

A review on plant diversity and forest management of European beech forests

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Abstract The impact of historical and present drivers on forest biodiversity is poorly understood. A better understanding is mandatory to ensure conservation and appropriate management of biodiversity and ecosystem functions in the face of climate warming and increasing demand for wood products. Here, we assess forest management strategies for maintaining plant biodiversity in Central European beech forests, with a focus on Germany. We show that (1) diversity of the German vascular plant flora increased exponentially during the Holocene reaching 3874 species mainly through apomictic and hybrid speciation. Vascular plant species confined to forests comprise about 10 % of this flora. No loss in vascular plants restricted to forests occurred over the past 250 years despite of forest management; (2) the indigenous arboreal flora has a low

diversity (64 tree species) compared with other continents due to environmental changes in the last 2 million years; (3) forest management has maintained a high plant diversity in the past. It should be an aim of silviculture to ensure this in the future; and (4) only 22 of the indigenous tree species are commercially used; nine of these commercially used species are threatened by diseases. We introduce the concept of *palaeo-neophytes* to address genera that existed in Central Europe during the latest Cenozoic. The introduction of species of palaeo-neophytic genera and sub-Mediterranean species is discussed as a measure to buffer negative effects on native species caused by climate change and spread of novel diseases.

Keywords Temperate deciduous forests · Management · Nature conservation · Tree diversity · Palaeo-history · Pest species · Climate change

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Introduction

The UN Convention on Biological Diversity (CBD) was established to counteract the increasing loss of biodiversity due to human activities at the global scale (Global Biodiversity Assessment 1995; Pimm et al. 2014). However, biodiversity is not evenly distributed: there are regions that are naturally rich in species, while others are naturally poor in species (Joppa et al. 2013). Also, greenhouse gas emissions, nitrogen deposition, land management, trade and mobility vary considerably at regional and local scales, affecting biodiversity (IPCC-WGII 2014). Therefore, national strategies for the conservation and sustainable use of biological diversity were initiated (e.g. German Biodiversity Strategy 2007). Protecting less intensively used forests from human use has been suggested as a strategy for preventing diversity loss. At the same time, forest management may also play an important role in maintaining plant diversity. Thus, in the following, we investigate the role of forestry in this context. We investigate strategies for maintaining ecosystem functioning and plant biodiversity of European beech forests, with particular reference to Germany.

The study region has a climate favouring temperate broad-leaved deciduous forests with maximum rainfall during the growing season and warm summer temperatures (Köppen-Geiger climate type Cfb: warm temperate, fully humid with warm summer months). Despite the current favourable conditions for forest growth, the forest vegetation of Europe only partially recovered from the dramatic floristic losses during the late Cenozoic (Röhrig and Ulrich 1991; Latham and Ricklefs 1993; Lang 1994; Ellenberg and Leuschner 2010) which left the region with a low floristic diversity compared with other regions of the world with a similar climate. Moreover, the young and species-poor postglacial European indigenous forest flora has been affected by humans for thousands of years, starting in the Pleistocene (Heybroek 2015; Schulze et al. 2010). It has also been affected by a variety of forest pathogens (Fisher et al. 2010) and, since the discovery of the Americas in 1492, by introduction of non-European forest tree species (Burschel and Huss 2003). However, despite considerable changes in the vegetation over historical times (Rüther and Walentowski 2008), the narrow spectrum of forest species comprising both r-strategists (which typically live in unstable, unpredictable environments) and K-strategists (occupying more stable environments) has been maintained in Europe over centuries. One reason for this is that different kinds of goods were needed from forests to meet the demands for manufacturing products before the industrial revolution (Schulze et al. 2010), and the question arises, to what extent this will change in future. The present area

distribution of coniferous and deciduous forest in Europe is mainly determined by the national and global demand for wood and other ecosystem goods and services, but not by natural succession. Thus, Germany may serve as an interesting case to study interactions between human management, vascular plant species diversity and biotic exchange with other regions.

The main aim of this review is to examine the role of forest management, including the introduction of new species, in the context of biodiversity. Since biodiversity is inherently affected by land management, we assess the impact of forest management on plant diversity on the basis of historical and biogeographic evidence. Our focus is on vascular plants, but mosses and lichens are considered as well when data were available. Our approach is an investigation of the present forest vegetation in relation to its pre-Holocene and Holocene history and a comparison of the German vascular plant diversity with the diversity of deciduous forests on other continents. The historical and biogeographic background can provide the basis for further improving strategies of forest management.

Historical changes in vascular plant diversity in Germany

Historical changes in vascular plants

When assessing biodiversity in forests, it is essential to understand the role of forests in the context of the respective flora. The historical changes in vascular plant diversity have been assessed by Wisskirchen and Haeupler (1998), who listed 3874 plant species for Germany and distinguished indigenous species, archaeophytes, neophytes and hybrids. Until 7000 BP, the flora of Germany is assumed to have been entirely composed of indigenous species. Archaeophytes (human-facilitated species) accumulate until 1500 AC (Gregorian calendar) when Columbus re-discovered America, and neophytes, hybrids and apomicts represent additional components until the present time. Despite all uncertainties of this approximation, Fig. 1a shows an exponential increase in diversity since 7000 BP from about 2074 indigenous species to about 3874 species at present. Clearly, invasions did not happen in a continuous manner, but may have occurred in steps with the introduction of agriculture (about 5000 BP) and forest clearings (until about 700 BP). In addition, improved taxonomy of the last century contributed to the slope.

The total number of plant species that have temporarily occurred in Germany since about 500 BP is even greater: according to published observations about 12,000 exotic species germinated along railways, roads and harbours, but

