLE INFO

Keywords:

Forest management
Birds
Xylobionts
Saproxyllic beetles
Forest plant species
Forest protection
Endangered forest species
Natura-2000 responsibility species

ABSTRACT

This overview of relationships between biodiversity and management focuses on Central European *Fagus* forests. Present management and conservation activities are embedded in the geographic and historic background of Central European forest flora, including endangered, protected, and plant species for which Germany has taken special responsibility to ensure their future survival. Managed and unmanaged forests are compared with respect to plants and other organisms. Based on the floristic background, management for climate change and consequences of conservation on a global ecological footprint will be discussed.

The Central European tree flora contains only about 7% of the tree diversity of East Asia. Only a few genera re-migrated to Central Europe after the Pleistocene, while others were lost during the Pleistocene, e.g. the genus *Pseudotsuga*.

In this study the forest flora is characterized by specialized plant species that only grow in forests. These forest specialists contribute only 10% of the plant species of the total German flora. This fraction is even less (4–5%) for Romania which is generally regarded as a region with close to “natural” forest conditions. Also, the forest flora of Germany and Romania contains fewer apomictic and hybrid plant species than the non-forest flora. No forest plant species have gone extinct in Germany in the past 250 years, which is the time since the first floristic documentation of a plant species that was lost in Thuringia, despite intense forest use including changes in dominant tree species.

With respect to the Natura 2000 goals of maintaining species diversity of Europe, the deciduous forest, as managed by rotation forestry, contain more protected and endangered species, and species for which Germany has taken responsibility than protected forest. Forests managed with permanent forest cover (so-called “management close-to-nature”) contain fewer plant species than age-class (rotation) forestry. The abundance of dead wood-fungi and of soil bacteria is higher in rotation forest than in protected forests. For the initial phase of decay, a dead wood experiment identified two important tree species, *Carpinus betulus* and *Picea abies*, as the most preferred tree species for xylobionts. *Carpinus* has the most diverse fungal flora among all wood types and is a typical species for managed forests.

The Natura 2000 habitat types were defined by plant species, but the assessment of ecosystem health is based on bird species in Central Europe. A time series extending from 1927 until 2015 indicates that most non-migratory forest bird species show an increasing abundance since 1970. Adding migrating and rare bird species populations resulted in constant average abundances since 1970. There is no evidence that sustainable forest management has led to decreased biodiversity in Central Europe. In view of climate change and increasing presence of tree diseases, Europe should avoid enlarging its ecological footprint by taking Central European forests out of management.

1. Introduction

It is generally accepted that biodiversity is in decline, and it has been proposed that biodiversity can only be maintained through conservation of specific ecosystems or of larger land areas (Global Biodiversity Assessment, 1995; Pimm, Jenkins, & Abell, 2014; WBGU,

2001). However, biodiversity is not equally distributed across the globe. The highest plant species numbers are found in the humid tropics and subtropics, and species numbers strongly decline towards the temperate and polar zones. Along this gradient about 35 hot spots of plant diversity have been identified as regions with high numbers of endemic species and rapidly changing land use (Mittermeier, Turner,

E-mail address: dschulze@bgc-jena.mpg.de.

<http://dx.doi.org/10.1016/j.jnc.2017.08.001>

Received 10 February 2017; Received in revised form 20 July 2017; Accepted 8 August 2017
1617-1381/ © 2017 Published by Elsevier GmbH.

Larsen, Brooks, & Gascon, 2011). It is quite clear that major efforts are needed to maintain genetic resources in these regions (Hilger et al., 2015a, 2015b). In this context Central Europe is not a hot spot of diversity, whereas the Mediterranean Basin is a hotspot linked to the Caucasus and Irano-Anatolian regions, and thus connecting to the Mountains of Central Asia including the Himalaya and merging into the Mountains of Southwest China (see also Akhmetiev and Zaporozhets, 2014). The global map of hot spots should be a baseline for global conservation efforts. In Central Europe forest biodiversity is closely linked to human activities (Küster, 1998).

In contrast to this global knowledge, the German “Strategy for Biodiversity” aims at taking 5% of the forest land out of management (Nationale Strategie zur Biologischen Vielfalt, 2008) since “forestry” is regarded as the second most important factor endangering species after agriculture (BfN, 2015). In addition to taking forests out of management for conservation, a certification by the Forest Stewardship Council (FSC) is recommended for managed public forests, which should result in a further 10% of unmanaged land as a baseline for “natural” development and in the identification of 10 habitat trees ha⁻¹. Additionally, there are restrictions on management, despite all observational and experimental knowledge about biodiversity of re-wilding forests. The main review of the past that compared unmanaged with managed forest sites in Europe (Paillet, Bergès, & Hjalten, 2010) concluded that age class (rotation) forestry does not differ from unmanaged forest with respect to species richness of major groups of organisms (see Paillet, Table 4). Individual organismic groups had higher species richness in unmanaged forest (see Paillet, Table 2) because of the unequal distribution of study plots and due to merging age class management with “permanent forest cover”, a methodology that resulted in an apparent decline of species richness under management.

In order to further investigate the effects of management on biodiversity, a large scale observational study was initiated in Germany in 2008, where organismic diversity was investigated in southern, central and northern Germany, comparing in each region unmanaged forests with different types of managed forest using experimental plots that are part of a grid-based inventory (Fischer et al., 2010). The investigation is centered on *Fagus* forests, which are a major focus of the European Habitats Directive (<http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:01992L0043-20070101>, accessed 18.07.17) in which 12 *Fagus*-habitat types have been listed to be of European interest (European Commission, 2007). In addition, *Fagus sylvatica* is a UNESCO cultural heritage species (whc.unesco.org/en/list/1133/documents, accessed 18.07.17). At present, *Fagus* forests make up only about 15% of the actual forest cover in Germany (1.7 Mill ha, <http://bwi.info/start.aspx>, accessed 18.07.17; Grossmann, 2012) even though they could cover about 60% of the area (www.EUFORGEN.org, accessed 18.07.17). The area of *Fagus* in Germany is 20% smaller than the area of *Fagus* in Romania (2.1 Mill ha, <http://roifn.ro/site/rezultate-ifn-1/>, accessed 18.07.17). A large fraction of the potential distribution of *Fagus* in Germany was converted into coniferous forest in the past century. Despite the suggested importance of *Fagus* forests in the Habitats Directive, Central European *Fagus* forests contain only one out of 46 forest plant species of the Annex II plant list (<http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:01992L0043-20070101>).

In the following, data from the German biodiversity-management project will be reviewed in the context of the floral history of forests in Central Europe and of future climate change. I am aware that this analysis is valid only for sustainable forest management of deciduous forests, and it cannot be expanded to exploitation forestry in other regions of the world. The focus will mainly be on plants, because plants were the basis for distinguishing the habitat-types in the Habitats Directive. I will present data on other organisms as they are available, extending the analysis beyond the project boundaries. All study plots were located inside Natura 2000 sites. It is the aim of this study to show the multiple facets of effects of management and conservation, and to draw conclusions about future development for maintaining diversity in

Table 1
Number of tree species in the temperate climate of Central Europe, Eastern North America and East Asia (Schulze et al., 2015).

Number of tree species	Central Europe	Eastern North America	Northeastern Asia
Broad leaved	55	203	733
Coniferous	8	33	94
Total	63	236	827

Central Europe’s Forests.

2. The floral history of central europe

Biodiversity of Central European forests can only be discussed in a historic context, because the flora was impoverished during the Pleistocene, and all forest tree species of Europe have a post-glacial migratory background. In a comparison to the tree diversity of temperate deciduous forests elsewhere in the Northern Hemisphere (Schulze et al., 2015), East Asia is by far the most diverse broad-leaved forest region of the Northern Hemisphere, containing almost 4 times as many tree species as North America and more than 10 times as many tree species as temperate Europe. The differences are larger than possible effects of taxonomic nomenclature (e.g. a tendency to split genera into many species exists in East Asia, contrasting with a tendency to lump species in North America) (Table 1).

In Europe, the main genetic source for forests is East Asia. Many of the temperate zone tree species migrated from East Asia via the Caucasus and invaded Europe via the Balkans in the Cenozoic. Examples include the genera *Fagus* (Denk and Grimm, 2009) and *Pseudotsuga* (Kunzmann, 2014; Yabe, 2011; Fig. 1). Both genera evolved in Northwestern North America (Oregon) and migrated to Japan and China during the course of the Cenozoic. *Fagus* and *Pseudotsuga* reached the Caucasus and Europe from China via the Central Asian Mountains. In the Cenozoic, there were 4 *Fagus* species and 3 *Pseudotsuga* species growing in Central Europe forming mixed deciduous-coniferous forest stands.

The ancestor of the contemporary *Fagus sylvatica* is the Eocene *Fagus castaneifolia* (Fig. 2A) which gave rise to *Fagus gussonii* in the Oligocene, a species that went extinct about 5 Mill years ago. *Fagus castaneifolia* then split into the contemporary *Fagus crenata* and *Fagus haidingeri* about 23 Mill years ago, and it is *Fagus haidingeri* which split into the contemporary *Fagus sylvatica* and *Fagus orientalis* only about 9 Mill years ago (Grímsson, Grimm, Zetter, & Denk, 2016; Renner, Grimm, Kapli, & Denk, 2016). In fact, *Fagus sylvatica* and *F. orientalis* are the youngest of all contemporary *Fagus* species. *Fagus lucida* and *F. grandifolia* are evolutionarily much older species (38 and 45 Mill years old respectively). After the last glaciation, *Fagus sylvatica* invaded Northern Europe from Italy and possibly from refugee regions in Southern and Southeastern Europe (Magri, 2008), and the migration of *Fagus sylvatica* into northern Europe is closely related to the spread of agriculture (Endrodi and Gyulai, 2000).

The history of *Pseudotsuga* is very similar to that of *Fagus*. The contemporary *Pseudotsuga sinensis* has cones that are similar to those of European *P. jehorekiae* and *P. loehrii* in Cenozoic Europe (Kunzmann, 2014; Fig. 2), even though the cones became larger in contemporary *P. sinensis*. In contrast to *Fagus*, *Pseudotsuga* did not reach the Caucasus and Europe after the Pleistocene, despite its presence in Europe in the Miocene. Thus, *Pseudotsuga* may be regarded as a Palaeo-neophyte (Schulze et al., 2015) in the modern forest flora of Europe. It is a genus that was part of the European flora in the late Cenozoic under similar climatic conditions as those that exist today. Only by chance, this genus did not reach Europe again. There is no science basis to reject cultivation of *Pseudotsuga* by nature conservation.

Fig. 2 bottom: Cones of the European Cenozoic *Pseudotsuga*



Moving from single species migration at a global scale to the floral history of specific regions, the floral history of Germany contains a continual increase of plant species with very few losses (Fig. 3). Most plant species exist in open habitats. Typical forest species (forest specialists that are restricted to forests and forest edges according to Schmidt, Kriebitzsch, & Ewald, 2011) contribute only about 10% to the total flora. The flora of Central Europe has been classified into “indigenous species” that invaded Europa after the Pleistocene contributing about 74% to the total flora, “archaeophytes” that arrived in Europe with the early farmers contributing about 8%, and the “neophytes” that reached Europe after the discovery of America by Columbus representing about 17% of the total flora. This classification remains arbitrary, as the role of human activities may be underestimated (Lyons et al., 2016). There is an additional group of plant species, which is distinct but which has mostly been neglected in plant

Only 37 plant species (27 indigenous species, 8 archaeophytes, and 2 neophytes) were lost in Germany in historic times (Korneck, Schnittler, & Vollmer, 1996). In forests, the Red Lists records 2 extinct species, but *Carex depauperata* was rediscovered (Hickler et al., 2012), and *Veronica paniculata* is a steppe species of Southeastern Europe (Bozga, Indreica, & Lazar, 2013) and not a forest specialist. Thus, no forest species in the strict sense were lost during a floral record of the past 250 yrs (Schulze and Ammer, 2015), where the time-frame is based on the last record of the wetland species *Gladiolus palustris* in Thuringia by Förster in 1768 (Korsch and Westhus, 2011). During all of this time forests were heavily used (Hess, 1898) and managed (Köstler, 1934).

