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RESEARCH ARTICLE

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Can multi-taxa diversity in European beech forest landscapes be increased by combining different management systems?

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Abstract

1. Forest management greatly influences biodiversity across spatial scales. At the landscape scale, combining management systems that create different stand properties might promote biodiversity due to complementary species assemblages. In European beech forests, nature conservation and policy advocate a mixture of unmanaged (UNM) forests and uneven-aged (UEA) forests managed at fine spatial grain at the expense of traditionally managed even-aged shelterwood forests (EA). Evidence that such a landscape composition enhances forest biodiversity is still missing.
2. We studied the biodiversity (species richness ^{0}D, Shannon diversity ^{1}D, Simpson diversity ^{2}D) of 14 taxonomic groups from bacteria to vertebrates in 'virtual' beech forest landscapes composed of varying shares of EA, UEA and UNM and investigated how γ-diversity responds to landscape composition. Groups were sampled in the largest contiguous beech forest in Germany, where EA and UEA management date back nearly two centuries, while management was abandoned 20–70 years ago (UNM). We used a novel resampling approach that created all compositional combinations of management systems.
3. Pure EA landscapes preserved a maximum of 97.5% γ-multidiversity (^{0}D, ^{1}D) across all taxa. Pure and mixed UEA/UNM landscapes reduced γ-multidiversity by up to 12.8% (^{1}D). This effect was consistent for forest specialists (^{1}D: −15.3%). We found only weak complementarity among management systems.

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4. Landscape composition significantly affected γ-diversity of 6–9 individual taxa, depending on the weighting of species frequencies with strongest responses for spiders, beetles, vascular plants and birds. Most showed maximum diversity in pure EA landscapes. Birds benefited from UNM in EA-dominated landscapes. Deadwood fungi showed highest diversity in UNM.
5. *Synthesis and applications*. Our study shows that combining fine-grained forest management and management abandonment at the landscape scale will reduce, rather than enhance, regional forest biodiversity. We found an even-aged shelterwood management system alone operating at intermediate spatial scales and providing stands with high environmental heterogeneity was able to support regional biodiversity. However, some taxa require certain shares of uneven-aged and unmanaged forests, emphasizing their general importance. We encourage using the here presented resampling approach to verify our results in forest landscapes of different composition and configuration across the temperate zone.

KEYWORDS
complementarity, even-aged forests, forest specialists, gamma-diversity, landscape composition, resampling, uneven-aged forests, unmanaged forests

1 | INTRODUCTION

Land-use change and intensification are major drivers of global biodiversity loss (Sala et al., 2000) and their pressures on biodiversity are expected to further increase (Pereira et al., 2010). Temperate broadleaved forests have been frequently replaced by conifer plantations across Central Europe affecting biodiversity in multiple ways (Spiecker et al., 2004). Nevertheless, European beech (*Fagus sylvatica*) forests, which naturally would dominate Central European landscapes, were preserved on a considerable area (Ellenberg, 1988), but were managed over centuries. Since the 19th century, shelterwood systems resulting in naturally regenerated even-aged (EA) stands were predominantly applied (Röhrig, Bartsch, & von Lüpke, 2006). Untouched primeval beech forests rarely exist in Central Europe today and are mainly restricted to the Carpathian Mountains (Korpel', 1996). Their multi-aged stand structure largely differs from EA managed beech forests, with many microhabitats and high amounts of deadwood of differing quality favouring several taxonomic groups (Dymytrova, Nadyeina, Hobi, & Scheidegger, 2014; Lachat & Müller, 2018). The increasing awareness of the importance of biodiversity and structural heterogeneity for ecosystem functions and services (e.g. Felipe-Lucia et al., 2018) made biodiversity conservation an important part of forest management programmes across Europe (Harrison et al., 2014; Kraus & Krumm, 2013). To restore beech forests with a high structural complexity, to ensure habitat continuity and to promote the diversity of multiple taxonomic groups (Boch, Prati, Hessenmöller, Schulze, & Fischer, 2013; Müller et al., 2019; Purahong et al., 2014), close-to-nature forest management with single tree or group selection cutting has been favoured over the traditional shelterwood system. In addition, there is a call for large UNM forest reserves to promote for example, fungi, carabids, bryophytes, lichens or saproxylic beetles (Bässler et al., 2014; Paillet et al., 2010). The mixing of small-scale forest management with up to 5% UNM forests within a landscape is thought to preserve forest biodiversity by simultaneously fulfilling timber demands (BMEL, 2017). Current forest management concepts across Europe, thus, combine land-sharing and land-sparing approaches (Bollmann & Braunisch, 2013; Doerfler, Gossner, Müller, Seibold, & Weisser, 2018).