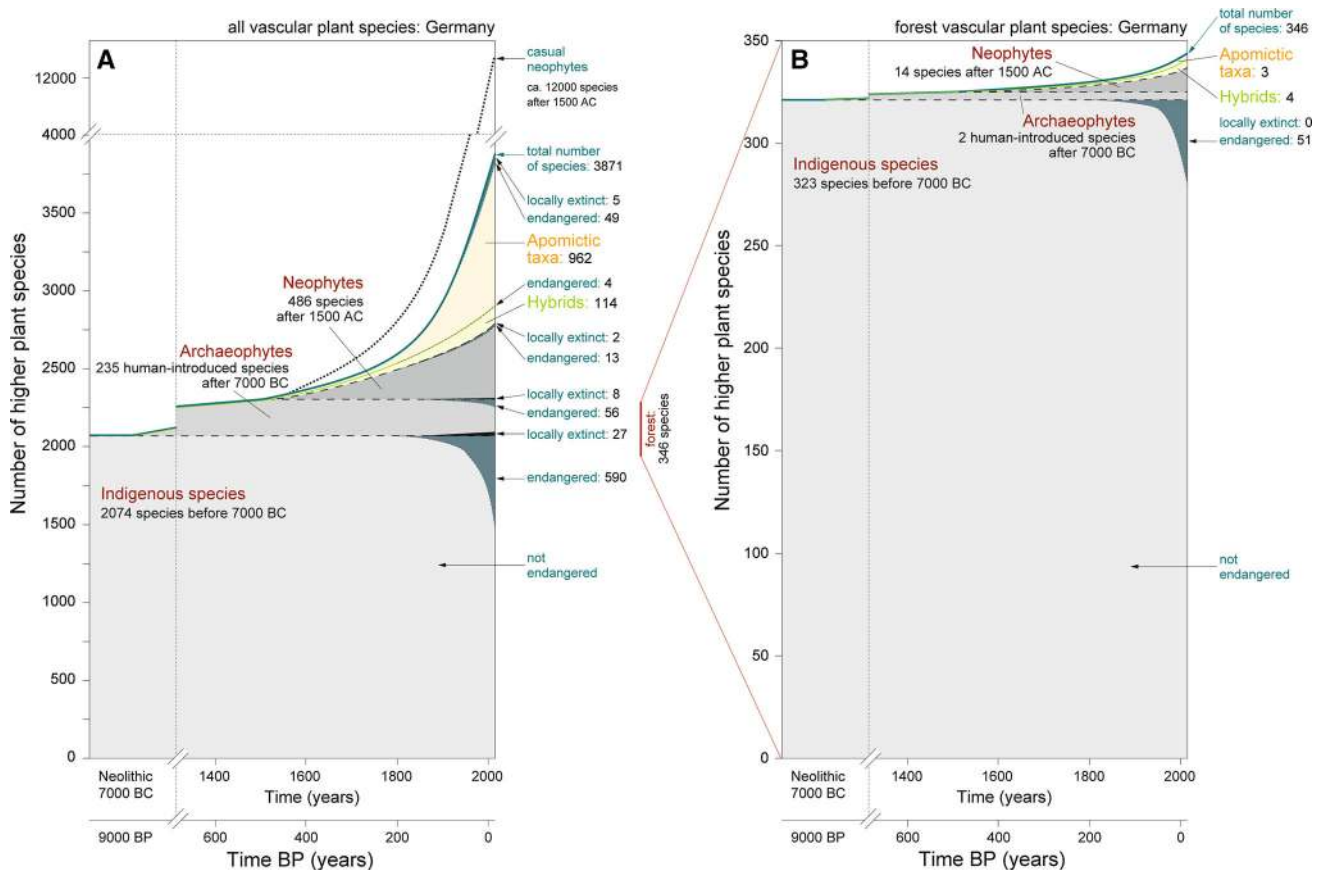


Fig. 1 Historical change in the total German plant flora (left) and for the subset (right) of the German forest flora (Category 1.1 and 1.2 according to Schmidt et al. 2011) since about 7000 BC (Scherer-Lorenzen et al. 2000). The exact curvature of the change in Neophytes and apomictic species remains unknown; it results in part from an

advanced taxonomy of the last century. Species and hybrid numbers follow Wisskirchen and Haeupler (1998), Red List and protected species follow Korneck et al. (1996). Main apomictic genera included *Alchemilla*, *Hieracium*, *Oenothera*, *Rubus*, *Taraxacum* following Wisskirchen and Haeupler (1998)

could not permanently establish themselves for various reasons (Sukopp 1976). After 500 BP, the number of species increased also as a consequence of a more reliable taxonomic framework for describing species based on the nomenclature by Linné (Leopoldina 2014). More recently, molecular systematic studies have helped to re-circumscribe species by (1) lumping morphologically separated Eurasian entities (e.g. *Fagus sylvatica-orientalis* complex, Gömöry and Paule 2010), (2) identifying new potential species (*Lathyrus pannonicus-collinus*, Schlee et al. 2011), (3) recognizing “cryptic” species (e.g. *Acer ortho-campstre*, Grimm and Denk 2014), (4) clarifying the state of debated species (e.g. *Acer ibericum*, Grimm et al. 2007) or (5) identifying suspected hybridization as in the case of oaks (e.g. Curtu et al. 2009). Overall, refined plant species identification and invasions contributed to the exponential increase in numbers of species over time in Germany, and the Neolithic biodiversity may be underestimated.

Problems related to the distinction between indigenous species, archaeophytes and neophytes become evident

when the group of apomictic “micro-species” is considered (Hand and Koltunow 2014). Most apomicts are associated with open landscapes and established themselves after disturbances (Schulze and Mooney 1993), but we are not sure when these apomicts emerged and how long they would remain in a specific plant community. For the genus *Rubus*, a genetic analysis indicates that the main ribotypes (sequence variants of fragments of the nuclear-encoded ribosomal DNA) separated already in the Miocene: a dynamic “cloud” of apomictic species in combination with mutations developed and disappeared again until present (Sochor et al. 2015). Thus, these species can be considered to be time-limited “events”, while the evolutionary lineage is maintained by a highly dynamic species “cloud”. Some of these apomicts may re-enter into the pool of hetero-sexual reproduction by chance and under certain environmental conditions (see also Hand and Koltunow 2014). Taking into account the particular nature of apomictic lineages, we hence classified the following genera showing a high degree of apomictic speciation as a separate

category, namely *Alchemilla* (53 species), *Hieracium* (170 species), *Oenothera* (53 species), *Ranunculus* (76 species), *Rubus* (303 species) and *Taraxacum* (353 species), following the approach of the Red Lists of Thuringia (Fritzlar et al. 2011). This selection leads to a conservative estimate since additional apomicts exist in other genera. Endemic species as indicated by Korneck et al. (1996) were not listed separately.

In addition to apomicts, hybrid species such as *Quercus* × *streimii* (= *Q. petraea* × *Q. pubescens*; Aas 1993; Curtu et al. 2009; Salvini et al. 2009) and new crossings between alien and native species (e.g. Scholz 2007; Pyšek et al. 2012) may affect species counts, leading to an overestimation of biodiversity, and hinder temporal and regional comparisons. The total number of true hybrids remains unknown (e.g. in oaks: Aas 1993; Nixon 1997; Denk and Grimm 2010). Nevertheless, hybridization and polyploidy are major mechanisms for adaptation and evolution in a changing world.

Of the over 3800 contemporary species, about 1100 are apomicts or hybrids, representing about 30 % of the present taxa. This affects any evaluation that is based on species counts. The number of non-hybrid plant species with heterosexual reproduction thus reduces the total species number to about 2800 species. Therefore, a conservative estimate would be an increase in species richness from about 2000 plant species in 7000 BP to around 2800 species today.

Historical changes in plant diversity in forests

Schmidt et al. (2011) distinguished between species confined to forests (obligatory forest species) and species also occurring in open habitats (facultative forest species); category 1.1 includes species that only grow under forest canopies; category 1.2 are species occurring at internal and external forest edges. Category 2.1 includes forest species that may also grow in open habitats, while category 2.2 refers to species of open habitats, which may also occur under forest canopies. In the following, we regard only category 1.1 and 1.2 as “true”, obligatory forest species, because the focus of this study is on *Fagus* forests. We therefore excluded facultative species, which may also occur in open habitats. Figure 1b shows that the total number of obligatory forest species (including hybrids and apomicts) of 346 taxa represents only 9 % of the total number of vascular plants in Germany. Although forests cover over 30 % of the land area in Germany, their contribution to regional plant species richness thus appears to be small.

Most of the Holocene plant species richness increase was linked to open habitats (Walentowski and Zehm 2010). Populations of tundra and steppe plants survived

postglacial forest expansion in semi-open habitats such as alluvial river plains, wetlands, gorges and ravines, rock outcrops and at elevations above treeline. Alternatively, the pristine forest cover may not have been as dense as commonly assumed (Feurdean et al. 2015), and humans may have interacted more than previously thought (Heybroek 2015). The low number of forest archaeophytes (only two species) may indicate that human activity was low (Hasel and Schwarz 2006). On the other hand, considering the large-scale human-induced changes of hunters during the Neolithic period (since about 7000 BP: Haber 2011) and of early farmers (Szécsényi-Nagy et al. 2014), the effect of humans may have been underestimated for forest vegetation.