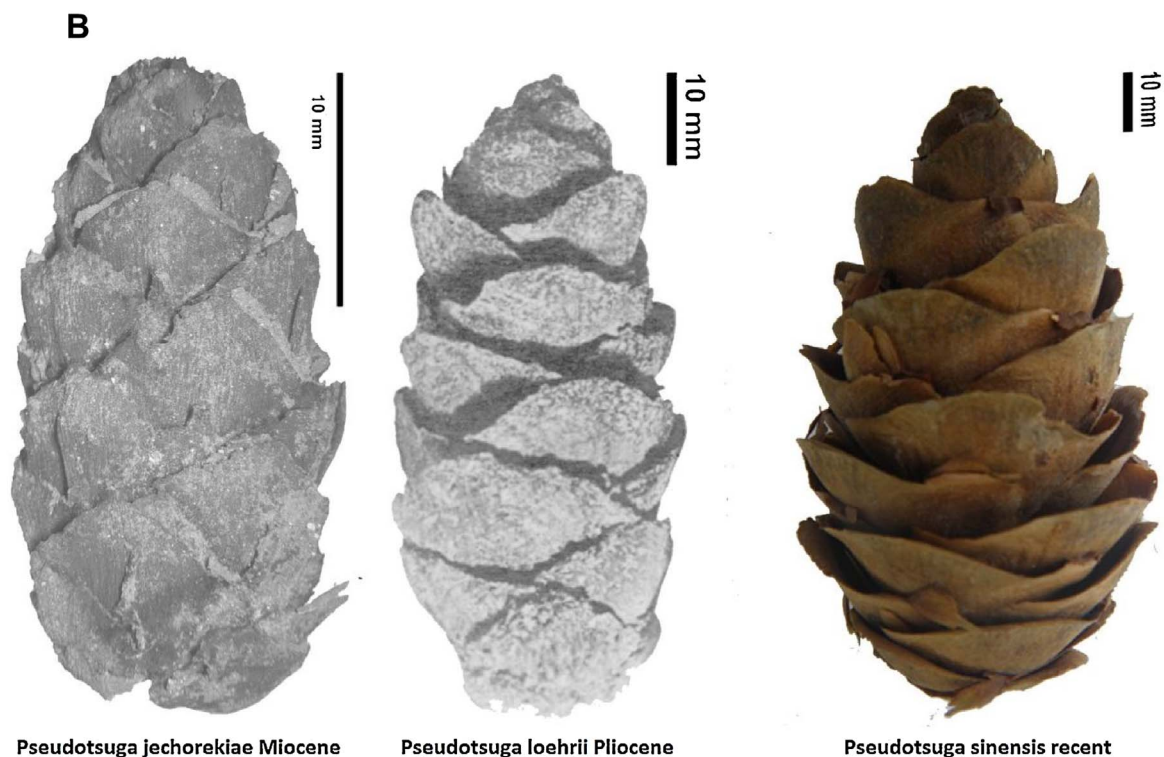
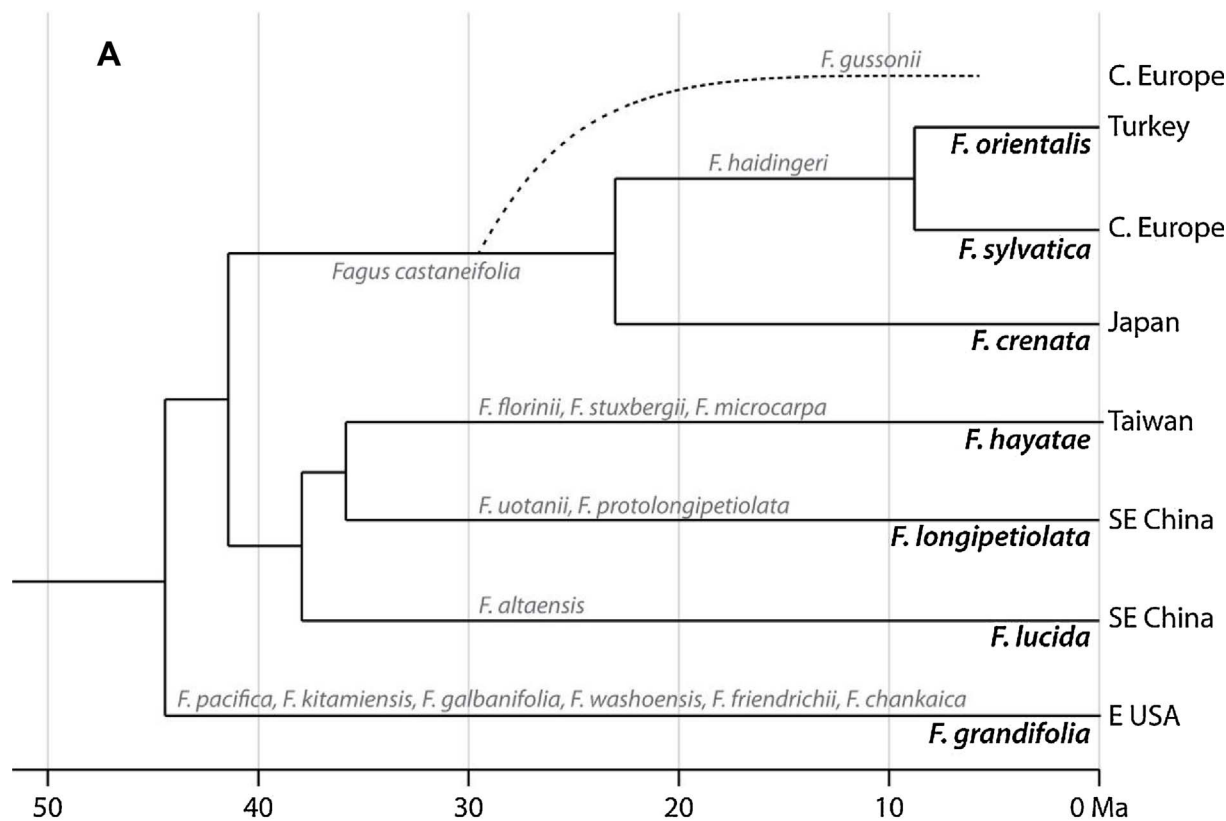


Fig. 2. top: Phylogeny of *Fagus sylvatica* and closely related *Fagus* species (modified from Renner et al., 2016).

Species losses are larger at smaller spatial scales (e.g. the red lists of Thuringia enumerates 107 lost species) and decrease at larger spatial scales (only 3 plant species are lost in Europe from the Mediterranean region, Schulze et al., 2015).

From the historic changes in biodiversity of the German flora we

may learn that the protection of the flora as a whole cannot be achieved only by protecting forests, because 90% of the species exist in non-forest habitats. In addition, the Central European tree flora has relatively little to offer. It is an impoverished “arm” of the Near East and Asian hotspots, despite of all landscape legacies on plant diversity that

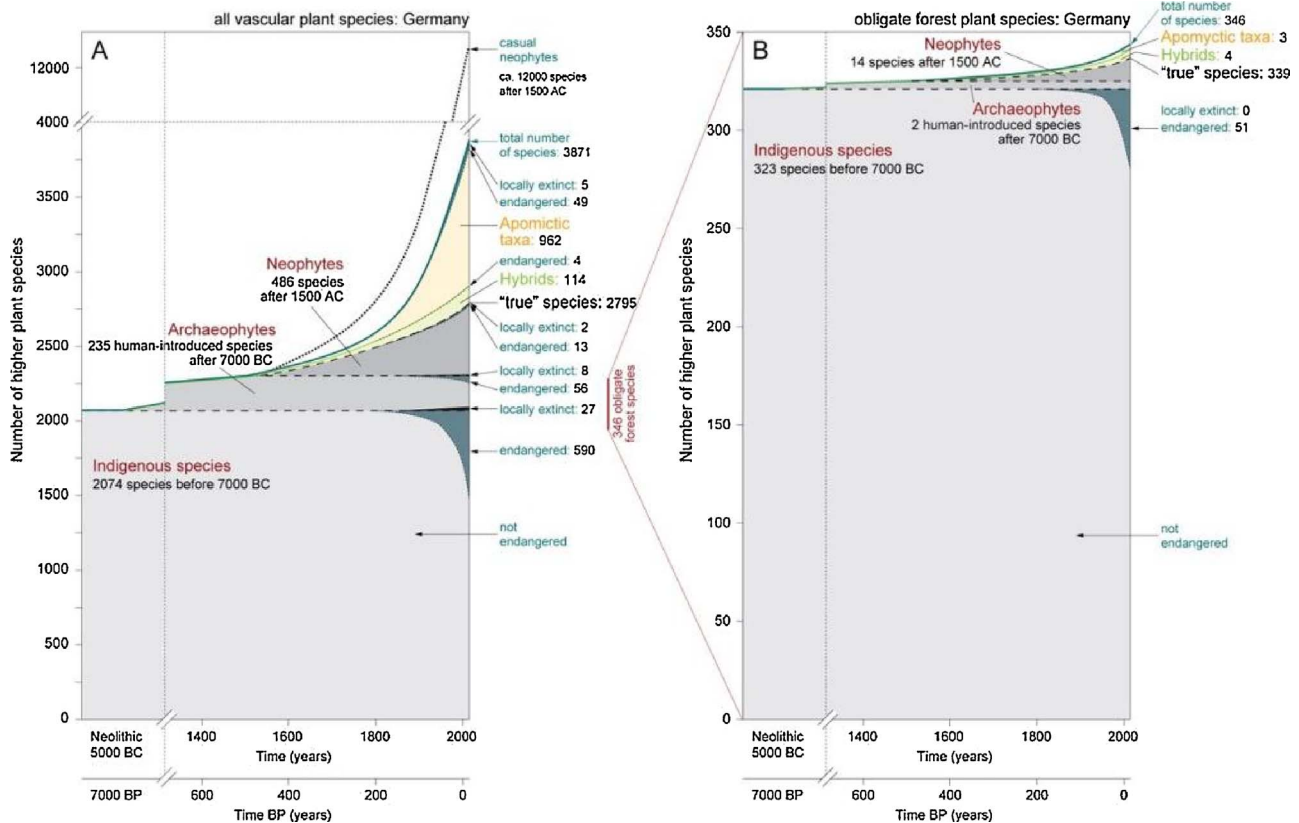


Fig. 3. Historic change of the biodiversity of the German plant flora (left) and for the German forest flora (right, Category 1.1 and 1.2 according to Schmidt et al., 2011) since about 7000 BCE (from Schulze et al., 2015). The exact curvature of changes in neophytes and apomictic species remains unknown. Species numbers follow Wisskirchen and Haeupler (1998).

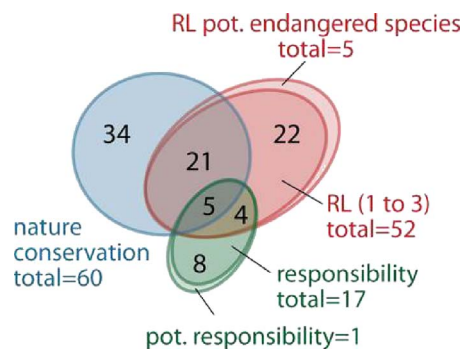


Fig. 4. Numbers of plant species occurring in forests with their association to nature conservation, red lists of IUCN, and to responsibility species according to the European Natura-2000 Habitats Directive. Numbers indicate the number of plant species in the respective sector (after Schulze and Ammer, 2015).

may delay immediate environmental effects (Sitzia and Trentanovi 2011). The starting conditions for management and conservation are set by the present flora (Sitzia et al., 2012).

3. The effects of forest management on endangered, protected and responsibility plant species, and on natura 2000 plant species of community interest

Based on the floral history I will focus in the following sections on the distribution and fate of endangered and protected plant species in Germany, because it is this group of species which has received attention in conservation activities, and which has resulted in major concerns regarding management.

