

Among stand heterogeneity is key for biodiversity in managed beech forests but does not question the value of unmanaged forests: Response to Bruun and Heilmann-Clausen (2021)

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Abstract

- Schall et al. (2020) assessed how a combination of different forest management systems in managed forest landscapes dominated by European beech may affect the biodiversity (alpha, beta and gamma) of 14 taxonomic groups. Current forest policy and nature conservation often demand for combining uneven-aged managed and unmanaged, set-aside for nature conservation, beech forests in order to promote biodiversity. In contrast to this, Schall et al. (2020) found even-aged shelterwood forests, represented by different developmental phases, to support highest regional (gamma) diversity.
- By pointing out that unmanaged forests included in our study are not old-growth forests, Bruun and Heilmann-Clausen (2021) challenge our conclusion as not providing sound scientific advice to societies. It is true that the studied unmanaged forests are not representing old-growth forests as defined in the literature. However, we demonstrate the representativeness of our unmanaged forests for current beech forest landscapes of Central Europe, where managed forests were more or less recently set-aside in order to develop old-growth structures. We also show that the managed and recently unmanaged forests in our study already differ distinctively in their forest structures.
- We use this response to stress the role of forest reserves for promoting certain species groups, and to emphasise their importance as valuable research sites today and in the future.
- Synthesis and applications.* We see two main conclusions from our study. First, unmanaged forests still matter. We agree with Bruun and Heilmann-Clausen (2021) on the general importance of unmanaged, old-growth or long-untouched forests, and we do not question the importance of set-aside forests for biodiversity conservation. However, a complete complementarity to managed systems may only

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reveal after many decades of natural development. Second, safeguarding biodiversity in largely managed forest landscapes should focus on providing a landscape matrix of different developmental phases with varying environmental conditions rather than on maximising the vertical structure within stands. Such landscapes can partly compensate for structures that are still missing in vital, dense and closed forests recently set-aside or for unsuitable phases that may occur due to a cyclic synchronisation of forest structures in unmanaged forests.

KEYWORDS

deadwood, even-aged forests, gamma diversity, landscape composition, old-growth structures, strict forest reserves, tree related microhabitats, uneven-aged forests

1 | INTRODUCTION

Schall et al. (2020) investigated the biodiversity (alpha, beta and gamma diversity) of 14 taxonomic groups in response to varying shares of three different forest management systems (even-aged, uneven-aged and recently unmanaged forests) in 'virtual forest landscapes' of European beech. Taxonomic groups were sampled in 43 1 ha plots within the largest contiguous beech forest in Germany.

We used a new resampling approach to create these 'virtual landscapes' by drawing samples out of plots belonging to the different forest management systems. Two of these forest management systems have a long tradition in the study region: First, a traditional even-aged shelterwood system (EA) without clear-cuts and relying on natural regeneration where stands differ in developmental phase ranging from thickets to mature stands (Figure S1); second, uneven-aged selection forests where forest management operates on a fine spatial grain, creating vertically structured stands by selective logging of individual trees or small groups of trees (UEA, so-called 'Buchen-Plenterwälder', Figure S2). Unmanaged forests (UNM), as part of the Hainich National Park and the UNESCO World Heritage Sites 'Ancient and primeval beech forests of the Carpathians and other regions of Europe', represented the third management system (Figure S2). In these protected forests, management was abandoned some decades before biodiversity sampling took place between 2008 and 2011 (about two decades for five plots located outside and several decades for the eight plots located within the World Heritage Site) to allow natural development and the establishment of old-growth structures. Thus, the unmanaged forests represent a passive management regime for nature conservation. As a mixed forest landscape of uneven-aged managed and unmanaged, set-aside forests is advocated by current forest policy and nature conservation, we were particularly interested in how such a 'virtual forest landscape composition' would influence biodiversity in contrast to managed forest landscapes with varying shares of the coarse-grained EA shelterwood system.

We found that managed forest landscapes of even-aged stands, comprising different forest developmental phases, promoted gamma diversity of most taxonomic groups and preserved a maximum of multidiversity calculated across the investigated taxonomic groups.