In view of the distribution of species in all kinds of land types versus forests only (Fig. 1a vs. b), the floristic diversity of Germany appears to depend mainly on the rate of speciation and of new taxonomic descriptions in open habitats. One may argue that this view is biased because molecular systematic studies predominantly focused on herbaceous taxa and not on trees and shrubs. However, considering existing studies on *Quercus*, *Fagus*, *Acer* and *Picea* (Denk and Grimm 2010; *Quercus*, Gömöry and Paule 2010; *Fagus*; Grimm et al. 2007; Grimm and Denk 2014; *Acer* sections *Acer*: Lockwood et al. 2013; *Picea*), the total number of new arborescent European species will nevertheless remain much lower than that of herbaceous genera. Also apomicts are much more frequent in herbaceous than in arborescent genera (Hojsgaard et al. 2014) because first flowering occurs later in woody species, and woody species are less affected by disturbances than herbaceous species.

Endangered species

Endangered species are registered in the Red Lists, and they are partly protected by law. In addition, Germany has taken responsibility for the maintenance of species with local distribution centres in Germany (see Supplement S1). Following the Red List of Germany, endangered vascular plant species represent 19 % of the flora. Neophytes, hybrids and apomicts contribute with only few species to the Red Lists. Indigenous species and archaeophytes contribute the largest fraction to the Red Lists even though these “old” species have seen large variations in climate in the past. Notably, a large fraction of the endangered old species are just rare (Walentowski and Zehm 2010), and not threatened by climate change but rather by extinction of the habitat through changes in land use and through atmospheric pollutants (see lichens in Fritzlar et al. 2011). Although legal plant protection, the Red List of endangered species and the responsibility by nations in the framework of EU-Natura2000 aim jointly at protecting vulnerable

species, the number of species that are common to all three lists is surprisingly low (55 species for the entire vascular flora). The total number of vascular plant species, i.e. 1044, that occur across all three schemes amounts to 37 % of the flora excluding apomicts.

In forests, the number of endangered plant species is small (57 species, which is 15 % of the obligatory forest flora), consisting mainly of rare species with local distribution. There are no endangered forest archaeophytes or neophytes. Although our emphasis is on vascular plants, comparative figures for mosses and lichens should be considered. For these groups, we refer to the Red List of the federal state of Thuringia (Fritzlar et al. 2011), which is more recent than the Red List of Germany (Korneck et al. 1996) and represents the core area of *Fagus* forests in Germany. According to that list, 26 % of the 805 mosses and of the 1148 lichens are endangered. Most of the endangered mosses and lichens are from open habitats, mainly soils, rocks and constructions, but not from forests, although several mosses and lichens do depend on forest continuity, and these species are in the focus of conservation strategies. Mosses and lichens are mainly affected by atmospheric nitrogen deposition—as recently also shown for grassland plant communities (Stevens et al. 2004, 2010), and by land-use change. Even in remote areas of the Alps, lichens decline because of nitrogen deposition from the atmosphere (Mayer et al. 2013). Lichens were also heavily affected by acid rain in the twentieth century and presently re-invade new habitats in Central Europe.

Extinctions

Fewer extinctions are expected at the European scale compared to Germany or sub-national scales. Indeed a low number of the 11,557 vascular plant species (Flora Europaea 1964 to 1993 including the Mediterranean region) are lost at the European scale (IUCN 2014: <http://www.iucnredlist.org/>). IUCN distinguishes between total extinction (category EX) and extinction in the “wild” (category EW), which indicates that these species were lost at natural stands but remain alive under cultivation (botanical gardens, nurseries, etc.). In 2014, there were only three category EX species listed in Europe: *Astragalus nitidiflorus*, *Euphrasia mendoncae* and *Viola cyana*, all of which grew in southern Europe. Extinct in the wild are four additional species: *Betula szaferi*, *Bromus bromoideus*, *Bromus interruptus* and *Lysimachia minoricensis*, which were growing in Belgium, France, Luxembourg, Poland, Spain and the UK, but not in Germany.

In Germany, vascular plant species extinctions have been rather low in general over the past 250 years (Fig. 1) and particularly low in forests (Korneck et al. 1996). The 250-year time frame is based on the last record of *Gladiolus palustris* in Thuringia by Förster in 1768 (see Zündorf et al. 2006). This

species thus became the oldest extinct species in this area (Fritzlar et al. 2011). Two putatively extinct forest species are *Rosa abietina* and *Carex depauperata*, but both have recently been re-discovered (Hickler et al. 2014). Thus, there are only 45 species (rather than 47 officially recorded species) that disappeared during the past 250 years in the whole flora of Germany. This is 1.1 % for the total flora (including apomicts) and 1.6 % for the flora excluding apomicts. There is only one putative forest extinction: *Pseudolysimachion spurium* (synonyms: *Veronica spuria*; *Veronica paniculata*) which was already rare in the eighteenth century. Although *Pseudolysimachion* was classified by Schmidt et al. (2011) as category 1.2 (forest edges) it grows in Austria in open grasslands of steppe vegetation, and on rocky places [see Flora Europaea 1964–1993 and Flora of Austria (Fischer 1994)]. Thus, *P. spurium* appears to be falsely classified (group 2.2 instead of 1.2). With this correction, not a single obligatory forest vascular plant species went extinct over the past 250 years. The low number of extinctions contrasts the fairly large number of endangered vascular plants of the Red List.

In Thuringia, the total number of extinctions in the whole flora is higher. The Red List of Thuringia (Fritzlar et al. 2011) lists 107 species that are not found any more in Thuringia. Twelve out of these species are apomictic, and five are obligatory forest species. Besides vascular plants, 6 % of the mosses and 10 % of the lichens are extinct. These were species with very local distributions in open habitats (e.g. succession along an abandoned railway track caused the extinction of a lichen species). Only 2 % of the extinct lichen and 8 % of the extinct moss species were obligatory forest species.

The extinction data suggest either that plants can cope with relatively fast changes in their growing environment or that, given that 1044 species are under some kind of protection, the protection efforts are effective. For example, all of the 266 nature conservation areas of Thuringia were established with the aim to protect species of the herbaceous flora. Animal protection has not been an objective when creating conservation areas. Only for the National Park Hainich special protection for some amphibians, a butterfly and few bats was demanded by law in addition to plant succession (Wenzel et al. 2012). This may illustrate that the protection of the flora had high priority in conservation in the past even though many forest trees are older, and management of these forest has commenced much earlier than protection measures.

Origin of forest species since the Cenozoic

Past distribution patterns including range extensions and contractions caused by tectonic and climatic changes are essential for understanding present numbers of tree species

in Europe. Here, we take three genera, *Quercus* (Group Quercus, ‘white oaks’), *Fagus* and *Pseudotsuga*, as examples as their evolutionary histories are well known.