"Protected species" are sheltered by law, and their selection is based on decisions by a governmental administration. In contrast,

"endangered species" are classified by Non-Governmental Organizations under the rules of the IUCN. In addition, there are species for which Germany has taken special responsibility to ensure their survival (Ludwig, May, & Otto, 2007). The rules of conservation in Europe are set by the European Habitats Directive (<http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:01992L0043-20070101>, accessed 18.07.17, see European Commission, 2015) and its Annex II (<http://eur-lex.europa.eu/legal-content/EN/ALL/?uri=CELEX:01992L0043-20070101>, accessed 18.07.17), which lists a total of 46 plant species, some of which have "priority status" (European Commission, 2015). There is only one Annex II species growing in Central European *Fagus* forests, the protected and endangered *Cypripedium calceolus* (European Commission, 2015), which grows not only in habitat type 9150 (*Cephalanthro-Fagion*), but also in open pine and spruce forests and in many other habitats. Thus, in the following I will focus on those species that are rare, under conservation or under national responsibility (RCN species).

The different conservation regimes are not "nested" entities (i.e. some endangered species are protected, and for some of these protected species Germany takes the responsibility to assure their further existence). Instead, the three "columns" of conservation are almost independent schemes with minute overlap (Fig. 4). The Annex II species of Natura 2000 and the "priority species" add additional levels of complexity by adding further independent entities. In German forests there are 52 endangered and 5 potentially endangered plant species, 60 protected plant species, and 17 plant species under national responsibility. According to the official classifications, the overlap is only 5 plant species, two of which turn out not to be typical forest plant species (*Asplenium adnigrum* grows on serpentine rock, and *Hymenoptera thunbergensis* on wet sandstone cliffs). The three remaining plant species that are endangered, protected, and under national responsibility are *Pulmonaria collina* (various deciduous forests and hedges in South Germany), *Chimaphila umbellata* (open Pine forests) and *Epipogium*

aphyllum (*Fagus* forests; Schulze and Ammer, 2015). One option for conservation would be to focus on these three species.

RCN species represent 42% of the total flora (1177 out of 2795 species, neglecting apomictic species). In forests, this number is lower, namely 29% (99 out of a total of 346). However, about every third plant species seen by a forest visitor could be contained in one of the conservation schemes. This large fraction makes management difficult, and it appears not to reflect the reality.

In this context it may be of interest to compare the German situation with other countries in Europe. Here I take Romania as a contrast, because Romania is generally regarded as being more “natural” in its management, and as a link to Southern and Eastern Europe it is to be expected that it has a more diverse flora. Romania contains a total of 3136 natural plant species and 600 plant subspecies (Ciocalan, 2009). Thus, surprisingly, the Romanian flora is only about 12% more rich than that of Germany, but Romania has a lesser number of subspecies, which may result from a lesser intensity of management, i.e. forests in Romania are managed to a large extent by a “cut and run” (Schulze, Bouriaud, Bussler, et al., 2014) which results in high stand densities and a very scarce ground flora. The forest flora of Romania (forest specialists) contains only about 142 forest specialists, which is only 4.5% of the flora, and a considerably smaller number of species than in Germany (Candrea-Bozga, Indreica, & Lazar, 2013). Only 7 forest species are endangered (red list), but only 1 species is endangered and protected. One may take this as an indication that reduced intensity of forest use results in lesser number of forest species and lesser number of RCN-species. Semenik National Park may serve as an example for a decrease in plant species diversity with conservation in *Fagus* forests (Fig. 5). *Fagus sylvatica* remained on large areas as the sole tree species. Any canopy gap is filled by *Fagus* regeneration. The rich herbaceous flora of the forest floor of managed forests is missing, and there is surprisingly little grounded dead wood, possibly due to the effects of *Fomes fomentosus*, a fungus that decomposes the wood of *Fagus* while the trees are still alive. The Romanian data are supported by studies in Switzerland (Brang et al., 2009), which identify a reduction in forest diversity caused by reduced management. This indicates that the floral situation in Germany, Switzerland and Romania represents a broader geographic pattern in Europe.

To further investigate the effects of management, a grid-based inventory of *Fagus* forests was established in Germany along a 100 × 100 m grid containing about 3000 grid points of 400 m² at each point (Hessenmöller, Nieschulze, Lüpke, & Schulze, 2011). The species under conservation or enumerated in the Red List, or being declared as species under national responsibility (the RCN-species) were recorded and accumulated with an increasing number of sample plots.

Management types were age-class rotation forestry (75% of the inventory points), where *Fagus* regenerates naturally under a shelter of a few seed trees, selectively cut forest (14% of the inventory points), where individual trees of harvestable dimensions are extracted (*Plenterwald*), and unmanaged forest (natural parks and reserves; 11% of the inventory points). Species accumulation curves were constructed by repeated subsampling of the total number of inventory points. This method allows an assessment of a 95% confidence interval, and an extrapolation to equivalent inventory numbers (see Schulze, Boch, Müller, Levick, & Schumacher, 2016).

Species accumulation curves for RCN plant species in the Hainich region of Thuringia increased rapidly with increasing inventory plot numbers (Fig. 6), but reached saturation or a continuously increasing trajectory with larger inventory plot numbers. The confidence interval indicates the highest variability for observations in unmanaged forests, and the lowest variability in selectively cut forests. The confidence limits of all management forms overlap, i.e. there is no significant difference between any of these management forms. Selectively cut forests may be separated from rotation forestry at high observation numbers with lower RCN-numbers under selective cutting. Managed forests had the highest number of RCN plant species even at comparable numbers of observation plots. Selectively harvested forests had the lowest number of RCN species. Apparently, in unmanaged and in selectively cut forests the permanent canopy cover out-shades numerous plant species (Mölder, Streit, & Schmidt, 2014).

The number of mosses and lichens is also not significantly different between management types, but unmanaged forests had a slightly higher number of RCN species at low numbers of observations. Selectively harvested forests had the lowest number of RCN species. The initial increase in numbers is steeper than for vascular plants.

The foregoing data focused on RCN-plant species only. However, the total flora of vascular plants, mosses and lichens is more diverse than the RCN-species indicate, and we need the total flora to understand the diversity of other organisms (Scherber et al., 2010). Thus, Table 2 contains data on the total floristic biodiversity of these sites. Plant diversity is higher in managed than in unmanaged forests, and Boch, Prati, Müller, et al. (2013) interpret this as a result of higher disturbances. Structural diversity is important (Schall, Ammer, Ayasse, Schulze, & Fischer, 2017), and not only the RCN-species gain from management. Since it is the objective of Natura-2000 to maintain European Biodiversity (Preamble of the Habitat Directive), with Article 2 stating that it is “the aim of this Directive...to contribute towards ensuring bio-diversity through the conservation of natural habitats”, conservation activities may have to be re-considered in view of the field observations. To ensure that biodiversity is maintained at large



Fig. 5. The “virgin” forest of Semenik Natl. Park in Romania with monotypic stands of *Fagus sylvatica* showing very little grounded dead wood and almost no herbaceous plant species. Semenik National Park is famous for its animal species that are linked to water (Foto ED Schulze, May 2017, from Schulze, 2017).

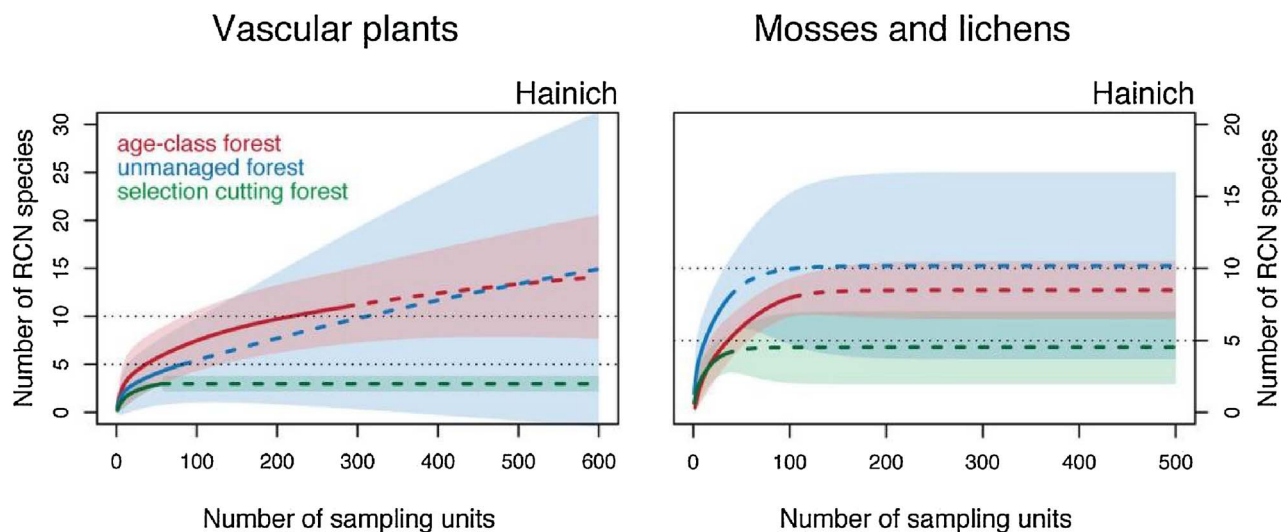


Fig. 6. Species accumulation curves for RCN-forest species in the Hainich region (Schulze, Boch, et al., 2016). 95% confidence interval is indicated by colored shades. Dashed lines are extrapolations based on the measured data (solid lines).

geographic scales, sustainable forest management appears to become an even more important contributor. The Romanian and Swiss example indicates that the results based on German observations may in fact be extended to all of Central and Eastern Europe.

4. Effects of management on forest biodiversity of other plant- and other organismic groups

The effects of management on other organismic groups have rarely been studied on a grid based scale, and in this study, complete grid based data are only available for plants. However, fungi and soil bacteria were studied on a subset of grid points.

The available data on fungi and bacteria (Table 2) confirm that deciduous rotation forests show a trend of a higher diversity than unmanaged forests. Also Paillet et al., 2010 did not find a significant effect of management (clear-cutting) on fungi. Paillet et al. (2010) found a significant negative effect for fungi only under “selective cutting close to nature”. The variation for microorganisms is very high. Thus, the differences are not significant for bacteria, but significant for fungi. The variation can be explained by soil pH and rainfall, and by the diversity of herbaceous plants on the forest floor (Felsmann et al., 2015; Wubet et al., 2012). Lichens appear to be a special case due to the effects of SO₂ in the past century. The re-migration is still ongoing. Nevertheless, a forest structure containing dead wood and snags is important in this process (Nascimbene, Dainese, & Sitzia, 2013).

The small number of plots used for investigating fungi and bacteria makes apparent that most other organismic groups cannot be investigated using a large grid. The level of detail required by such work is prohibitive. Thus, approaches other than regional distributions were used to identify mechanisms for differences in diversity. In this context, one major group of organisms that has been of conservation concern is the xylobiontic beetles. These are the most species rich organisms in forests, and it has been hypothesized that these organisms require large

quantities of dead wood (Müller and Büttler, 2010), which may only exist after major forest disturbances. Meanwhile it becomes apparent that it is not just the amount of dead wood but also the temperature that determines the presence of rare dead wood beetles (Müller, Boch, Blaser, Fischer, & Prati, 2015; Müller, Brustel, et al., 2015). 100 m³/ha can be lowered to about 12 m³/ha if the temperature on the forest floor increases by about 0.5 K. This amount of dead wood is lower than the average in managed forests of Germany. Thus, additional factors limit the distribution of dead wood beetles. To study the food preference of xylobionts, a dead wood experiment was established on a subset of inventory points. Logs of 4 m length and with a diameter of > 30 cm were exposed under different types of management (14 species, 3 regions, 5 replications, 5 management types for a total of 1050 logs). Wood-dwelling insects were collected over 5 years at regular intervals during each growing season (see Gossner et al., 2016). Multiple regression models were calculated to explain the observed number of xylobionts for each log.