Results were consistent when focusing on species richness (Hill number 0D) or when accounting for species frequencies (higher order Hill numbers, i.e. Shannon 1D and Simpson 2D diversity) and were valid across all available species as well as across forest specialists only. Pure and mixed landscapes of uneven-aged and recently unmanaged forests reduced multidiversity by up to 13% across all taxa. We concluded that biodiversity benefits from management systems providing high environmental heterogeneity across stands, rather than from landscapes characterised by fine-grained forest management mixed with set-aside forests. We, however, also made clear in the synthesis and application section of the abstract that some groups 'require certain shares of uneven-aged and unmanaged forests, emphasising their general importance' (Schall et al., 2020). In fact, deadwood fungi were maximised in a pure unmanaged forest landscape and birds (species richness 0D , Shannon diversity 1D), ectomycorrhizal fungi (Simpson diversity 2D), forest specialist beetles (1D , 2D) and forest specialist multidiversity (1D , 2D) displayed a complementarity in species composition between EA and UNM (see table 1 in Schall et al., 2020). This indicates that mixing a coarse-grained management system (EA) with forests set-aside for nature conservation (UNM) may be an effective tool for biodiversity conservation in contrast to focusing on a diverse vertical stand structure (UEA).

Although Bruun and Heilmann-Clausen (2021) appreciate the way our data were analysed, they challenge our conclusions by criticising that the unmanaged forests used in our study are not representative of 'long-unmanaged old-growth stands'. They see the danger that our study may prevent the establishment of new forest reserves or may even initiate the management of still existing primeval forests. We agree that the inclusion of well-established, long-unmanaged forests on areas large enough to allow a natural disturbance regime or even of large primeval forests may have changed the outcome in terms of unmanaged forests. As such beech forests are, however, nearly inexistent in Central Europe, they cannot be regarded as an intrinsic part of current forest landscapes.

As our study aimed to be representative of currently existing managed forest landscapes of Central Europe, we appreciate the opportunity to better explain the overall goals of our study and to present common ground for further discussion. We also want to use this reply to clarify the important role of unmanaged forests

in intensively managed landscapes of Central Europe. At the same time, however, we reaffirm our main conclusion that, given the current forest situation in Central Europe, various even-aged forest stands of different developmental phases can promote landscape level biodiversity, while a combination of fine-grained forest management with recent management abandonment does not.

2 | WHAT DO UNMANAGED FORESTS STAND FOR—A REFERENCE FOR PRIMEVAL FORESTS OR A PASSIVE MANAGEMENT SYSTEM FOR ACHIEVING CONSERVATION GOALS?

The main criticism raised by Bruun and Heilmann-Clausen (2021) is that the unmanaged forests investigated by Schall et al. (2020) have been unmanaged for only a relatively short period and therefore provide 'little conditions that characterise long-unmanaged old-growth stands' that could be seen as a reference for primeval forests. Indeed, according to the definition by Burrascano et al. (2013) the unmanaged forests used in our study cannot be considered as old growth since they do not meet the criteria of a stand age older than 200 years (about 160 years in UNM), of a high density of large living trees (median: 75.5 trees >50 cm dbh ha⁻¹ vs. 55 in UNM) and a high amount of deadwood (median: 157.3 m³/ha vs. 20 in UNM). Nevertheless, parts of the Hainich National Park have been acknowledged by the UNESCO as important ancient beech forest sites in Europe based on the evaluation of the IUCN (2011) stating that: 'The nominated sites [Jasmund, Serrahn, Grumsin, Hainich, Kellerwald] are the best conserved, most natural and closest to beech-dominant primary forest sites remaining in Germany and have not been exploited for many decades'. Parts of the National Park have also been classified as long-term untouched based on a literature survey (Sabatini et al., 2018). The aim of our study, however, was not to contrast two differently grained management systems with a long-untouched reference resembling primeval forests, but to be representative of current managed forest landscapes of Central Europe, where forest management abandonment represents one management strategy for nature conservation (Bollmann & Müller, 2012). In these landscapes, unmanaged forests are indeed 'production forests, in which logging has been halted (Bruun & Heilmann-Clausen, 2021)' and which can be characterised by a quite diverse management history. Forests within the Hainich National Park, for example, have been managed as coppice-with-standards from 1,600 until the beginning of the 20th century, when a transition to high forests with a selection system started in the 1920s to produce large timber. In 1965, an already existing military training area was enlarged, including our study sites. This provided large areas that remained free of any harvesting since then. In the surroundings, selection management by the federal forestry administration lasted until the establishment of the National Park (Mund, 2004). Thus, the National Park consists of forests that provide a gradient of time since management abandonment as can be found in different landscapes of Central Europe. In Germany, for example,

the mean time since management abandonment in strict forest reserves currently existing is 34 ± 24 years (mean \pm SD; $n = 747$). Of these reserves, only seven beech forests have been unmanaged for more than 80 years (BLE, 2000). This means that our study area is representative for set-aside beech forests of Europe, but that our results are limited to such managed forest landscapes.