The Cenozoic, the past 66 million years (Ma), was a time of major diversification of the angiosperms. The Northern Hemisphere mid-latitude climate changed from nearly tropical conditions in the Eocene (56–34 Ma) to warm temperate conditions in the Miocene (23–5 Ma; Mai 1995). Most genera presently observed in the temperate humid zone of North America and East Asia were present in Europe during most of the Cenozoic, including *Carya*, *Catalpa*, *Liquidambar*, *Liriodendron*, *Mahonia* and *Nyssa* (Mai 1995; Manchester 1999). Exceptions are *Euptelea* and *Thujaopsis* with fossil records only in East Asia (Manchester et al. 2009). Although global patterns are well resolved at the genus level, taxonomic relationships between Cenozoic and contemporary species have been established for only a few genera (*Fagus*: Denk and Grimm

2009; *Pseudotsuga*: Yabe 2011; Kunzmann 2014, *Quercus*: Grímsson et al. 2014).

The oldest *Fagus* species is known from British Columbia and Northeast China from the Eocene (Fig. 2). In the later Cenozoic, *Fagus* spread and diversified in subtropical and temperate East Asia and migrated via the Eurasian mountain regions to Europe. The two late Cenozoic European species, *Fagus haidingeri* and *Fagus gussonii*, show a mosaic of morphologies that comprise both East Asian and modern European types, but both vanished. Genetic evidence shows that *Fagus sylvatica* evolved from *Fagus orientalis* (Gömöry and Paule 2010). Both remain very similar to the Japanese *Fagus crenata* (Denk and Grimm 2009).

The evolutionary history of *Pseudotsuga* is similar to that of *Fagus* (Florin 1963; Hermann 1985; Yabe 2011; Kunzmann 2014). The oldest reliable record (Schorn and Thompson 1998; Wei et al. 2010) is from the early

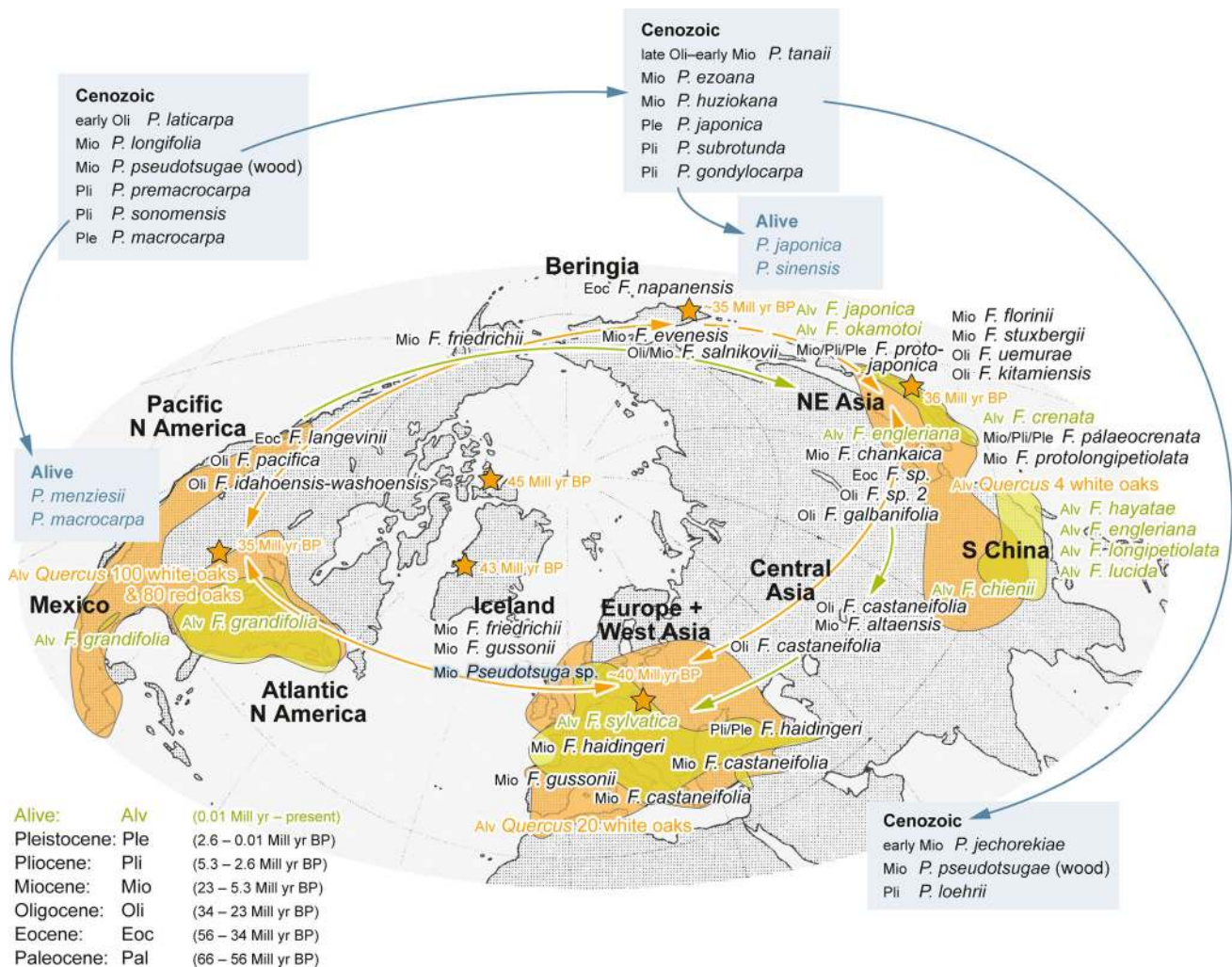


Fig. 2 Palaeogeography of *Fagus*, *Pseudotsuga* and *Quercus* (modified from Denk and Grimm 2009; Yabe 2011; Kunzmann 2014 and Denk unpublished)

Oligocene of western North America. Subsequently, the genus migrated to East Asia via Beringia from where it reached Europe in the early Miocene (Strauss et al. 1990). There are fossil records (e.g. the localities Thierbach and Wiesa, Germany: Kunzmann 2014), proving that *Fagus* and *Pseudotsuga* contributed to mixed forests in Europe during the Miocene. Miocene fossils of *Pseudotsuga* at Tetta-Buchholz, Germany, closely resemble the modern *Pseudotsuga chinensis* var. *forrestii* (Czaja 2000). Fossils of leaves and reproductive structures of *Pseudotsuga* show that the genus occurred in Iceland during the middle and late Miocene (Denk et al. 2011). In Europe, *Pseudotsuga* persisted until the onset of the Pleistocene (Mai 1995, p. 511). Other genera that are currently confined to East Asia and/or North America and persisted into the Pleistocene in Europe include *Sciadopitys*, *Tsuga*, *Carya*, *Eucommia* and *Magnolia* (Lang 1994; Kunzmann 2014).

The evolution of white oaks (*Quercus* Group *Quercus*, a group comprising the lobed deciduous oaks of Eurasia and both evergreen entire-leaved and deciduous lobed oaks of America) followed a different biogeographic history (Grímsson et al. 2014). In contrast to *Fagus* and *Pseudotsuga*, the oldest fossils of white oaks (45 million years, McIntyre 1991; McIver and Basinger 1999) were found on Axel-Heiberg Island, Nunavut, Canadian High Arctic (Fig. 2). From this location, deciduous oaks migrated to western Greenland and Northern Europe via the North Atlantic Land Bridge to central North America (east of the Rockies) and to Kamchatka and Japan via Beringia. Thus, a circumpolar northern hemispheric distribution emerged, allowing unhindered gene flow between populations resulting in a very low genetic differentiation in modern white oaks although they are morphologically distinct (Denk and Grimm 2010). The migration of different *Quercus* subgroups is discussed by Bouchal et al. (2014), indicating that the present distribution of *Quercus* subgroups took place in the Cenozoic. The red oaks (*Quercus* Group Lobatae), including *Quercus rubra*, are a parallel line in oak evolution (Fig. 2).