Carpinus betulus and *Picea abies* turned out to be the woody species most preferred by xylobionts (Fig. 7). 90% of all captured beetles were found on these two woody species. *Quercus* added 5% to the diversity of observed species, and *Fagus* added an additional 1%. The maximum number found on single logs was not different for these 4 tree species. It was not possible to statistically separate the preference of RCN species among observed woody species, i.e. rare beetle species occurred on each tree species. It is possible that rare xylobionts prefer other species at later stages of decomposition. However, comparisons are difficult, because *Carpinus* has the highest decay rate of 13 woody species. The lowest decay rates were found in *Fraxinus* and *Quercus*. In nature, by the time that *Carpinus* has decomposed, remnants of *Fraxinus* and *Quercus* still exist and still house xylobionts. Nevertheless, species richness of Fungi and Coleoptera, and the mineral composition, determined the decay rate (Kahl et al., 2017). Thus, forest structure and changes with management determines beetle communities rather than conservation

Table 2
Comparison of species numbers (average ± standard deviation) of various organismic groups under different types of management. Plot size was 20 × 20 m. Number of plots was 1500 for plants, but only 3 for fungi, and 9 for bacteria.

	Conservation	Rotation forestry	Reference
Herbs (number/plot)	27 ± 1.3	32 ± 0.8	Boch, Prati, Müller, & Socher, (2013)
Mosses (number/plot)	7 ± 1.6	10 ± 0.8	Müller, Boch et al., 2015; Müller, Brustel, et al., 2015
Lichens (number/plot)	5 ± 0.5	5 ± 0.5	Boch, Prati, Hessenmöller, Schulze, & Fischer, (2013)
Fungi (number/plot)	17 ± 3.9	27 ± 3.5	Blaser, Prati, Senn-Irlt, & Fischer (2013)
Soil bacteria (OTUs/plot)	1296 ± 330	1337 ± 130	Felsmann et al. (2015)

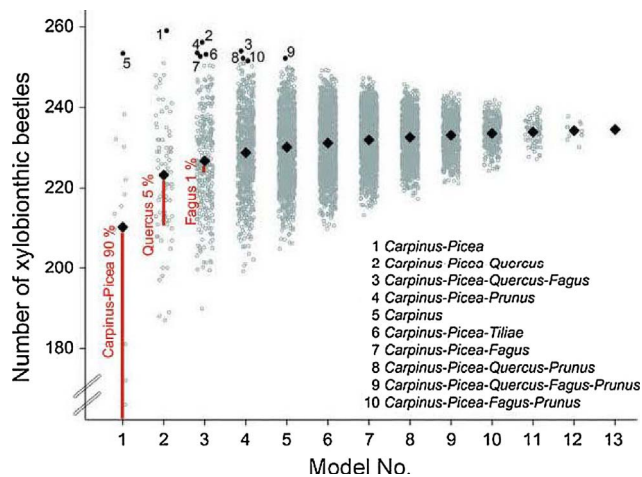


Fig. 7. Number of xylobiontic beetles as observed in single logs of freshly cut timber over 5 years of exposure. Each dot represents a log of a specific tree species. The diversity was explained by multiple regression models (1–10) using different tree species and tree species combinations as independent variables (see Gossner et al., 2016).

(Sitzia, Campagnaro, Gatti, Sommacal, & Kotze, 2015). The effects of climate remain unknown, but there are indications that rare xylobionts favor warmer climates (Müller et al., 2015b; Gossner personal communication), or exposure to the sun, as it is the case in managed forests (Seibold et al., 2014).

Carpinus occurs mainly in managed forest, and it is generally out-competed by *Fagus* in unmanaged forest (Burschel and Huss, 2003). It is unclear how the hornbeam-oak forests of Natura 2000 (habitat type 9170) can be maintained at all without management. *Picea* has been introduced into montane *Fagus* forests by planting in Germany. Thus, the type of wood and not wood mass attracts and maintains xylobionts, and the preferred tree species assembly is linked to management (Sitzia

et al., 2015). The same observations have been made for fungi (Purahong, Wubet, Krüger, & Buscot, 2016)

In this context it may be of interest to note that saproxylic beetles are known to increase in abundance and species richness in Eastern Europe. Defilkeul Jiului National Park in Romania was established based on the presence of 115 rare xylobionts representing the complete saproxylic beetle fauna of this region (Bussler, Müller, & Dorka, 2005). Defilkeul Jiului is a former coppice forest that supplied charcoal to the nearby iron industry in Petrosani. Thus, a history of intensive use and not protection was the historical basis for the high diversity of saproxylic beetles, and it remains unclear if these organisms will survive under protection. The Romanian forest reserve may serve as an example that present species richness is affected by historic management. In the case of Defilkeul Jiului, the rare species survived probably because of intensive management. However, once rare species are lost, or if by chance rare species were never present, comparing managed and unmanaged sites or plots will not lead to a conclusion of a negative effect of management. Thus, in the case of the wood-decay experiment by Gossner et al. (2016), history could have biased the result in that saproxylic were lost in the past in Thuringian forests, when forest management changed from coppice to high forest. Rare saproxylic species still exist in Thuringia in parks, road side trees, and other open habitats. Thus, the wood-decay experiment was repeated in southern, central and northern Germany, representing a gradient in forest history and climate, and making sure that rare dead wood xylobionts were still present in the associated fauna.

In a meta-analysis of the exploratory-experiment (see Fischer et al., 2010; Schall, Gossner, et al., 2017) compared alpha, beta and gamma diversity of 15 organismic groups along the same study sites of the wood-decay experiment, which is indeed the most comprehensive study on effects of management in Central Europe. The main result is that a coarse-grained heterogeneity of forest landscapes provided by different ages of tree cohorts is the major driver for biodiversity and makes sustainably managed forests superior to uneven-aged and unmanaged

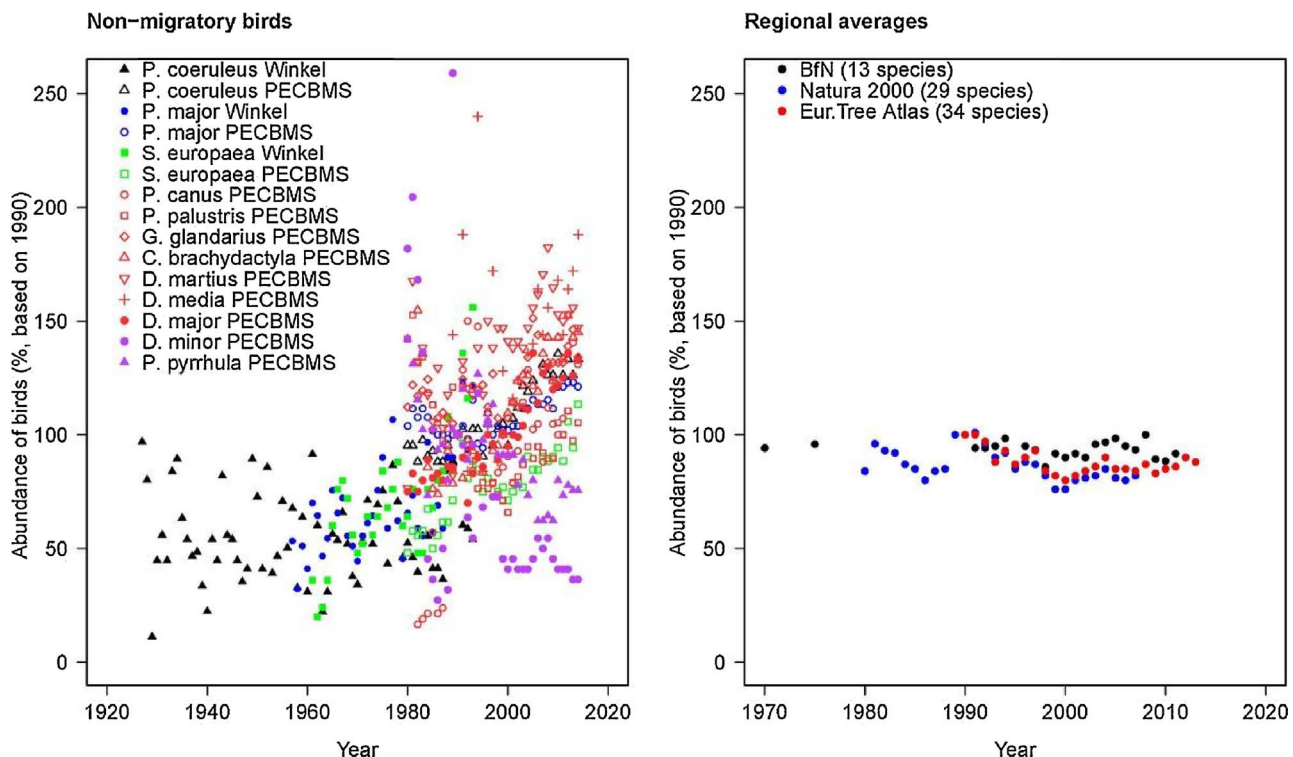


Fig. 8. (left panel): Time series of abundance of *Parus caeruleus* since 1927 (Berndt and Winkel, 1979), of *Parus major* and *Sitta europaea* since 1957 (Winkel, 2002), and of the following PECBMS European bird observations (www.wbcc.info/index.php?ID=612): *Picus canus*, *Parus palustris*, *Garrulus glandarius*, *Certhia brachydactyla*, *Dendrocarpus martius*, *Dendrocarpus media*, *Dendrocarpus minor*, and *Pyrrhula pyrrhula*.

forest. Plant diversity even determines the diversity of soil organic compounds (El Moujahid, Le Roux, Michalet, Bellvert, & Weigelt, 2017).

Even though the definition of the Natura 2000 Habitat Types is made on the basis of plant species, the assessment of biodiversity is made via bird species in Germany (BfN, 2015). Thus, it is of great interest to know about the trend in bird populations for forest ecosystems in Central Europe as an indicator for ecosystem “health”. This, however, is not easily possible because birds are not observed on a grid basis, and long-term population studies rarely extend before 1990. Fig. 8 summarizes studies for deciduous and coniferous forests in Germany based on the data available from several bird watching institutions, and from the Pan-European Common Bird Monitoring Scheme (PECBMS, 2016; <http://www.wbcc.info/index.php?ID=612>), which averages observations across Europe. Both approaches have their own high intrinsic uncertainties at the level of the individual observation (Berthold, pers. communication). Clearly, a grid-based observation system could improve our knowledge of bird-life (Sitzia, Dainese, Clementi, & Mattedi, 2014).

(right panel): Meta-analyses of forest bird populations of the German Biodiversity report (BfN, 2015) based on 13 rare and common, as well as migrating and non-migrating bird species, the European Natura 2000 report on forests (European Commission, 2015) based on 29 forest species, and of European Tree Atlas (San-Miguel-Ayabz, De Rigo, Caudullo, Tracy, & Mauri, 2016) based on 34 forest species.

The longest record is available for the Blue Tit, *Parus caeruleus*, which extends from 1927 until 2015 (Berndt and Winkel, 1979; Winkler, 2002, PECBMS-database, Fig. 8 left panel). Therefore *P. caeruleus* was included in this study even though it is not a strict forest specialist (PECBMS-database). The Blue Tit was initially studied using 3000 artificial nesting-holes that were placed over 1200 km² of *Fagus* forest near Braunschweig in northern Germany. The authors discuss that the numbers may be an overestimate of natural populations due to the nesting support. Nevertheless, the data show large annual variations, and the data merge into the PECBMS-data of natural populations. A linear regression through the data of Winkel reaches 56% abundance in 1970 and a linear regression through the PECBMS data predicts 55% abundance in 1970. Thus, the earlier observations are representative. The Blue Tit time series was complemented by observations on *Parus major* and *Sitta europaea* extending from 1957 until 2016 (Winkler, 2002), and by adding common non-migratory bird species since 1980 (PECBMS-data). Here we selected the data of all true forest species that are under observation in the European network and which do not migrate (Peterson, Mountfort, & Hallom, 1966; Tucker and Evans, 1997). We are aware that the number of species is limited by the observation system. All data were scaled to 1990 as 100% because 1990 is the endpoint of observations by Winkler (2002), and the beginning of the PECBMS observations. It should also be kept in mind that the population dynamics of individual bird species may be quite different for forests and for non-forest land. The Blue Tit may serve as an example of stable populations in forests, but the same bird species shows severely declining populations in non-forest land due to an increasing lack of nesting holes (Berthold, pers. communication).