In contrast, Kaufmann et al. (2018) found a higher species richness of bryophytes and lichens in primeval beech forests of Slovakia compared to production forests. Eckelt et al. (2018) identified a list of saproxylic beetle species that show high population densities in primeval forests of Europe, so-called 'Primeval forest relict beetles', highlighting the uniqueness of such primeval forests. However, these landscapes are restricted to very few and local examples across Europe due to Europe's long history of settlement.

When it comes to the few existing, often small-sized, long-untouched old-growth forests in Central Europe it has to be emphasised as well, that their suitability as a reference for primeval forests and for the availability of old-growth structures depends on their ecological continuity and may be questioned for some specific old-growth structures such as deadwood (see e.g. Ruffer, 2018). According to Vandekerckhove et al. (2009) "an undulating sequence of rejuvenation cycles and dead wood pulses can be expected'. Similarly, Von Oheimb et al. (2007) concluded for an old-growth forest in north-eastern Germany (Serrahn, 200 to 230 years old) that 'the current high levels of dead wood [...] are a major result of the synchronisation of the stand structure [...], and it must not be assumed that they reflect the average long-term dead wood levels of the natural beech forests of Central and north-western Europe'. Instead, the authors expect low levels of coarse woody debris for about 100 years after several decades of high dead wood volumes. Thus, the strongly phase-dependent forest properties observed in long-unmanaged, but often rather small-sized reserves call for careful interpretation of their validity as references for primary forests and old-growth structures.

With about 3,600 ha, the forests of the Hainich National Park are 100-fold larger than average German strict forest reserves (median: 34.2 ha) which should allow for natural dynamics and a continuous availability of different developmental stages. However, due to being in optimum growth phase, horizontal heterogeneity representing a small-scale mosaic of developmental phases has not yet developed (see Figure S3 comparing Hainich National Park with Serrahn forest reserve, Suserup Skov reserve and Havešová primeval forest). This is in line with other former managed forests recently left for natural development (Heiri et al., 2009).

The choice of reference also matters when it comes to the question which kind of biodiversity is relevant. While some see the purpose of nature conservation in 'securing natural ecosystems with whatever levels of species diversity that entails' (Bruun & Heilmann-Clausen, 2021), others find it worthwhile to also secure species which reflect the cultural heritage (see e.g. Mölder et al., 2019) and again others find promoting or even maximising species richness itself an important goal. Our intention as scientists is to provide information on the numbers and types of species maintained in landscapes with

various forest type configurations. We have, for example, distinguished forest specialists from all species to account for specific habitat needs within the 'virtual managed forest landscapes'. Focusing even more on those species that benefited or suffered from varying landscape composition will be worth to be analysed in more detail in the future. While this is of scientific interest and informs society and decision-makers, it is not intended as a normative message as to which conservation goals should be prioritised.

If biodiversity conservation in forests not only aims at supporting species of late successional 'natural ecosystems' but also species with a different ecological amplitude and specialisation, our results suggest that a matrix of different developmental phases can support this goal. Protected areas and uneven-aged managed forests are an important part of such a landscape as they promote specialised groups. We thereby agree with Bruun and Heilmann-Clausen (2021) that only unmanaged beech forests providing a continuous availability of sufficient amount of old-growth structures can sustain high population densities of 'Primeval forest relict species' (Eckelt et al., 2018), in turn providing important sources for the surrounding managed landscapes. While we have never questioned this view, it will take some time to develop these structures and the research in the established network of forest reserves with its long-term monitoring sites as established in the National Park Hainich will help to clarify (a) how fast important structures such as canopy gaps or substantial amounts of deadwood will develop and (b) what the spatio-temporal dynamics of these structures will be in the long run. The recent drought years show that not only (no) management but also climatic events will shape these structures. Our results are therefore valid for a short-term perspective after management abandonment but should not be extrapolated to the future. With increasing natural dynamics and old-growth attributes a higher complementarity of species assemblages between unmanaged and managed forests may emerge also for overall multidiversity. Providing a sufficient heterogeneity at the landscape scale by forest management will, however, also be key for supporting forest biodiversity across time because (a) management abandonment can decrease the habitat suitability, particularly for forest species adapted to more open canopy structures, in the first decades (Braunisch et al., 2019), (b) the provision of old-growth structures in unmanaged forests can be phase dependent (Von Oheimb et al., 2007) and (c) the recovery of old growth structures can take very long (see Paillet et al. (2015) for French reserves set-aside for a mean time of 46 years).