In the light of the biogeographic history, the modern Central European forest is species poor, irrespective of management. Compared with other regions of the world

with similar climate, the European forest vegetation appears also not to be “species saturated”. Given this situation, we suggest that species of genera, which were growing in Central Europe during the late Cenozoic under environmental conditions similar to modern ones, are not classified as “neophytes” but rather as “Palaeo-neophytes”. Palaeo-neophytes should not be confused with early neophytic species that emerged as German house garden flora in the Renaissance and which Hempel (1990) classified as “palaeophytes”. Palaeo-neophytes are species of genera that were present in the European flora of the Cenozoic and are anatomically close or even identical to their extinct European congeners. The anatomical distance—caused by chronological disjunction—between extinct and extant species has only been established for *Fagus* (Denk and Grimm 2009). Future research is needed to investigate the closeness of extinct and extant species of other tree genera.

Tree diversity and forest management

Number of tree species in a global comparison

Geographic comparison (Table 1) shows that with 64 tree species Central Europe has the lowest number of indigenous tree species as a result of environmental changes during the Neogene (see also Ellenberg and Leuschner 2010). The number of tree species almost triples to 169 if the Mediterranean species are included. The flora of eastern North America and temperate East Asia contains, however, about 6–15 times as many tree species and about twice as many genera and families as Central Europe (see also Röhrig and Ulrich 1991; Latham and Ricklefs 1993). These differences remain, irrespective of different taxonomic traditions (splitting in China, lumping in North America and Europe, see Supplement S2). Despite the much larger number of tree species in East Asia, some genera are endemic to Europe (*Laburnum*) or North America (*Robinia*). These are “neo-endemic” genera according to the definition in Manchester et al. (2009) due to their wider distribution in the past.

Table 1 Geographic comparison of tree species numbers

	Central Europe	Geographic Europe minus Mediterranean	Geographic Europe plus Mediterranean	NE North America	East Asia	Röhrig and Ulrich (1991) East Asia
Species total	64	114	169	398	990	833
Broad leaved	55	101	139	363	879	835
Conifers	9	13	29	35	110	2
Genera	28	36	40	52	78	59
Families	16	21	23	28	37	41

Total number of tree species and commercially used species in Germany

There are 64 native and 21 non-native tree species in Central Europe (Table 2). This number is higher (85 vs. 71) than that listed by Schmidt et al. (2011) and Wisskirchen and Haeupler (1998) who overlooked some non-native commercial forest tree species. About one-third of the tree species are used in forestry as major wood resource. Additional species are still used for artwork and furniture (e.g. the genus *Pyrus*). However, about 40 % of the 22 native commercial species and 10 % of the non-native species commercially used are affected by regional or local diseases, which may restrict the abundance and the range of distribution of native species in the future (Allen et al. 2015; Wingfield et al. 2015). The relative lower effect of diseases on non-native species may only be a temporary time lag (Müller et al. 2015). The low diversity, the spread of mainly new diseases and the uncertainty of the intensity of further climate changes strongly limit tree species choice for forest management. Following Raffa et al. (2008), a healthy forest is one that encompasses a mosaic of

successional patches representing all stages of the natural range of disturbance and recovery. However, Trumbore et al. (2015) pointed out that the ability to recover from disturbances varies with the type of disturbance and with species, and for some of the pathogens, a recovery of affected tree species may not even be foreseen. Thus, with some of the species the European tree flora may be at an edge of an unhealthy condition (Müller et al. 2015).

The effects of management on forest vascular plant diversity

Most studies on the effect of forest management on plant diversity contrasted managed and unmanaged stands (see e.g. Paillet et al. 2010a). Duguid and Ashton (2013), for example, found no clear influence of management on understory plant biodiversity when contrasting managed and unmanaged stands, but observed management effects by taking the harvesting regime into account. Paillet et al. (2010a) found that management types which created canopy openings were more diverse in plants than unmanaged forest. Other studies suggest highest

Table 2 Tree species of Central Europe

Native Tree species Germany			
<i>Acer campestre</i>	Fraxinus excelsior	<i>Rhamnus carthatica</i>	Sorbus domestica
<i>Acer monspessulanum</i>	<i>Hippophae rhamnoides</i>	<i>Salix alba</i>	Sorbus torminalis
<i>Acer opalus</i>	<i>Ilex aquifolium</i>	<i>Salix appendiculata</i>	Tilia cordata
Acer platanoides	<i>Malus sylvestris</i>	<i>Salix caprea</i>	Tilia platyphyllos
Acer pseudoplatanus	<i>Populus alba</i>	<i>Salix daphnoides</i>	Ulmus minor
Alnus glutinosa	<i>Populus nigra</i>	<i>Salix dasyclados</i>	Ulmus glabra
Alnus incana	Populus tremula	<i>Salix elaeagnos</i>	Ulmus laevis
Betula pendula	Prunus avium	<i>Salix fragilis</i>	Abies alba
<i>Betula pubescens</i>	<i>Prunus mahaleb</i>	<i>Salix myrsinifolia</i>	<i>Juniperus communis</i>
Buxus sempervirens	<i>Prunus padus</i>	<i>Salix pentandra</i>	Larix decidua
Carpinus betulus	<i>Pyrus nivalis</i>	<i>Salix purpurea</i>	Picea abies
<i>Crataegus laevigata</i>	<i>Pyrus pyrastrer</i>	<i>Salix triandra</i>	Pinus cembra
<i>Crataegus monogyna</i>	<i>Quercus cerris</i>	<i>Salix viminalis</i>	Pinus nigra
Fagus sylvatica	Quercus petraea	<i>Sambucus nigra</i>	Pinus sylvestris
<i>Frangula alnus</i>	<i>Quercus pubescens</i>	<i>Sorbus aria</i>	<i>Pinus mugo</i>
<i>Fraxinus angustifolia</i>	Quercus robur	Sorbus aucuparia	<i>Taxus baccata</i>
Non-native Tree species			
<i>Abies grandis</i>	Fraxinus pennsylvanica+	Pinus strobus	<i>Sequoiadendron giganteum</i>
<i>Abies nordmanniana</i>	<i>Juglans regia+</i>	Populus x canadensis+	<i>Thuja plicata</i>
<i>Abies procera</i>	<i>Juglans nigra</i>	<i>Prunus serotina+</i>	<i>Tsuga heterophylla</i>
<i>Aesculus hippocastaneum+</i>	Larix kaempferi	Pseudotsuga menziesii+	
<i>Castanea sativa+</i>	<i>Liriodendron tulipifera</i>	Quercus rubra+	
<i>Chamaecyparis</i>			
<i>Lawsoniana</i>	Picea sitchensis	Robinia pseudacacia+	

Hybrids of forest use are included. Trees managed for forest use are printed in bold letters. Species that are affected by diseases in such a way that the existence of the species is endangered are marked in purple. *Alnus* is affected by *Phytophthora*, *Fraxinus* by *Hymenosyphus*, *Buxus* by *Cylindrocladium*, *Pinus strobus* by *Cronartium*, *Ulmus* by *Ophiostoma* and *Picea* by *Ips* sp. Locally endangered species are marked in yellow: *Acer* spp. are affected by *Verticillium* and other fungi in Thuringia, *Quercus* sp. and *Pinus sylvestris* by *Thaumetopoea processionea* and *T. pinivora* in NE Germany. The non-native forest species (for Germany) follow Burschel and Huss (2003). Non-native forest species that are listed by Wisskirchen and Haeupler (1998) are marked by “+”

organismic diversity for unmanaged forests (Müller and Leibl 2011).