In the PECBMS dataset, all but two species significantly increase in their abundance after 1970. The slope of increase is 1.5% of relative abundance per year since 1970. The increase appears to be related to climate change, providing longer growing seasons and milder temperatures in winter. The two species not participating in the increase but showing stable populations after 2000 are *Dendrocarpus minor* and *Pyrrhula pyrrhula*. *Parus palustris* is intermediate; its populations decreased since 1980 but increased again since 2000. The large variation of the relative abundances of the declining species could be due to absolutely low populations. The decrease in population of *Dendrocarpus minor* may have resulted from effects of forest decline in the 1980s providing a high number of dead trees at that time, while *Pyrrhula pyrrhula* appears to be affected by an intestinal disease (Berthold pers. communication).

Obviously most non-migratory bird species take advantage of climate change with warmer winters and longer growing seasons (Richardson et al., 2013), while migratory birds face increasing risks of hunting along the migration route, of land-use change in the winter habitats, and of a mismatch between breeding and food supply in the summer habitats (Bairlein, 2016). The mismatch of food supply and migration time may occur along the outgoing route in autumn as well as on the return route in spring. For instance, *Turdus philomelos* generally aggregates in large flocks to feed on fruits of *Sorbus aucuparia* in successional montane forest of Thuringia in October. In 2016 *Sorbus aucuparia* had a mast year, but only a few birds were feeding on the fruits. The swarms of *Turdus philomelos* arrived in December and visited the same *Sorbus* stands as every year but at a time when all the fruits had already dropped to the ground and been eaten by other ground-dwelling animals (Schulze, personal observation).

In contrast to the recent increase in abundance of non-migratory forest species, meta-analyses containing migratory and non-migratory, and common as well as rare species, show a constant level of bird populations since 1990 (Fig. 8, right panel). The German biodiversity assessment shows an average relative abundance of $95 \pm 1\%$ standard deviation for 13 forest species as related to 1990 abundance (BfN, 2015). The German BfN-data were officially scaled to about 80% in 1970 with the expectation that by taking forests out of management bird abundance would increase. However, this did not happen based on the selected “basket” of birds. The trend of stable average bird populations was confirmed by the EU-Natura 2000 Forest Report (European Commission, 2015), which shows decadal variations of $87\% \pm 7\%$ of the 1990 value for 29 forest bird species. Also, the European Atlas of Forest Tree Species (San-Miguel-Ayabz et al., 2016) shows a constant level for 34 forest bird species since 1995 ($88\% \pm 5\%$ based on 1990 abundance). The averages decline with an increasing number of species under consideration due to the increased fraction of migratory bird species. Thus downscaling of the German data to 80% taking 1970 as a baseline by the German Biodiversity Report (BfN, 2015) has no scientific basis in view of the other European meta-analyses, which are based on a larger set of bird species. It is unlikely that the abundances of migrating birds can be increased solely by conservation or management in Germany, because the populations of these species are regulated by conditions encountered during migration. However, the non-migrating forest bird species increased since 1970 by 57%, which is more than the German 20% correction factor.

Taking birds as indicator for “ecosystem health” in forests may contain a bias because other top predators declined, e.g. snakes (Serfling and Serfling, 2017). However, there is no European snake that is confined to forests. They all require open habitats. Thus, snakes may suffer from a loss of habitats under continuous canopy cover as it is the case under non-management or under management “close to nature”. Thus, snakes will not represent “ecosystem health” as we expect from birds. Also, the losses of wolves, bear and lynx (Hess, 1898) are not caused by a decline in ecosystems, but by intentional extinctions (Ott, 2004).

5. Effects of deer populations

Forest biodiversity is regulated not only by forest management or conservation, but also by hunting and deer populations. Hunting has its own legislation. Free living deer have no owner in Germany; they become the property of a hunter only when shot. Thus, effects of management and strategies for conservation cannot be discussed without recognition of the abundance of ungulates, which affect tree species composition (Ammer, 1996). In Europe, the roe-deer (*Capreolus capreolus*) feeds selectively on rare plant species and on species of preferred taste, which results in a shift of tree species dominance in deciduous forest. The effects of ungulate browsing on tree composition are far larger than the effects of management in deciduous forests (Schulze, Bouriaud, Wäldchen, et al., 2014).

Table 3

Loss of tree species due to ungulate browsing in the regeneration of forests under various types of management (632 plots protected, 1967 plots selection cutting, 670 plots age class, and 140 plots fenced forest). The specific effects of ungulates can be seen from fencing experiments (Schulze, 2014a; Lüpke et al., 2011).

No. tree species	Canopy	Regeneration 20–50 cm	Regeneration > 1.3m	Species loss %
Protected	18	11	6	67
Selection forest	20	18	7	65
Age class forest	21	16	10	52
Fenced plots	20	20	19	1

Here I present data (Table 3) based on the same inventory-grid mentioned above. Tree species richness decreased in managed and unmanaged forest with increasing height of regeneration. Compared to the canopy, the relative loss of tree species > 1.3 m height during regeneration is between 52 and 67%, with the highest losses under unmanaged conditions due to the higher ungulate populations following termination of hunting in the absence of any predators (Schulze, Bouriaud, Wäldchen, et al., 2014). With fencing, this loss of species disappears (Schulze, 2014). As discussed by Schulze, Bouriaud, Hessenmoeller (2016), there is a broad public consensus for maintaining large ungulate populations despite the obvious effects on diversity with all its biological consequences. There is no change in hunting policy visible, even in protected areas where the strategy of “letting nature be nature” enhances the problem, and despite of the fact that it is well-known that increased hunting activities could solve the problem (Hothorn and Müller, 2010).

Concerning conservation, the national parks focusing on temperate deciduous forest in Germany are located in former state hunting areas (details for Serrahn Natl. Park are summarized by Spieß, 2013; Kellerwald Natl. Park was even fenced for state hunts and the author participated in such hunts when he was young). The exception is Hainich Natl. Park, which was intensively used by local villages for wood, charcoal, soot, ash, and grazing during a time of unclear property rights of the nobility (Witticke and Biehl, 2009). In contrast, the monotypic stands of *Fagus* in Serrahn, Grumsin, Ascona, and Kellerwald compared to the tree species richness of Hainich are a consequence of deer browsing.

6. Expected effects of climate change

The need for forest diversity has been recognized as major tool for maintaining ecosystem services under conditions of climate change (Isbell, Craven, & Connolly, 2015) and for climate mitigation. Biomass production was chosen in most studies as major parameter to quantify effects of diversity (Hickler, Bolte, & Hartard, 2014) despite the fact that biomass production is controlled to a large extent by management in temperate and boreal ecosystems (Birdsey and Pan, 2015; Campioli et al., 2015; Noormets et al., 2015).

For grasslands it is well established that productivity increases with plant species diversity (Hector, Schmid, & Beierkuhnlein, 1999). It was also established for grasslands that abundance and species richness of all other organisms depends on plant diversity (Scherber et al., 2010). This holds even for belowground organisms that rely on root exudates and fungal biomass (Eisenhauer et al., 2017). Plant diversity promotes temporal stability (Proulx, Wirth, & Voigt, 2010) and supports numerous additional ecosystem functions in addition to productivity (Allan, Breshherds, & McDowell, 2015).

It remains difficult to reproduce these diversity effects for forests, due to their legacy in structure and composition (Sitzia and Trentanovi, 2011). A major attempt was made by Liang et al. (2016), who established a productivity-diversity relationship from a global forest database. Thus, a loss of forest species could potentially have a “cost” in mitigation capacity via productivity. The productivity-diversity

Table 4

The fraction of total forest area (%) as occupied by different forest species and being affected by drought under present climate conditions and as expected in the future (Spellmann et al., 2015).

	1981 to 2016 (% of forest area)	2041 to 2070 (% of forest area)
<i>Picea</i>	8.9	62.5
<i>Fagus</i>	5.6	56.0
<i>Quercus</i>	< 1	< 1
<i>Pinus</i>	< 1	< 1

relationship of Liang et al. (2016) is still under discussion, because managed forests with few species reach the highest productivity in a global comparison. Thus, the conflict between achieving the highest level of climate mitigation via conservation or via intensive management remains. However, climate change will affect ecosystem structure and composition beyond productivity. According to a model analysis of Spellmann et al. (2015) only 6–9% of spruce and beech forest grew in habitats with a high risk of drought in 2015. This situation will change in the future. By 2050, 55% to 65% of spruce and beech forest will experience a high risk of drought. Only pine and oak forests appear to be more drought-adapted. All species are expected to decrease in productivity. Based on these predictions, major changes in forest composition are to be expected in the next decades, and these changes will be preceded by an increasing spread of tree diseases prior to climate change (Schulze et al., 2015) (Table 4).

The predicted change in climate and forest species distributions has major consequences for nature conservation of Natura 2000, which aims at maintaining the present diversity in geographically confined regions without allowing for invasion by non-native species even though such species may be indigenous and fill open niches (see Pearce, 2015). The concept of Natura 2000 is based on a phyto-sociological classification (Braun-Blanquet, 1964), a concept which has been questioned in population biology due to the fact that species move individually (e.g. Day, Hutchings, & Watkinson, 1987). Nevertheless, the concept was maintained in conservation as a tool of communication between practitioners. Maintaining phyto-sociological units will probably not be possible under global change. This will also make Appropriate Assessments of Natura 2000 regions (Article 6.3 of the Habitat Directive) rather difficult (Sitzia, Campagnaro, & Grigolato, 2016). Especially endangered are large blocks of protected areas, which cannot be moved. In fact, protected areas may serve as a baseline of increasing species change where an interaction among climate change, invasion, ungulate effects, and modern pests and diseases exists. These changes are not recognized by the Natura 2000 Directive, which tries to avoid any deterioration of habitats (Article 6.2) despite of know effects of diseases. The present flora and fauna could probably be best supported by a grid-based regional network of small plots, representing a diversity of structures, or by sustainable forest management maintaining a diversity of tree species under strict control of ungulate populations (Rösch, Tscharnke, Scherber, & Bara, 2015). After all, the present diversity of temperate European forests results from management in the past centuries. Given this situation, most likely the native species assemblage will need support from non-native or palaeo-neophytic tree species in the near future because the temperate European forest tree flora consists mostly of genera that are mono-specific, and many of these species are endangered by pests and diseases. In fact, the East Asian and North American deciduous tree flora may be more resilient to climate change due to the species richness within genera and the associated possibility of evolution via hybridization (see Huang et al., 2016), which is not possible among the monotypic genera of Europe's forests (Soltis, Clayton, & Soltis, 2014). Thus, if European species fail due to climate change, the open niche may be filled by closely related species that still exist in East Asia or North America (Schulze et al., 2015).

7. The ecological footprint of taking forests out of management

In a world of increasing human needs and activities, and global trade under conditions of uneven distribution of species richness across the globe, there are effects of conservation at one location on other places of this globe, which may be non-linear. In the following I try to point at such linkages.

The German Strategy of Biodiversity (Nationale Strategie zur biologischen Vielfalt, 2008) plans to set aside 5% of the forest area to be unmanaged, focusing on broad-leaved forests. In addition, there is a political pressure for FSC certification in public forests. Since forest growth is balancing the wood demand neither in Germany nor in Europe (Seintsch and Weimar, 2013; Forest Europe, 2015), the request of setting aside 5% of the forest area has immediate consequences for imports. Since the wood balance is assessed at a national level, an estimate about the external cost of conservation and certification is not possible at an ecosystem or regional scale. Therefore, here I present an estimate of the effects of conservation and certification at the national level of Germany, assuming that extra wood would be exported from boreal forests, mainly in Russia or Eastern Europe (Schulze, Frör, & Hessenmöller, 2016).