3 | THERE ARE UNIQUE STAND STRUCTURAL PROPERTIES EVEN IN UNMANAGED FORESTS THAT WERE RECENTLY SET-ASIDE

Although the time since management abandonment has not been long enough for the development of natural dynamics or old-growth attributes comparable to primeval forests, differences have already

evolved between the studied unmanaged and managed forests. This is in accordance with results presented by Paillet et al. (2015). Thus, we do not agree with the statement that UNM 'do not really represent a management class distinct from EA [managed even-aged] and UEA [managed uneven-aged]' (Bruun & Heilmann-Clausen, 2021). Unmanaged forests of the Hainich National Park displayed a higher density of large living trees (>65 cm dbh) and a higher maximum diameter than the active management systems. Furthermore, the volume of large deadwood items was highest in the unmanaged forests (Schall, Gossner, et al., 2018), while deadwood in managed forests comprised mainly of stumps and harvest residuals. Large deadwood is known to be an especially important resource for saproxylic beetles (Gossner et al., 2013) and a range of fungal communities (Lonsdale et al., 2008; Purahong et al., 2018), although generally all sizes are of importance for deadwood-dependent fungi (Heilmann-Clausen & Christensen, 2004). When excluding stumps, deadwood volume was higher in the unmanaged forests than in the even-aged and uneven-aged stands in 2012 (Figure 1). The difference had further increased at the time of re-inventory in 2017 with diameters >40 cm increasing in volume in the unmanaged forests, while the total volume decreased in the even-aged stands due to reduced harvesting operations. This underlines the increasing dynamics towards old-growth structures and the limited time-scale of our study. For the inventory in 2012 deadwood volumes in the even-aged stands exactly corresponded to average values recorded by the National Forest Inventory in the same year with a comparable distribution of diameters showing that values in even-aged forests were as well representative for managed forests of Central Europe (Figure 1). Stands of UEA have been exposed to the extraction of firewood for centuries, contributing to low amounts of deadwood (Fritzljar & Biehl, 2006; Wäldchen et al., 2011).

Nevertheless, we agree that deadwood amounts of the unmanaged forests investigated by Schall et al. (2020) are rather low (mean \pm SD: 21.6 ± 13.5 m³/ha for all plots, 27.9 ± 13.3 m³/ha within the World Heritage Site and 12.0 ± 6.7 m³/ha outside). This remains true when compared to the mean value of 64.9 ± 58.0 m³/ha reported by Vandekerkhove et al. (2009) for beech forest reserves in Central Europe with a mean time span of non-intervention of 35 years. Across 107 beech forest reserves in Germany and Switzerland, a mean value of 50.1 ± 44.8 m³/ha was found (59.6 ± 43.8 m³/ha for reserves with at least 30 years of non-intervention, Table S1). However, the high standard deviation of the reported values shows a high variation in deadwood amount across studied reserves with the Hainich National Park lying within the reported ranges. In addition, we detected an annual deadwood accumulation rate of 0.6 m³ ha⁻¹ year⁻¹, which is quite similar to the modelled accumulation rate of 0.4 m³ ha⁻¹ year⁻¹ reported by Paillet et al. (2015) and lies within the range of the rate reported by Vandekerkhove et al. (2009) for beech forests (2.13 ± 2.05 m³ ha⁻¹ year⁻¹). Thus, the values presented in Schall et al. (2020) are low but not atypical for Central European unmanaged beech forests few decades after management abandonment.