Clearly, there is not only a range of management strategies, but also a range of nature conservation goals. Conservation strategies include the preservation of natural monuments; there are protection areas where careful management continues or certain management practices are even requested (e.g. coppice systems), and national parks and biosphere reserves, where an unmanaged core area exists without extraction of biomass by humans (Scherzinger 1996). Management strategies range from rotation forest (also termed age class forest) with even-aged stands to selectively cut forests and “selective felling close to nature” (Paillet et al. 2010a, b; Burschel and Huss 2003). Age class forest is the dominant management type in Europe.

Irrespective of management and conservation strategies, the problem remains that the number of studies designed to distinguish between different forest management types on a reasonable number of replicates is rare. Moreover, most studies are additionally inherently biased by site-specific differences in biodiversity. One of the few examples in which different management is sufficiently replicated and site-specific differences are minimized is the so-called Biodiversity Exploratory Project in north, central and south Germany, where plots were selected from a regional grid-based inventory of about 3000 grid points to represent similar soils, topography and edaphic conditions in stands with different forest management and un-managed stands. This approach allowed investigating the effect of management and protection under standardized conditions of a wide range of organisms including animals and microbes (Fischer et al. 2010), but it also contains a limitation in the age of un-managed forests. There is no true “old-growth” forest in Germany. Until now, the results of this study have only been compiled for the Hainich region, which contains a large range of management types in close vicinity. For plant species diversity, as summarized by Boch et al. (2013a, b), Schall et al. (2015) and Schulze and Ammer (2015), it is shown that even-aged forest management increased plant species number by creating a variety of forest structures and management types on a relatively small scale. Thus, not only alpha- but also beta- and gamma-diversity were higher in managed than in un-managed forests. Similar observations were made in the other regions of this experimental set-up (Schmidt 2013; Gossner et al. 2014).

Under uniform edaphic conditions, bryophytes (Müller et al. 2015), lichens (Boch et al. 2013a, b) and wood fungi (Blaser et al. 2013) increase with the amount of dead wood. The expectation was that un-managed sites would have higher stores of dead wood due to missing wood extraction. However, contrary to this expectation higher amounts of

deadwood were found in a grid-based inventory of the Biodiversity Exploratories in managed forests (dead wood: 9.7 vs. 15.0 m³ ha⁻¹ in un-managed versus managed forest of north, central and south Germany: Müller et al. 2015). The difference is smaller for a selected number of experimental plots of the Exploratory study. We are aware that the absolute number is smaller than published by Vandekeerkhove et al. (2009) for un-managed forests. Nevertheless, consistent with the dead wood stores mosses increased from 6.6 species per plot in un-managed forest to 10.1 species in managed deciduous forest (Müller et al. 2015). Lichen diversity was independent of management and protection in the central and northern study region (Boch et al. 2013b), possibly indicating that atmospheric pollution rather than management determines lichen diversity (Mayer et al. 2013). Dead wood and soil fungi were measured by molecular methods and characterized as operational taxonomic units (OTU) as measure for biodiversity, including ectomycorrhizal and general fungal communities. Dead wood fungal communities showed no significant difference between selectively cut and un-managed forest, but both had higher OTU richness than age class forest. For litter decomposers, no differences in fungal community structure were found between managed and unmanaged forest (Wubet et al. 2012). Soil fungal diversity, however, decreased in unmanaged forests compared with young and old age class forests at two of the exploratory study regions and remained independent of management and protection in the third region where the unmanaged forest was a former “coppice with standards” (Goldmann et al. 2015). Thus, soil fungi remain controversial. Lazaruk et al. (2005) and Gömöryová et al. (2013) showed that management increases soil fungal diversity. However, a large spatial variability of soil fungi makes comparisons of management types and species composition difficult.

In contrast to even-aged forests, selectively harvested forests can be disadvantageous for many forest species because of a higher frequency of disturbance and the property of beech to rapidly close small gaps created by single-tree harvests, which causes homogeneity at landscape scale (Schall et al. 2015). This contrasts to an earlier study by Brunet et al. (2010), who concluded in their review on biodiversity in European beech forests that only selectively harvested stands may reach the diversity of old-growth beech forest. The comparisons between managed and unmanaged sites may additionally be biased by the fact that many initially species-rich forest ecosystems were set aside for protection in the past (Halme et al. 2010, and response by Paillet et al. 2010b), and by the fact that selective management may have been quite extensive. Old woodlands have been shown to be of importance for ecologically diverse taxa, such as ground beetles (Assmann

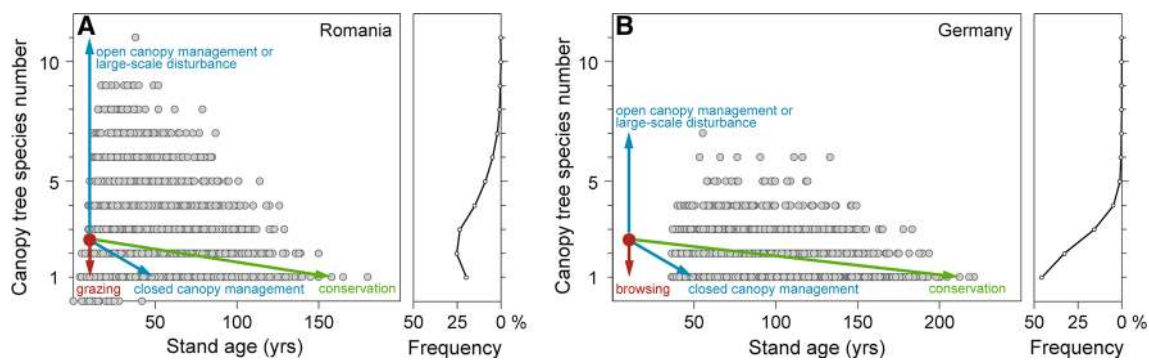


Fig. 3 Changes in canopy species composition during stand development based on Romanian and German grid-based inventories with plots of 500 m² in size (1000 m² in old-growth stands) in both countries. The Romanian inventory contains 4515 inventory plots; the German inventory is based on 1924 inventory plots. At the right-hand side of each plot, there is a frequency plot of observed tree species biodiversity levels. The red dot illustrates the average starting

conditions of a regenerating stand (2.5 species). The arrows indicate trends of various factors that affect tree diversity. Grazing reduced tree diversity to 1 remaining species in Romania and browsing in Germany at a very early stage of regeneration (Schulze et al. 2014), and selective thinning (mainly in Germany) cuts non-target species during stand development and succession. Species number increases by open canopy management and disturbance

1999; Descender et al. 1999; Sroka and Finch 2006), saproxylic beetles (Alexander 1998; Müller et al. 2005), spiders (De Bakker et al. 2000, 2001) and some plants (Wulf 2003; Petit et al. 2004). Thus, species communities in most parts of the managed landscape in Central Europe are affected by a legacy effect of the past (Tobias 2015). In addition, not only unmanaged forests, but also even-aged forest management systems can facilitate development of important structures (e.g. dead wood, veteran trees, cavities) and therefore contribute to regional diversity by creating landscape heterogeneity.