The forest area of Germany is about 11 Mill ha with an average annual volume increment of $11 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$ being harvested and a loss of residues of about 20%. If 5% of this forest area is taken out of management following the German Biodiversity Strategy (Nationale Strategie zur biologischen Vielfalt, 2008), and only 3% (and not the newly required 10%) of the forest area is taken out of management as baseline for FSC-certification, with additional 10 habitat trees ha^{-1} as requested by FSC, and a change in forest management from rotation forest towards “permanent forest cover”, this will result in an estimated loss of harvested wood of about 26 Mill $\text{m}^3 \text{ year}^{-1}$ for Germany. In order to close demand with supply, additional wood needs to be imported by Germany, and the source is most likely the boreal forest region of Asia or Eastern Europe, where volume increment is on the order of $1\text{--}1.5 \text{ m}^3 \text{ ha}^{-1} \text{ yr}^{-1}$, and harvest residues exceed 50%. There is a 20-fold difference in growth and harvesting efficiency between Germany and Eastern Europe. Thus, taking 5% of forest out of management requires an area equivalent to the total forest area of Germany to be clear cut in Eastern Europe each year, enlarging the ecological footprint of Germany significantly. If this import strategy will remain in the future, a sustainable clear-cutting in Russia will require a 200-fold of the German forest area due to a 200 year rotation in Siberian forests.

Similar considerations about the effects of conservation on the ecological footprint are also most likely applicable to Europe as a whole, due to the fact that the demand for wood and wood products is higher than forest growth (Forest Europe, 2014). The increased imports from boreal forests in Asia and North America are an immediate indicator of these effects (SRREN, 2011; EUWID, 2017). The footprint could be reduced by imports from tropical plantations.

8. Synthesis

The present study is an attempt to summarize the multiple facets that determine biodiversity in managed and unmanaged forest, and most likely, the number of interactions in nature is even more diverse. Nevertheless, the numerous parameters tend to point in the same direction. Sustainable forest management, as it is exercised in Europe, promotes rather than diminishes organismic diversity, even for endangered species, as compared to unmanaged forests. The number of plant species in unmanaged forest or selection forests decreases compared to rotation forestry. Creating large openings and larger cohorts of different-aged trees and diverse canopies appears to be a major driver for most, if not all other organisms. This also includes the creation of larger openings in the canopy by harvesting, which are opportunities for species migration and changes in mixture as well as generating logging residues. These openings should be large enough to create a

northern and a southern edge, which results in a microclimate that is equivalent to several degrees of latitude. Clear cuts are presently forbidden by German forest law, but the existing evidences on biodiversity may have to change this act. Also, taming and thinning of young stands, where wood below 10–15 cm diameter is not used but left on site, has major ecological implications. The plant diversity of forests is not only determined by tree diversity, but consists to a large extent of herbaceous species that require light at the forest floor, and these light conditions are reduced in un-managed and in selectively cut forest. The decadal change in canopy density of managed forest also allows a re-establishment of species under conditions of permanent change. Only rarely, a single species may become dominant, such as *Allium ursinum* or *Mercurialis perennis*, but these stages are not permanent in managed forest. Under conditions of changes in available light, some species are even stimulated to flower and to set seed after thinning, e.g. *Lilium martagon* or *Cephalanthera rubra* and *C. longifolia*, which flower and set fruits abundantly after thinning (Schulze, personal observations).

It also emerges that forests contain ecosystem properties that were described in detail for grasslands. Most other organisms follow the diversity of plant species. Thus, it remains of ultimate importance that management maintains a coarse-grained canopy mixture in rotation forests. The presence of *Carpinus* dead wood and the dynamics of bird populations may be the living example for the importance of mixed forests, which are endangered mainly by insufficient deer regulation.

Two major problems remain:

Firstly, one expectation of nature conservation is that managed forests do not get old enough, and miss the age of so-called “old-growth forest”. In analyzing the grid based inventories of deciduous forests in Thuringia it emerges that unmanaged forest is not different from managed forest along a volume versus tree age plot (Fig. 9). One could argue that unmanaged forests in Germany have not yet reached the stage of old growth forest, which is expected in a few centuries. Therefore, Fig. 9 also contains the volume/age data of plots from the

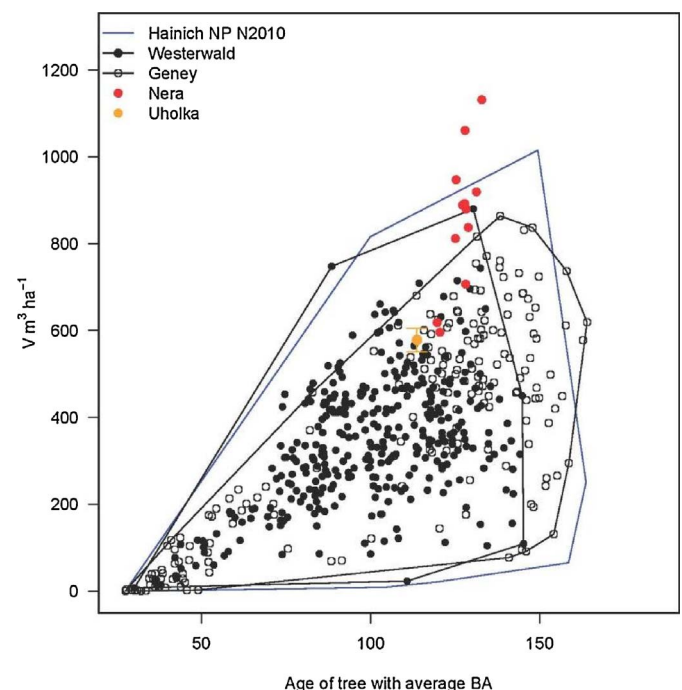


Fig. 9. Scatter plots and border lines of stand volumes as related to the age of the stem with average basal area of the age class forests of Westerwald and Geney in Thuringia and of Hainich National Park in Thuringia (Schulze, 2017). The Thuringian data are from grid-based inventories. Also included are existing plots of the *Fagus*-dominated Nera National Park in Romania (Turcu, 2012) and the average and standard deviation of a grid based inventory at Uholka (Commermot: www.wsl.ch/fe/Waldressourcen/projekte/uholka/index_DE).

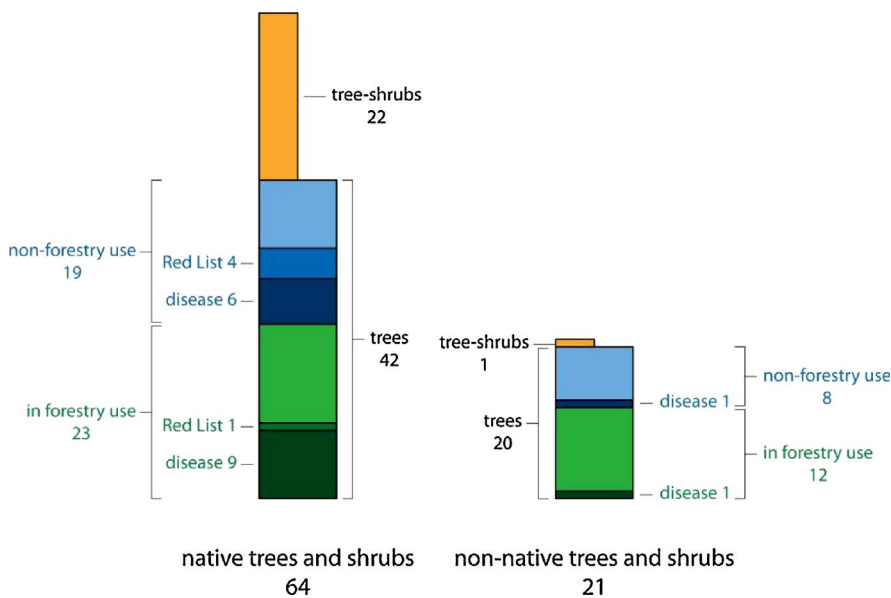


Fig. 10. The distribution of major tree diseases among trees in forest use and in trees not in use for native and non-native species (after Schulze et al., 2015).

“old” virgin forest, such as Nera National Park (=Semenic, see Fig. 5) in Romania and of Uholka in the Ukraine (Hobi, Commarmot, & Bugmann, 2015). Both parks are dominated by *Fagus sylvatica* canopies. Unexpectedly, the wood volumes on inventory plots of managed age class forests in Germany are larger than in Uholka, and in the same range as in Nera, and trees are older in managed forest than in the reference national parks. Apparently, the age of trees under unmanaged conditions is limited by wood-decomposing fungi, mainly of *Fomes fomentaria* in the aboveground parts of the tree and of *Armillaria mellea* belowground (Schulze, 2017). This does not rule out that some very old trees exist in unmanaged but also under managed conditions. Thus, it is predicted that plot-scale volumes and ages will decrease rather than increase with conservation.

Fig. 9 is based on the age of the tree with average basal area which neglects the plot-scale variation in age and in volume, even though the average of the quadratic mean diameter tree favors larger diameter trees. In the case of Fig. 9 the lower threshold of DBH was 7 cm. In order to further investigate the effect of management on tree size, Schulze (2017) selected the largest diameter tree from a total of about 2 million measured DBHs of the grid based inventory. The largest beech tree standing in a closed canopy had a DBH of 116 cm and this forest was managed by selective cutting. The largest DBH of unmanaged forest was lower, namely 110.5 cm. The same relation was true for the 10 and the 100 largest beech trees. In all cases the managed forest had larger DBH than the unmanaged forest. Based on a DBH-age relation (Schöning et al., 2013) the age of the largest tree was estimated to be 186 years, the average age of the 10 biggest trees was estimated to be 179 years, and the average age of the 100 biggest trees was estimated to be 171 years, and these ages were similar for the slightly thinner trees under non-management (Schulze, 2017). As mentioned above, the age of beech is limited by wood-decaying fungi. The oldest beech tree that has been sampled in Thuringia on a limestone cliff (Dün region, North Thuringia) was 286 years old, but this cliff was not included in the grid based forest inventory, due to an open canopy.

Secondly, the European tree flora contains a major hidden risk that may become increasingly apparent under conditions of global change: an impoverished flora that migrated to Europe from genetic refugia in the Caucasus and the Mediterranean Basin. Most species are monotypic representatives of genera that are much more diverse in North America and East Asia. Essentially all tree species in Central Europe have a post-glacial migratory background, which makes distinguishing between native and alien species an obsolete mindset. Since diseases are an early warning sign of climate change, we should be aware that almost 50% of

the European tree species carry lethal diseases that seriously endanger these species in the future, the elm and ash disease may serve as examples (Fig. 10). Thus, we should be more open towards so-called “alien” species that, in part, were present in Europe before the Pleistocene. The hotspots of diversity for Europe are the Caucasus and East Asia, and we may need these genetic resources in the future to maintain our forests (see also Allen et al., 2015). At this moment, conservation enlarges the ecological footprint of Europe into Asia, and we are in the process of destroying our genetic background. Thus, maintaining diversity by use may be more rational than pure conservation efforts in Europe.

The question remains whether data from Europe can be extrapolated to other regions of the world. In this context it is of interest to realize that an anthropogenic basis of existing forest vegetation is increasingly emerging, even in the tropics. A recent study by Levis et al. (2017) shows that even the Amazonian rain forest contains a persistent effect of pre-Columbian plant domestication. The situation in Europe appears to be special, in that sustainable management has reached a level of diversity that is beyond un-managed situations. This makes sustainable management rather than conservation necessary.

9. Conclusions

Biodiversity of forests contains only about 10% of the plant species that exist in the flora of Germany, and this low fraction is similar in other European countries. The majority of plant species (and most likely also most other organisms) also exist in non-forest habitats.

In temperate deciduous forests, sustainable forest management provides habitats for endangered, protected and responsibility species of various organismic groups at similar or even higher abundance than in unmanaged forest.