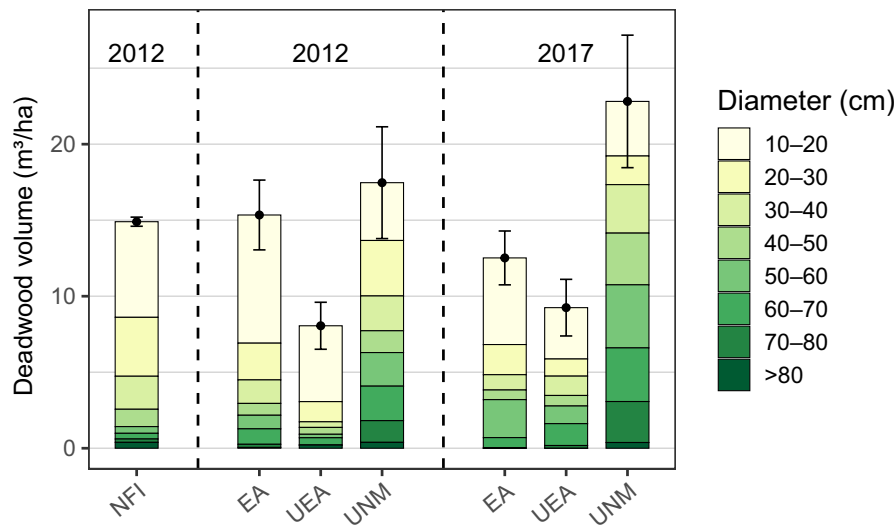


FIGURE 1 Deadwood volume of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forest management systems measured in 2012 and 2017 in the study system of Schall et al. (2020) and of the German national forest inventory (NFI, Thünen-Institut, 2020) measured in 2012. Deadwood volume was corrected for stumps, which account for 5.7 m³/ha in NFI and 8.0 and 4.8 m³/ha in EA, 6.5 and 5.0 in UEA, and 1.9 and 0.6 m³/ha in UNM, in 2012 and 2017 respectively. To comply with NFI standard, we considered only deadwood with a minimum diameter of 10 cm

There is no doubt that the deadwood volume in the reserves will further increase with increasing time since abandonment, but this may take many more decades or require disturbances. However, total deadwood volume alone is not a sufficient indicator of saproxylic biodiversity (Lassauce et al., 2011) since microclimate and deadwood quality determined by tree species and decomposition stage are also important (Gossner et al., 2016; Müller et al., 2015; Seibold et al., 2016; Vogel et al., 2020). Still, there are many open questions concerning deadwood and related forest structures. Thus, more research is needed on (a) how the overall community of all types of deadwood-dependent organisms is affected by the loss of important structures, (b) which structures are essential for promoting diversity in general and highly demanding species in particular and (c) which structures are available as alternative habitats in managed forests surrounding unmanaged ones (Runnel & Löhmus, 2017). In this view, our results are encouraging since managed forest landscapes seem to provide sufficient habitats for most recorded species. Silvicultural measures such as deadwood enrichment in managed forests may further improve the habitat suitability for these specialised species (Doerfler et al., 2018) in addition to unmanaged forests set-aside for nature conservation.

Next to standing and lying deadwood, tree-related microhabitats are considered important for biodiversity and become increasingly relevant in forest nature conservation and management (Larrieu et al., 2018). We recorded tree-related microhabitats on 2,000 m² across each plot (five subplots of 20 m × 20 m) following the reference catalogue of Kraus et al. (2016) in 2017 and found the highest microhabitat abundance per plot for each broad microhabitat type in unmanaged forests (Figure 2A). Unmanaged forests also displayed the highest richness of microhabitats across management systems (using the same resampling approach as in Schall et al. (2020);

Figure 2B), while pure even-aged forest landscapes provided the lowest richness of microhabitat types. Birds responded to this high microhabitat density and diversity by showing the highest alpha diversity in unmanaged forests (Schall et al., 2020). As their gamma diversity was, however, largely driven by different species assemblages in the developmental phases of even-aged stands, this species group benefits from a mixed landscape of even-aged and unmanaged forests.

Saproxylic beetles sampled in 2008 (see Schall, Gossner, et al., 2018; Schall et al., 2020 for details) displayed the same gamma diversity pattern as birds benefiting from a 20% share of unmanaged forests in an even-aged landscape (Figure 3). In our study the importance of unmanaged forests for saproxylic beetle diversity depended on the vertical stratum. The formation and accumulation of crown deadwood as an important tree-related microhabitat seems to mainly occur in unmanaged forests (Figure 2) and its associated saproxylic beetle community obviously complements species assemblages of even-aged forests (Figure 3). This finding shows that the development towards old-growth structures is ongoing in our unmanaged forests and that the initiation of comprehensive deadwood-dependent trophic networks has already started. The results, however, also underline the importance of the considered time-scale, even though results can be assumed representative for current forest landscapes of Central Europe.

Despite the positive effect of old-growth characteristics for some species groups in the recently set-aside forests, the even-aged forests provided suitable habitats for most of the recorded species including producers, herbivores and carnivores (Figure 4). We therefore hypothesise that the abundance and diversity of primary producers is likely to cascade up to higher trophic levels.