In temperate forests of Central Europe (Fig. 3), tree diversity decreases with stand age and terminates in a mono-dominated stands of *Fagus* (Schulze et al. 2014; Hobi et al. 2015). It is one effect of management to counteract the negative effects of canopy closure on tree diversity by creating canopy openings—shelterwoods, larger gaps or even clear cuts with and without retention trees—or large-scale natural disturbances. The latter can compensate the potential effects of deer browsing. It might be that very rare species, for example those depending on large snags, are underrepresented in managed forests (Werner and Raffa 2000; Müller et al. 2005; Nascimbene et al. 2013). However, in the above-mentioned Biodiversity Exploratory experiment, the diversity of Coleoptera dead-wood specialists was significantly higher in age class forests than in stands with selective cutting or in unmanaged forests due to the higher amounts of dead wood (Schall et al. 2015). Müller et al. (2014a) suggested an additional mechanism: temperature and the amount of dead wood interact in such a way that high temperatures promote species richness of dead wood organisms. Thus, temperature in part compensates for low amounts of dead wood. Promoting more open forest canopies by forest

management would be beneficial not only for vascular plants (Tinya et al. 2009), but also for other organisms such as true bugs (Gossner 2009) and saproxylic beetles (e.g. Franc and Gotmark 2008; Bouget et al. 2013; Horak and Rebl 2013). Additionally, increased structural diversity can promote the diversity of different trophic levels (Gossner et al. Gossner et al. 2013a, b; Müller et al. 2014b; Lange et al. 2014). On the other hand, intensively used managed forests may lack veteran trees and other “habitat trees”, i.e. the late forest development phases with over-mature trees, which are habitat for many dead wood organisms (Walentowski et al. 2014). Thus, retention measures such as setting aside habitat trees are needed to compensate intensive management (Lindenmayer et al. 2012; Nascimbene et al. 2013). Rösch et al. (2015) point at the importance of small habitat fragments for landscape-level diversity. Following Hulvey et al. (2013), intensively managed forests of Germany already contain admixed species and habitat trees at present to reduce the risk of losing entire stands by wind throw, by pests or by drought.

Maintaining biodiversity and sustainability of economically used forests, and the role of introduced tree species

Overall, diversity of many trophic levels is linked to the diversity of the plant species (Scherber et al. 2010), even though the correlation between plant diversity and the diversity of other trophic guilds in Central European beech forests seems to be less pronounced than in grasslands (Gossner et al. 2013a, b; Manning et al. 2014; Fraser et al. 2015). For some groups, other factors are important such as the input of atmospheric pollutants, mainly nitrogen compounds (Meinunger 2011; Mayer et al. 2013). For some

Table 3 Tree species diversity, wood volume and stem density of differently managed forests (von Lüpke et al. 2011)

Management type	Average and maximum number tree species Per 500 m ² plot	Wood volume (m ³ ha ⁻¹)	Stand density (number ha ⁻¹)
Coppice forest	3.7 (max 6)	632	1061
Coppice with standards	3.6 (max 6)	457	935
Small parcelled farmer's high forest	2.9 (max 6)	321	414
Unmanaged (former coppice with standards)	2.6 (max 6)	521	450
Age class forest	1.8 (max 6)	415	671
Selectively cut	1.3 (max 7)	339	334

Values correspond to mean values at stand maturity

groups habitat continuity and for others open canopies provide optimal conditions, even if tree species diversity is low (Müller et al. 2014a). In order to serve biodiversity demands for managed forests, heavy thinning resulting in low wood volumes and deeper light penetration, while maintaining a reasonable number of habitat trees and an amount of dead wood at various degrees of decay, seems to be an important conservation strategy to counteract decreasing age of harvested forests.

The hypothesis that sustainable management of forest ecosystems has maintained plant diversity in the past finds support from a comparison of tree species in different forest management systems of *Fagus*-dominated forest types in Germany (von Lüpke et al. 2011). The highest average tree species number on 500 m² plots was found in coppice forests, which were used for firewood and bark production during the past centuries (Table 3). Trees were harvested at small size every 25–30 years. The coppiced stumps are a major habitat for dead wood organisms. “Coppice with standards” had the second highest tree diversity. “Coppice with standards” is a management type of past centuries, in which two canopy heights are maintained: tall trees (about 80-year rotation) were used as saw timber at medium diameter for construction, and the lower shrub-like layer (about 25-year rotation) was coppiced for firewood (see Albert and Ammer 2012). Independent of the specific management approach, the lowest tree diversity is found in clear-felling systems and in selectively cut forests. The maximum number of tree species per inventory plot was similar among the different management types. This result indicates that certain management actions support tree diversity.

In this context, it must be kept in mind that management serves to supply goods on demand, and this demand has changed over time. Before the industrial revolution, wood of different arboreal species was required for medicine, food and construction. This demand maintained a high tree diversity in Europe (Schulze et al. 2010). In a book on wood technology, Soravia (1877) listed a total of 63 woody species (European shrubs and trees) used for 94 purposes:

52 species were used for medicine; 35 species were used for dyes; 32 species were used for firewood; 30 species were needed for furniture, constructions, fodder and food; and 20 species were used for ash production, nectar for bees, wood for barrels, carving, shoes, bird catching and making wheels and cogs. Most of these uses have been abandoned, and at present, only 27 are still in practice. Substitution by plastic and metal resulted in abandoning the use of 72 woody species. Twenty of these species are now used as ornamental plants, 25 species are used in landscaping, and 30 species are still used in medicine. Six species are now listed as being endangered. This enumeration illustrates the importance of woody species up to the nineteenth century and the importance of woody species as medicinal plants. It was in the general interest of the public to maintain *these* species, which were collected by private households. This has changed dramatically. Today, wood industries in Germany rely on four main species (*Fagus sylvatica*, *Picea abies*, *Pinus sylvestris*, and *Quercus robur/Quercus petraea*). Thus, the commercial importance of diversity has decreased over time, leading towards monocultures or less intensively mixed stands.

Within the economic frame of managing forests for wood products, the natural risks of windthrow, drought and diseases must be considered for long-lived crops. The (gale-force) windstorms Kyrill and Wiebke produced 50–70 million m³ each of windthrow wood in Germany (Behboud et al. 2013). This has caused forest legislation to promote diversity of forest regeneration, in order to (1) reduce the risk of forest losses due to climate extremes (e.g. Mund and Schulze 2005; Allen et al. 2010; Neuner et al. 2015) and (2) increase resistance against pests and pathogens (Jactel and Brockerhoff 2007; Scherer-Lorenzen 2014). Risk avoidance has become a major reason for growing species-rich mixed forest stands (Knoke et al. 2008; Pedro et al. 2015). Besides risk avoidance, plant mixtures were shown to have higher productivity as they can exploit a broader range of resources. There are longer legacy effects of climatic extremes in forests (Anderegg et al. 2015), and the effect of mixtures, for example on

productivity, varies considerably. In forests, productivity depends on species composition, site conditions and the silvicultural management of stand density (Pretzsch 2003, 2005). Resource utilization can, nevertheless, be improved by about 30 % by combining early and late successional species, or shade-tolerant and intolerant species (Pretzsch 2014; Pretzsch et al. 2013, 2014, 2015). When species compete for the same resource, productivity may, however, decline by 30 % (Pretzsch 2005). Thus, there are good incentives for managing tree diversity.