A grid based inventory of managed and unmanaged regions shows that wood volumes do not increase under unmanaged conditions, and the age of the tree with average basal area is even lower in unmanaged than in managed forests. This observation is confirmed by data on single trees. The largest and the oldest tree were found in managed forest. The present managed forest contains all features of “old growth stands” as components of a coarse-grained matrix of structural diversity.

There is no record of extinction of a plant species that was a forest specialist over the past 250 years in Germany. The record of other organismic groups is less clear. There is no organism that is confined in its distribution to unmanaged forest. We cannot confirm that sustainable

forestry is a major threat to diversity in temperate deciduous forests as suggested by the German BfN-report, but differences may emerge depending on the dominant tree species. The recent National Parks were established on areas where a limited number of species had been historically sustained by management, or in areas where past hunting regimes resulted in Beech-monocultures.

In view of climate change and the associated expected changes of ecosystems, the survival of specific habitats and species may only be possible by sustainable land management at large scales, and not by protection of fixed pieces of land which cannot be moved under climate change.

The present conservation schemes appear not to provide the necessary dynamic to cope with the expected situation of global climate change..

Acknowledgements

I greatly appreciate the help of Dr Franz Bairlein, Vogelwarte Helgoland, and Prof Peter Berthold, Vogelwarte Radolfzell, to finding data of long-term observations on bird populations. I also appreciate the help of Annett Boerner and of Marcus Guderle in preparing the figures. I thank Dr Andrew Durso for thorough English language text editing, and I thank the anonymous referees for very constructive suggestions. The work was supported by the > Max-Planck Society.

References

- Akhmetiev, M. A., & Zaporozhets, N. I. (2014). Paleogene events in Central Eurasia: Their role in the flora and vegetation cover evolution, migration of phytochore boundaries, and climate change. *Stratigraphy and Geological Correlations*, 22, 312–335.
- Allan, C. D., Breshherds, D. D., & McDowell, N. G. (2015). On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. *Ecosphere*, 6, 10 [article 129].
- Ammer, C. (1996). Impacts of ungulates on structure and dynamics of natural regeneration of mixed mountain forests in the Bavarian alps. *Forest Ecology and Management*, 88, 43–53.
- Bairlein, F. (2016). Migratory birds under threat. *Science*, 354, 547–548.
- Berndt, R., & Winkel, W. (1979). Zur populationsentwicklung von blaumeise (*Parus caeruleus*), kleiber (*Sitta europaea*), gartenrotschwanz (*Phoenicurus phoenicurus*) und wendehals (*Jynx torquilla*) in mitteleuropäischen untersuchungsgebieten von 1927 bis 1978. *Die Vogelwelt*, 1979, 55–69.
- BfN (2015). *Artenschutz-report 2015*. Bonn: Tiere und Pflanzen in Deutschland [61pp].
- Birdsey, R., & Pan, Y. (2015). Trends in management of the world's forests and impacts on carbon stocks. *Forest Ecology and Management*, 355, 83–90.
- Blaser, S., Prati, D., Senn-Irlt, B., & Fischer, M. (2013). Effects of forest management on the diversity of deadwood-inhabiting fungi in Central Europe forests. *Forest Ecology and Management*, 304, 42–48.
- Boch, S., Prati, D., Hessenmöller, D., Schulze, E. D., & Fischer, M. (2013). Richness of lichen species, especially of threatened ones, is promoted by management methods furthering stand continuity. *PlosOne*, 8, e55641.
- Boch, S., Prati, D., Müller, J., Socker, S., Baumbach, H., Buscot et al, F., et al. (2013). High plant species richness indicates management-related disturbances rather than conservation status of forests. *Basic and Applied Ecology*, 14, 496–505.
- Bozga, S. B. C., Indreica, A. V., & Lazar, G. (2013). *Flori din padurile romaniei. editura green steps, bracov*. [496pp].
- Brang, P., Hallenbarter, D., Rohrer, L., Commarmot, B., Heiri, C., & Bugmann, H. (2009). Insight from 50 years of research in natural forest dynamics in Switzerland. *4th symposium of the hohe tauern national park for research in protected areas* (pp. 41–44). Braun-Blanquet, J. (1964). *Pflanzensoziologie*. 3. aufl. Wien: Verlag [865pp]. 1. Aufl. 1928].
- Burschel, P., & Huss, J. (2003). *Grundriss des waldbaus*. Stuttgart: Ulmer Verlag [487pp].
- Bussler, H., Müller, J., & Dorka, V. (2005). European natural heritage: The saproxylic beetles in the proposed parcul national defileu jiuului. *Anale ICAS*, 48, 3–19.
- Campio, M., Vicca, S., Luyssaert, S., Bilcke, J., Ceschia, E., Chapin, F. S., III, et al. (2015). Biomass production efficiency controlled by management in temperate and boreal ecosystems. *Nature Geoscience*. <http://dx.doi.org/10.1038/NGEO2553>.
- Candrea-Bozga, S. B., Indreica, A. V., & Lazar, G. (2013). *Flori din padurile romaniei*. Brasov: Editura Geen Steps [495pp].
- Ciocalan, V. (2009). *Flora ilustrata a romaniei*. Bucurest: Editura Ceres1141.
- Day, A. J., Hutchings, M. J., & Watkinson, A. R. (1987). *Plant population ecology*. Blackwell Oxford [478pp].
- Denk, T., & Grimm, G. W. (2009). The biogeographic history of beech trees. *Review of Palaeobotany and Palynology*, 158, 83–100.
- EUWD (2017). *Russland hat 24% mehr Nadel-schnittholz exportiert*. Holz- und Holzwerkstoffe [7.2017:6.].
- Eisenhauer, N., Lanoue, A., Strecker, T., Scheu, S., Steinauer, K., Tharkur, M. P., et al. (2017). Root biomass and exudates link plant diversity with soil bacterial and fungal biomass. *Scientific Reports*, 7 [55641, 8pp].
- El Moujahid, L., Le Roux, X., Michalet, S., Bellvert, F., & Weigelt, A. (2017). poly F Effects of plant diversity on the diversity of soil organic compounds. *PlosOne*, 16. <http://dx.doi.org/10.1371/journal.pone.0170494>.
- Endrodi, A., & Gyulai, F. (2000). Hearths and other finds of the late copper age Baden culture at Budapest-Csepel Island (Gynaecomorphic vessels, Archaeobotanical remains). *Archaeological Értesito*, 125, 9–44.
- European Commission (2007). *Interpretation manual of European Union Habitats EUR 17*. 1–144.
- European Commission (2015). *Natura 2000 and Forests. Part I and II*. 112.
- Felsmann, K., Baudis, M., Gimbel, K., Kayler, Z. E., Ellerbrock, R., & Bruehlheide, H. (2015). Soil bacterial community structure responses to precipitation reduction and forest management in forest ecosystems across Germany. *PlosOne*, 10.
- Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., et al. (2010). Implementing large-scale and long-term functional biodiversity research: the biodiversity exploratories. *Basic and Applied Ecology*, 11, 473–485.
- Forest Europe (2015). *Sate of europe's forests 2015*. Madrid: Forest Europe Liaison Unit [314 pp].
- Global Biodiversity Assessment (1995). *Global biodiversity assessment UNEP*. 1140: Cambridge University Press.
- Gossner, M. M., Wende, B., Levick, S., Schall, P., Floren, A., Linsenmair, K. E., et al. (2016). Deadwood enrichment in European forests – Which tree species should be used to promote saproxylic beetle diversity? *Biological Conservation*, 201, 92–102.
- Grimsson, F., Grimm, G. W., Zetter, R., & Denk, T. (2016). Cretaceous and Paleogene Fagaceae from North America and Greenland: evidence for a Late Cretaceous split between Fagus and the remaining Fagaceae. *Acta Palaeobotanica*, 56, 307–327.
- Grossmann, M. (2012). alte buchenwälder deutschlands sind weltnaturerbe. *AFZ-Der Wald Special Issue*, 1–27 [Special Issue].
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., et al. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Hess, H. (1898). *Der Thüringer wald in alten zeiten*. Gotha: Perthes Verlag [72pp].
- Hessenmöller, D., Nieschulze, J., Lüpke, N., & Schulze, E. D. (2011). Identification of forest management types from ground based and remotely sensed variables and the effect of forest management on forest structure and composition. *Forstarchiv*, 82, 171–183.
- Hickler, T., Bolte, A., Hatard, B., Beierkuhnlein, C., Blaschke, M., Blick, T., et al. (2014). Folgen des klimawandels für die biodiversität in wald und forst. In V. Moosbrugger, G. Brasseur, M. Schaller, & B. Stritny (Eds.). *Klimawandel und biodiversität: folgen für deutschland* (pp. 164–221). (2nc ed.). Darmstadt: WBG.
- Hilger, T., Lewandowski, I., Winkler, B., Ramsperger, B., Kageyama, P., & Colombo, C. (2015a). Seeds of change—Plant genetic resources and People's livelihoods. *Intech*, 24. <http://dx.doi.org/10.5772/59984>.
- Hilger, T., Lewandowski, I., Winkler, B., Ramsperger, B., Kageyama, P., & Colombo, C. (2015b). Seeds of change – Plant genetic resources and people's livelihood. *Intech*, 24 [Chapter5].
- Hobi, M. L., Commarmot, B., & Bugmann, H. (2015). Pattern and process in the largest primeval beech forest of Europe (Ukrainian Carpathians). *Journal Vegetable Science*, 26, 323–332.
- Hothorn, T., & Müller, J. (2010). large-scale reduction of ungulate browsing by managed sport hunting. *Forest Ecology and Management*, 260, 1416–1423.
- Huang, X., Yang, S., Gong, J., Zhao, Q., Feng, Q., Zhan, Q., et al. (2016). Genomic architecture of heterosis for yield traits in rice. *Nature*, 537, 629–636.
- Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., Beierkuhnlein, C., et al. (2015). Biodiversity increases the resistance of ecosystem productivity to climate extremes. *Nature*, 526, 574–577.
- Köstler, J. (1934). *Geschichte des waldes in Altbayern*. München: Beck'sche Verlagshandlung [174pp].
- Küster, H. (1998). *Geschichte des waldes*. München: Beck Verlag [267pp].
- Kahl, T., Arnstadt, T., Baber, K., Bässler, C., Bauhus, J., Borken, W., et al. (2017). Wood decay rates of 13 temeptrate tree species in relation to wood properties, enzyme activities and organismic diversity. *Forest Ecology and Management*, 391, 86–95.
- Korneck, D., Schnittler, M., & Vollmer, I. (1996). Rote liste der farn- und blütenpflanzen (Pteridophyta et spermantophyta) deutschlands. *Schriftenreihe für Vegetationskunde*, 28, 21–187.
- Korsch, H., & Westhus, W. (2011). Rote Liste der Farn- und Blütenpflanzen (Pteridophyta et Spermatophyta) Thüringens. *Naturschutzreport*, 26, 365–390.
- Kunzmann, L. (2014). On the fossil history of *Pseudotsuga* Carr. (*Pinaceae*) in Europe. *Palaeobiodiversity and Palaeoenvironments*, 94, 393–409.
- Lüpke von, N., Hardtke, A., Lück, M., Hessenmöller, D., Ammer, C., & Schulze, E. D. (2011). Bestandesvorrat, Baumartenvielfalt und Struktur kleinparzellierter Privatwälder im Hainich. *Forstarchiv*, 82, 203–215.
- Levis, C., Costa, F. R. C., Boungers, F., Pena-Claros, M., Clement, C. R., Junqueira, A. R., et al. (2017). Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*, 355, 925–931.
- Liang, J., Crowther, T. W., Picard, N., Wiser, S., Zhou, M., Alberti, G., et al. (2016). Positive biodiversity-productivity relationship predominant in global forests. *Science*, 354, 196–208.
- Ludwig, G., May, R., & Otto, C. (2007). *Verantwortlichkeit deutschlands für die weltweite erhaltung der farn- und blütenpflanzen-vorläufige liste*. BfN-Skript 220. Bonn: BfN [102pp].
- Lyons, S. K., Amatangelo, K. I., Behrensmeier, A. K., Bercovici, A., Blois, J. L., Davis, M., et al. (2016). Holocene shifts in the assembly of plant and animal communities implicate human impacts. *Nature*, 529, 80–83.
- Mölder, A., Streit, M., & Schmidt, W. (2014). When beech strikes back: how strict nature