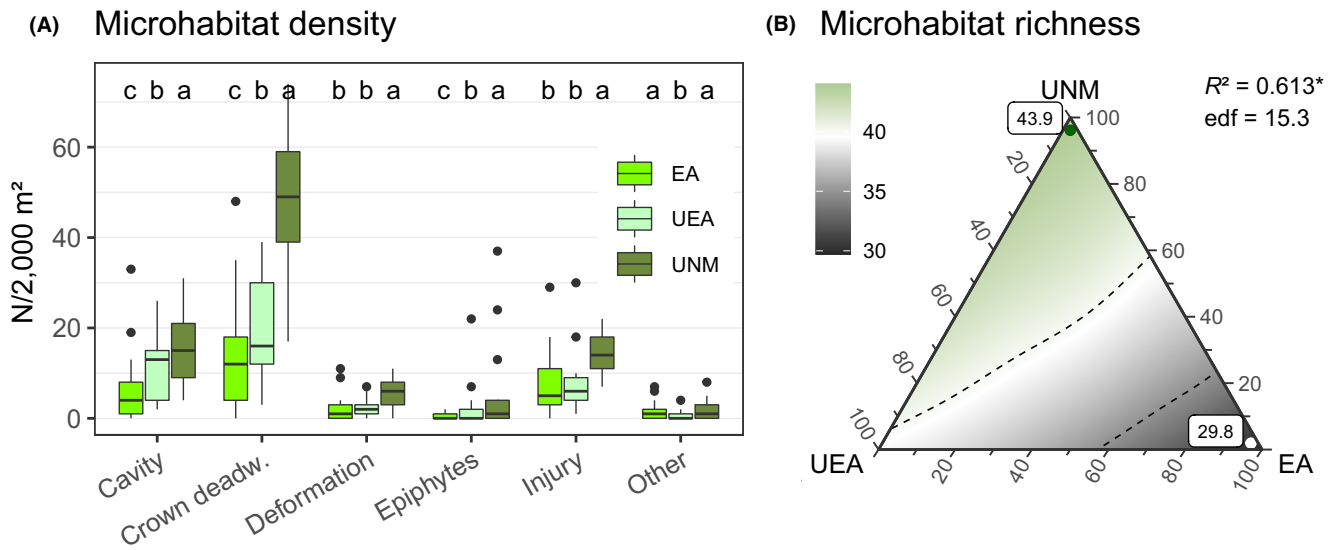


FIGURE 2 Density (A) and γ -diversity (richness⁰D) (B) of tree-related microhabitats in 2017, following the classification of Kraus et al. (2016). Differences of microhabitat density between EA, UEA and UNM management systems were tested using the Poisson distribution for count data. To estimate γ -diversity of mixed landscapes composed of EA, UEA and UNM, the composition of forest landscapes was varied in steps of 10% using 1,000 resamplings of 10 plots per step (66 unique landscape compositions), following the method of Schall et al. (2020)

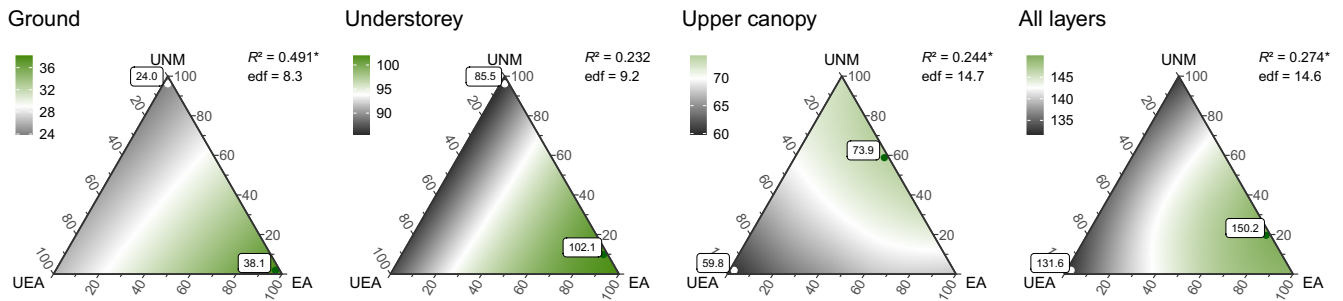


FIGURE 3 Gamma diversity (richness⁰D) of saproxylic beetles for different forest layers in 2008. Data were sampled using pitfall traps installed at the ground surface and flight interception traps installed in the understorey (1.5 m height above the ground) and the upper canopy. To estimate γ -diversity, the composition of forest landscapes was varied in steps of 10% using 1,000 resamplings of 10 plots per step (66 unique landscape compositions), following the method of Schall et al. (2020)