In reality, the common goal of diversifying future forests is difficult to reach, because of recent detrimental effects such as ungulate browsing, which attack all species but affect rare species more severely, and novel diseases, which affect a large fraction of the most important forestry species (Table 2). Even *Fagus sylvatica*, which remained relatively unaffected by modern diseases, suffers from occasional summer drought in a complex disease with phloem necrosis (Hartmann et al. 1995). In some cases, e.g. ash dieback (see caption of Table 2), the consequences are quite dramatic (Pautasso et al. 2013; Mitchell et al. 2014). A forest cover remains only in mixed, multi-species stands. On clay soils, the former ash forest turns into a shrub land (Millar and Stephenson 2015). The ash dieback case reveals that the species basis for forestry in Europe is extremely small to respond appropriately, even though the ecological range of ash is very large (Ellenberg and Leuschner 2010). Ash dieback is an example of so-called unpredictable surprises (Solbrig 1993). Thus, the resilience and recovery potential of European forests may even be already at its limits, considering local diebacks of *Acer*, *Quercus* and *Picea*. It has been predicted that climate will become suboptimal or even hostile for *Picea* and *Fagus* in Central Europe, even though their distribution covers a large range of ecological conditions (Kölling et al. 2009; Rubel and Kottek 2010; Hickler et al. 2014). In a situation where the need for future land to supply food, fodder, wood and fibre to a growing human population must be considered, it can be expected that forest use will have to encroach into remote areas and areas of low productivity in order to obtain sufficient biomass for various and increasing demands. Discarding any mitigation strategies, the entire terrestrial surface area of the globe is expected to be needed for safeguarding human survival by 2050 (Canadell and Schulze 2014).

The mitigation options for wood products and fibre supply are limited. Mainly, the rotation time may be decreased to the level of coppicing or short rotation crops (which only alleviates the situation for a short time period), or the productivity is being enhanced, e.g. by selection of appropriate species and mixtures or proper management to close the yield gap (Bolte et al. 2009, 2010; Canadell and Schulze 2014). Fares et al. (2015) suggest breeding of

drought-tolerant varieties of existing species, but this will take time even for the few main commercially used species. Thus, it becomes increasingly important to discuss the suitability of introducing additional species, because the latest disease on *Fraxinus excelsior* moved faster than it is possible to breed replacement species or search for tolerant genotypes (Vor et al. 2015). The use of genotypes of native species that are adapted to warmer climates, or the introduction of European sub-Mediterranean species, or the introduction of species from other temperate forest regions of the globe may present rational solutions. Palaeo-neophytic genera had been growing in Europe under very similar climatic conditions than today and expected for the near future during the late Neogene. *Pseudotsuga*, *Abies* and *Picea*, and other forest genera occurred before the last glacial maximum in mixed forest stands with *Fagus*. The main effect of introducing species of such genera should be that additional *K*-strategy species could compete with *Fagus* also in the late stages of succession, in order to avoid that European deciduous forests turn into quasi-monocultures of *Fagus* (Hobi et al. 2015). This assisted colonization would deliberately help North American or East Asian tree species to colonize habitats equivalent to their lineage's palaeo-habitats in Europe until the Plio-/Pleistocene, thus providing a much quicker alternative to the breeding of new tolerant variants of the (still) native species in order to respond to the present rapid environmental change ("the great acceleration"; Steffen et al. 2007; Pretzsch. 2014). We are aware that any attempt to increase the variety of tree species in Central Europe may be offset by the introduction of novel diseases, which affect both former native and novel species. Kegel (2013) gives a comprehensive account of unwanted events caused by invasion of new species. In forestry, one has tried to avoid such situations, even though a successful establishment of a new species for one reason may cause unwanted effects in other situations as seen for *Robinia pseudacacia* (Radtko et al. 2013) or *Pinus contorta* (Engelmark et al. 2001)

Clearly, before introducing new species, the genetic variation of existing native species should be explored. After all, most tree species are distributed over a large altitudinal range, which should provide amplitude to cope with a warmer climate. Despite this genetic variation, distribution models indicate that the distribution areas will change with climate change in relatively near future (Hickler et al. 2014). Thus, it seems appropriate to consider the introduction of species from the circum-arctic gene pool. This includes species of lineages that will eventually re-colonize Europe, as happened repeatedly in the past but over a timescale of millions of years.

In contrast to other parts of the world, forestry in Central Europe has only cautiously introduced non-native tree species. Nevertheless, some introductions have been quite

successful and are supported by management, with *Pseudotsuga menziesii* (Mirb.) Franco being one example. Douglas fir was introduced to Europe (Great Britain) in 1827, while provenance trials started in most countries early in 1900 (Lavender and Hermann 2013). Douglas firs are one of the few species cultivated on a larger scale. The cultivation of Douglas fir increased during the last 50 years, particularly in southwest Germany (Heidingsfelder and Knoke 2004). The species regenerates naturally quite well even though mast years are less frequent than for native conifers. Severe negative ecological impacts have not been encountered on a larger scale until now (Schmid et al. 2014). *Pseudotsuga menziesii* has become a naturalized component of European forests, but it suffers also from bark beetles and from deer. Among broadleaf trees, North American red oak, *Quercus rubra*, has been suggested as another suitable species (Burschel and Huss 2003; Vor et al. 2015).

Conclusions

The impact of forest management on biodiversity is controversially debated. Naturally, the impacts of management differ between biomes and forest types and need to be discussed in detail on a case-to-case basis. In this review, we focused on temperate beech forests and vascular plant species diversity. The situation in beech forests is comparatively well studied, given the economic and ecological importance of this forest type. We invite readers to think critically about the issues we have raised, and we hope to open further discussion with this review (Table 3).

We cannot decide if high diversity is an ultimate aim for maintaining ecosystem functions, but it is generally accepted that maintaining biodiversity is needed also to satisfy human demands. In this context, sustainable forest management seems to have little detrimental effect on plant diversity in central European beech forests. Recent studies show that this result may also be true for other organisms. The provision of habitats and specific structures are key measures for the conservation of biodiversity in forests, and these habitats exist in sustainably managed forests.

The low tree species diversity in Europe is the result of the tectonic/geographic and climate situation during the latest Cenozoic, culminating in the last glacial maximum (LGM) and subsequent extinctions of many European floral elements. Half of the total modern flora invaded Germany or evolved in Germany after 7000 BP, maintaining ecosystem functioning in a changing world. At present, however, a larger fraction of the 169 European tree species is affected by diseases.

We learn from the palaeontological record that the European forests had been much more diverse before the Pleistocene fluctuations. Genera, evolutionary lineages and possibly species, which existed in Europe (some until the LGM), still exist in the deciduous forests of Eastern USA and of East Asia. In order to maintain sustainable ecosystem functioning under conditions of global climate change and an increasing future demand for wood and fibre, it appears essential to investigate, carefully assess and discuss the reintroduction of such Cenozoic species along with genotypes of native species that are adapted to warm climates or Eurasian sub-Mediterranean species. Even though uncertainties of consequences of such re-introductions remain, modelling studies indicate that the genetic variability of the existing native species may not be sufficient to face potential impacts of future environmental conditions, but this needs further studies.

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