- conservation reduces herb-layer diversity and productivity in Central European deciduous forests. *Forest Ecology and Management*, 319, 51–61.
- Müller, J., & Büttler, R. (2010). A review of habitat thresholds for dead wood, a baseline for management recommendations in European forests. *European Journal of Forest Research*, 129, 981–992.
- Müller, J., Boch, S., Blaser, S., Fischer, M., & Prati, D. (2015). Effects of forest management on bryophyte communities on dead wood. *Nova Hedwigia*, 100, 423–438.
- Müller, J., Brustel, H., Brin, A., Bouget, C., Obermaier, E., Heidinger, I. M. M., et al. (2015). Increasing temperature may compensate for lower amounts of dead wood in driving richness of saproxylic beetles. *Ecography*, 38, 499–509.
- Magri, D. (2008). Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). *J Biogeography*, 35, 450–463.
- Mittermeier, R. A., Turner, W. R., Larsen, F. W., Brooks, T. M., & Gascon, C. (2011). Global biodiversity conservation: the critical role of hotspots. In F. E. Zachos, & J. C. Habel (Eds.). *Biodiversity hotspots* (pp. 3–22). Berlin Heidelberg: Springer.
- Nascimbene, J., Dainese, M., & Sitzia, T. (2013). Contrasting responses of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver for mature woodlands. *Forest Ecology and Management*, 289, 325–332.
- Nationale Strategie zur Biologischen Vielfalt (2008). *Bundesministerium für Umwelt, Bonn: Naturschutz und Reaktorsicherheit* [178pp].
- Noormets, A., Epron, D., Domec, J. C., McNulty, S. G., Fox, T., Sun, G., et al. (2015). Effects of forest management on productivity and carbon sequestration: a review and hypothesis. *Forest Ecology and Management*, 355, 124–140.
- Ott, W. (2004). *Die besiegte wildnis: wie Bär, wolf, luchs und steinadler aus unserer heimat verschwanden*. Leinfelden-Echterdingen: DRW-Verlag.
- PECBMS (2016). *Trends of common birds in Europe, 2016 update*. <http://www.ebcc.info/index.php?ID=612>.
- Paillat, Y., Bergès, L., Hjeltén, J., Ödor, P., Aron, C., Bernhardt-Römermann, M., et al. (2010). Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conservation Biology*, 24, 101–112.
- Pearce, F. (2015). *The new wild. why invasive species will be nature's salvation*. Icon books [330pp].
- Peterson, R., Mountfort, G., & Hallom, P. A. D. (1966). *A field guide to the birds of Britain and Europe German translation*. Hamburg: Parey [417pp].
- Pimm, S. L., Jenkins, C. N., Abell, R., Brooks, T. M., Gittleman, J. I., Joppa, L. N., et al. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science*, 344, 987–999.
- Proulx, R., Wirth, C., Voigt, W., Weigel, A., Roscher, C., Attinger, S., et al. (2010). Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands. *PUBLIC LIBRARY OF SCIENCE*, 5.
- Purahong, W., Wubet, T., Krüger, D., & Buscot, F. (2016). Molecular evidence strongly supports unexpected tree species preferences of deadwood-3 inhabiting fungi in temperate forests. *The ISME Journal* [in press].
- Rösch, V., Tscharnke, T., Scherber, C., & Baraty, P. (2015). Biodiversity conservation across taxa and landscapes requires many small as well as single large habitat fragments. *Oecologia* [10.1007/s00442-015-3315-5].
- Renner, S. S., Grimm, G. W., Kapli, P., & Denk, T. (2016). Species relationships and divergence time series in beeches: new insights from the inclusion of 53 young and old fossils in a birth-death clock model. *Philosophical Transactions of the Royal Society B*, 371 [20150135].
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M. (2013). Climate change, phenology, and phenological control on vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156–173.
- SRREN (2011). *Renewable energy sources and climate change mitigation. special report of the intergovernmental panel on climate change* Cambridge University Press Cambridge [2088 pp].
- San-Miguel-Ayabz, J., De Rigo, D., Caudullo, G., Tracy, H. D., & Mauri, A. (2016). *European atlas of forest tree species*. Luxembourg: Publication Office of the European Union [204pp].
- Schall, P., Ammer, C., Ayasse, M., Schulze, E. D., & Fischer, M. (2017). The impact of forest management on stand structure and productivity. *Basic and Applied Ecology* [in print].
- Schall, P., Gonner, M. M., heinrichs, S., Fischer, M., Boch, S., Prati, D., et al. (2017). Unforeseeable effects of forest management systems on biodiversity of temperate European beech forest – the habitat heterogeneity dilution. *J Applied Ecology*. <http://dx.doi.org/10.1111/1365-2664.12950> [Advance online publication].
- Scherber, C., Eisenhauer, N., Weisser, W., Schmid, B., Voigt, W., Fischer, M., et al. (2010). Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, 468, 553–556.
- Schmidt, M., Kriebitzsch, W. U., & Ewald, J. (2011). Waldartenlisten der farn- und blütenpflanzen, moose und pflanzen deutschlands. *BfN-Skript*, 299, 109pp.
- Schulze, E. D., & Ammer, C. H. (2015). Spannungsfeld forstwirtschaft und naturschutz. *Biuz*, 5, 304–314.
- Schulze, E. D., Aas, G., Grimm, G. W., Gossner, M. M., Walentowski, H., Ammer, C., et al. (2015). A review on plant diversity and forest management of European beech forest. *European Journal of Forest Research*, 135, 51–67.
- Schulze, E. D. (2014). Zuwachs und Entmischung der Verjüngung im Laubwald mit und ohne Wildverbiss. *AFZ-Der Wald*, 11, 26–27.
- Schulze, E. D. (2017). *Biodiversität und waldbewirtschaftung im laubwald. artenschutz report5* [in print].
- Schulze, E. D., Boch, S., Müller, J., Levick, S. R., & Schumacher, J. (2016). Seltene und gefährdete pflanzen wachsen im laubwald überall. *AFZ-DerWald*, 13, 35–38.
- Schulze, E. D., Bouriaud, L., Bussler, H., Gossner, M., Walentowski, H., Hessenmöller, D., et al. (2014). Opinion paper: forest management and biodiversity. *Web Ecology*, 14, 3–10.
- Schulze, E. D., Bouriaud, O., Wäldchen, J., Eisenhauer, N., Walentowski, H., Seele, C., et al. (2014). Ungulate browsing causes species loss in deciduous forests independent of community dynamics and silvicultural management in Central and Southeastern Europe. *Annals of Forest Research*, 57, 267–288.
- Schulze, E. D., Bouriaud, L., & Hessenmoeller, D. (2016). Wald vor wild oder wild vor wald. problematik der wildschäden. *Bündener Wald*, 69, 5–11.
- Schulze, E. D., Frör, O., & Hessenmöller, D. (2016). Externe ökologische folgen von Flächenstilllegungen im wald. *AFZ-DerWald*, 15, 24–26.
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidt, J., Thorn, S., et al. (2014). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29, 382–390.
- Seintsch, B., & Weimar, H. (2013). *Holzbilanzen 2010 bis 2012 für die bundesrepublik deutschland Thünen working paper*, 9, 1–37.
- Serfling, C., & Serfling, F. (2017). Untersuchungen zur bestandessituation der kreuzotter *Vipera berus* im Thüringer wald und seinen randbereichen im jahr 2015. *Landchaftspflege Und Naturschutz in Thüringen*, 54, 3–9.
- Sitzia, T., & Trentanovi, G. (2011). Maggengo meadow patches enclosed by forests in the Italian Alps: evidence of landscape legacy on plant diversity. *Biodiversity and Conservation*, 20, 945–961.
- Sitzia, T., Trentanovi, G., Dainese, M., Gobbo, G., Lingua, E., & Sommacal, M. (2012). Stand structure and plant species diversity in managed and abandoned silver fir mature woodlands. *Forest Ecology and Management*, 270, 232–238.
- Sitzia, T., Dainese, M., Clementi, T., & Mattedi, S. (2014). Capturing cross-scalar variation of habitat selection with grid sampling: an example with hazel grouse (*Tetrastes bonasia* L.). *European Journal of Wildlife Research*, 60, 177–186.
- Sitzia, T., Campagnaro, T., Gatti, E., Sommacal, M., & Kotze, D. J. (2015). Wildlife conservation through forestry abandonment: Responses of beetle communities to habitat change in the Eastern Alps. *Forest Ecology and Management*, 134, 511–524.
- Sitzia, T., Campagnaro, T., & Grigolato, S. (2016). Ecological risk and accessibility analysis to assess the impact of roads under Habitats Directive. *Journal of Environment Planning and Management*. <http://dx.doi.org/10.1080/09640568.2016.1140023>.
- Sochor, M., Vašut, R. J., & Sharbel, T. F. (2015). How just a few makes a lot: speciation via reticulation and apomixis on example of European brambles (*Rubus* subgen. *Rubus*, Rosaceae). *Molecular Phylogenetics and Evolution*, 89, 13–27.
- Soltis, D. E., Clayton, J. V., & Soltis, P. S. (2014). The polyploidy revolution then...and now: stebbins revisited. *American Journal of Botany*, 101, 1057–1078.
- Spellmann, H., Meessenburg, H., Schmidt, M., Nagel, R. V., Suttmöller, J., & Albert, M. (2015). Klimaanpassung ist vorsorge für den wald. *ProWald*, 4–10.
- Spieß, H. J. (2013). Das weltnaturerbegebiet serrahn – vom großherzoglichen wildpark zum nationalpark. *Artenschutzreport*, 31, 11–19.
- Stockstadt, E. (2013). The war against weeds down under. *Science*, 341, 734–736.
- Thompson, H. (2012). War on weeds loses grounds. *Nature*, 485, 430.
- Tucker, G. M., & Evans, M. I. (1997). Habitats for birds in Europe. *Bird Life Conservation Series*, 6 [200pp].
- Turcu, D. O. (2012). *Cercetări privind dinamica structurii făgetelor virgine și a mortalității arborilor din Rezervația Naturală „Izvoarele Nerei/Research on the structural dynamics of virgin beech forests and mortality of trees in the „Izvoarele Nerei Nature Reserve, PhD thesis*. Brașov: Transilvania University [156p].
- WBGU (2001). *World in transition: conservation and sustainable use of the biosphere*. London: Earthscan [435pp].
- Winkel, W. (2002). Sind Vögel anzeiger von umwelt- und klimaveränderungen? langzeitrends bei meisen und anderen kleinhöhlenbrütern im braunschweiger raum. *Milvus Braunschweig*, 21, 1–12.
- Wisskirchen, R., & Haeupler, H. (1998). *Standardliste der farn- und blütenpflanzen deutschlands*. Stuttgart: Verlag Eugen Ulmer [765pp].
- Wittiche, H., & Biehl, H. (2009). Hainch-aldungen 1785 und einige aspekte ihrer weiteren entwicklung. *Artenschutzreport*, 23, 32–55.
- Wubet, T., Christ, S., Schöning, L., Boch, S., Gawlich, M., Schnabel, B., et al. (2012). Differences in soil fungal communities between European beech (*Fagus sylvatica* L.) dominated forests are related to soil and underground vegetation. *PLOSOne*, 7, e47500.
- Yabe, A. (2011). *Pseudotsuga tanaii Huzioka from the earliest Miocene Shichiku Flora of northeast Japan: systematics and ecological conditions*. *Palaeontology Research*, 15, 1–11.
- Yakimowski, S. B., & Riesenberger, L. H. (2014). The role of homoploid hybridization in Evolution: a century of studies synthesizing genetics and ecology. *American Journal of Botany*, 101, 1247–1258.