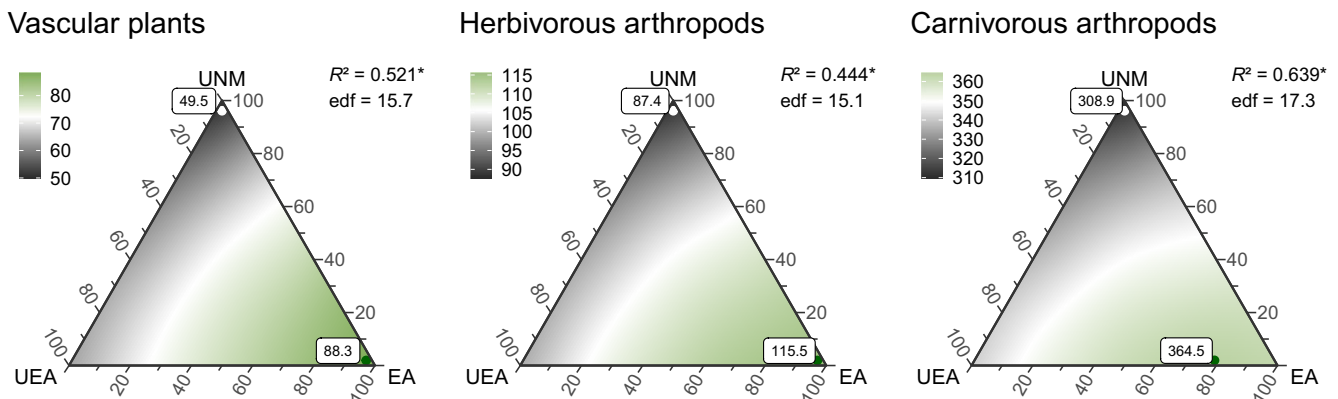


FIGURE 4 Gamma diversity (richness⁰D) across trophic levels of producers, consumers and predators in 2008/09 shows a bottom-up pattern. Arthropods comprise the groups of araneae, coleoptera, hemiptera, hymenoptera, neuroptera, opiliones and pseudoscorpiones. For method details see Figure 3

4 | COMPARING RESULTS—SCALE MATTERS!

Bruun and Heilmann-Clausen (2021) refer to an own study which they consider as very similar to ours, but with different outcomes. The study by Lelli et al. (2019) compared (a) forests unmanaged for more than 50 years with trees older than 200 years, (b) recently unmanaged forests (partly comparable to UNM in Schall et al., 2020), (c) extensively managed forests with a multi-layered stand structure (comparable to UEA) and (d) one (mature) developmental phase of the even-aged system. Thus, while our study was not able to consider a fully developed unmanaged forest with a mosaic of developmental phases, Lelli et al. (2019) have not considered the complete even-aged management system indicating limitations for both studies. The main difference of both studies is, however, the spatial scale considered. While Lelli et al. (2019) focused on stand-level diversity, we concentrated on landscape-level diversity. Interestingly, when referring to stand-level diversity, we found similar patterns as Lelli et al. (2019) for vascular plants, deadwood fungi and lichens. This emphasises the need to make comparisons at the same spatial scale.

At the landscape scale, it is crucial to represent all developmental phases if these inherently belong to the respective system. That is why we have included the different developmental phases of the even-aged system proportionally to their share in the rotation period. As uneven-aged forests harbour different developmental phases on the within-stand scale but not between stands, a pre-selection was not necessary and a stratified sampling design even not possible as each plot represented the same developmental phases. Our study was, however, limited to considering different developmental phases of the unmanaged forests in contrast to other study sites (Emborg et al., 2000; Friedel et al., 2006, see Figure S3). Our unmanaged forests still show impressive growth leading to closed canopies and to still relatively low amounts of deadwood (see above). The cessation of forest management also led to a dilution of intermingled developmental phases that dated back to the former selection forest management. As a result, the environmental heterogeneity was lowest in the unmanaged forests in terms of light availability (see fig. S2–S11 in Schall et al., 2020) or daily temperature range (Ehbrecht et al., 2017) compared to even-aged and uneven-aged forests. In order to reflect the existing heterogeneity as well as possible, we considered forests with a different management history and time since management abandonment within the unmanaged category.

The consideration of different developmental phases across stands for the even-aged system also explains differences in tree species composition that existed between even-aged and uneven-aged forests. As stated by Schall et al. (2020) a higher share of admixed tree species is an intrinsic characteristic of early developmental phases of the shelterwood system with a high light availability (table S1–S2 in Schall et al., 2020). Beech successively outcompetes admixed tree species in later developmental stages leading to monospecific stands. As uneven-aged forests are mainly characterised by single tree interventions, light availability is hardly

sufficient for admixed tree species. Differences in tree species composition are, therefore, causally related to the management system. Interestingly, a higher share of admixed tree species was not only observed after shelterwood cuttings but also following natural disturbances in self-sustaining beech forests on nutrient rich sites (Heinrichs & Schmidt, 2013). The high tree species diversity in the unmanaged forests of the Hainich National Park is, however, a result of the former coppice-with-standards management and is currently decreasing due to the competitiveness of European beech (Schall, Schulze, et al., 2018).

5 | CAREFUL INTERPRETATIONS ARE NEEDED

Unfortunately, Bruun and Heilmann-Clausen (2021) seem to interpret our conclusions as if 'biodiversity conservation is worse off in more natural ecosystems than in managed ones'. This is simply not true, as we clearly suggest that biodiversity conservation in a managed landscape like Central Europe requires both integrative and segregative elements in managed forests. Thus, the high biodiversity detected in the even-aged system should not be interpreted as a claim for using this system only. However, our study challenges the often-raised assumption that forest management inevitably leads to biodiversity loss and questions the complete focus on fine-grained management of beech forests. This focus leads to homogenised forest structures across landscapes (Angers et al., 2005) and thus to a reduction in biodiversity at the landscape level. In their current state, characterised by closed canopies while in development towards old-growth structures, the unmanaged forests in our study area, and in most of Central Europe, are not yet able to compensate for this structural homogenisation. This is in line with Sabatini et al. (2019) showing a trade-off between carbon accumulation in trees, as currently visible in the recent unmanaged forests, and biodiversity. Recent reserves, however, already support certain groups partly in combination with even-aged forests. Their contribution to landscape level biodiversity will presumably increase in the future with stand ageing and with increasing natural disturbances, although giving an exact time frame would be speculative (see Paillet et al., 2015). There have been suggestions to accelerate the process (Bernes et al., 2015) as also mentioned by Bruun and Heilmann-Clausen (2021). However, we consider it also important that current reserves are kept unmanaged to study how their contribution to landscape-level biodiversity changes with reserve age.

Overall, we see our results as a promising sign pointing towards options for successfully integrating important aspects of nature conservation into forest management. By this, they may contribute to overcoming the unsatisfying antagonism of 'forestry' versus 'nature conservation' as our results successfully exemplify integrative forest nature conservation (Bollmann & Braunisch, 2013; Doerfler et al., 2018). Beech forest landscapes managed to promote developmental phases characterised by different environmental conditions

can provide habitats for most sampled species including forest specialists. By combining heterogeneous stands in the landscape with forests where management was abandoned and where natural dynamics can take over after centuries of management, demands for timber production as well as biodiversity conservation of generalist and specialist species can be successfully integrated in the future (see also Penone et al., 2019). Our study therefore highlights the need to combine land-sparing and land-sharing approaches by maintaining a heterogeneity of structures in space and time within managed forests. The heterogeneity provided by forest management may also compensate for unsuitable phases that may occur early after forest management abandonment (Braunisch et al., 2019) or due to a cyclic synchronisation of forest structures in unmanaged forests (Vandekerckhove et al., 2009; Von Oheimb et al., 2007).

As our study was based on the—albeit very diverse—beech forest systems of the Hainich region, we reiterate our call for more studies addressing whole landscapes of different forest compositions and configurations and focusing on gamma diversity rather than on stand-scale diversity only. A variety of future studies including different management systems may clarify the optimised spatial scale of management units or necessary shares of protected areas for fully realising both sustainable timber production and forest biodiversity conservation at the landscape scale. By no means, however, such studies would question the importance of existing (and future) unmanaged forest reserves for biodiversity that still have only a small share on the total forest area of Europe, and the full and infinite protection of the remaining European primeval forests.

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CONFLICT OF INTEREST

The authors have declared no conflict of interest.

AUTHORS' CONTRIBUTIONS












S.H. and P.S. wrote the first draft of the manuscript; P.S., S.H. and M.M.G. compiled and analysed data; S.H., P.S., M.M.G., C.A., M.F.

and W.W.W. finalised the manuscript. All authors contributed to discussion and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data are publicly available from the Biodiversity Exploratories Information System (<https://doi.org/10.17616/R32P9Q>) at <https://www.bexis.uni-jena.de/ddm/publicsearch/index> with identifiers 30,979 (deadwood), 30,980 (microhabitats), 30,981 (saproxylic beetles) and 30,982 (trophic levels).

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SUPPORTING INFORMATION

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