A recent multi-taxa study in European beech forests revealed higher regional γ-diversity for many taxonomic groups, including forest specialist and deadwood-dependent species, in EA compared to uneven-aged (UEA) forests (Schall, Gossner, et al., 2018). This was explained by a high between-stand variation in environmental conditions compared to UEA stands. The latter are characterized by a high within heterogeneity but relatively homogenous stand structures at the landscape scale (Decocq et al., 2004; Werner & Raffa, 2000). Results were in accordance with studies conducted in forests across the temperate zone that underline the importance of heterogeneous forest structures within and among stands for biodiversity at the landscape scale (e.g. Angers, Messier, Beaudet, & Leduc, 2005; Sebek et al., 2015).

It is not known, however, whether the application of a single, but diverse, management system is sufficient to support maximum landscape-scale diversity. Previously reported positive effects of environmental heterogeneity on biodiversity at larger spatial scales rather indicate the necessity for a mosaic of different management systems as well as protected areas across the forest landscape (Nolet, Kneeshaw, Messier, & Béland, 2018). Such a mosaic would promote landscape-scale biodiversity when the different systems support complementary species assemblages (Colwell & Coddington, 1994; Schall, Gossner, et al., 2018). In tropical systems Edwards et al. (2014)

found that a segregative approach with forest reserves next to intensively logged sites conserves regional diversity of different taxonomic groups better than a land-sharing approach with selective forest management. For Europe, similar analyses across multiple taxa are still missing (Ammer et al., 2018).

Here we investigated the diversity of 14 taxonomic groups along compositional gradients of EA, UEA and UNM European beech forests based on data of an ancient forest landscape in Central Germany, where the EA system was found to be more diverse compared to the UEA one (Schall, Gossner, et al., 2018). In this landscape, EA stands result from uniform shelterwood cuttings, while UEA structures are created by single tree selection cutting. Thus, the two management systems represent the coarse- and fine-grained edges of continuous cover forestry in Europe (Brang et al., 2014; Röhrig et al., 2006). The UNM forests, where forest management has ceased 20–70 years ago, are representative of other strict forest reserves of Central Europe (Burrascano et al., 2018). The studied landscape represents a perfect real world model for analysing biodiversity effects of different compositions of the three management systems since shelterwood and selection systems have a long tradition in this forest region and coexisted for nearly two centuries (Wäldchen, Schulze, Schöning, Schrumpf, & Sierra, 2013). By using a novel approach we resampled forest stands within this landscape to create all compositional combinations of management systems (= 'virtual' forest landscapes) in steps of 10%.

Our main questions were:

1. Which composition of management systems maximizes regional multidiversity?
2. Are composition effects consistent among taxonomic groups?
3. Is regional biodiversity of taxonomic groups driven by mean local diversity or species turnover within or among management systems?

We expect a positive effect on biodiversity by combining the EA management system, which shows high environmental heterogeneity among stands (Schall, Gossner, et al., 2018), with certain shares of UEA and/or UNM at the landscape scale, as natural forest development or complex canopy structures have been shown to be important for particular taxonomic groups at the local scale. This effect is expected to be driven by species assemblages that rely on forest properties and structures that are provided by UEA and UNM.

2 | MATERIALS AND METHODS

This study was conducted within the framework of the Biodiversity Exploratories project (Fischer et al., 2010, www.biodiversity-exploratories.de) and is based on the same data as Schall, Gossner, et al. (2018). Plots were selected to (a) include forest management systems that cover large contiguous areas to eliminate effects of forest configuration on measurements, (b) be located within sufficiently large management units to provide habitat for the species under study, (c) be sufficiently spaced to ensure independence of measurements and (d) show similar environmental gradients between management systems to factor out environmental bias. We thus consider each forest management system to be represented by independent observations. For a graphical summary of our methodology see Figure S1-1 in Supporting Information document.

2.1 | Study area

Even-aged (EA, N = 17 plots), uneven-aged (UEA, N = 13) and unmanaged forests (UNM, N = 13) are located in Central Germany, Thuringia, along the forested hill chains of Hainich, Westerwald, and Dün (51°12′N, 10°22′E) on Triassic limestone. The natural vegetation is a mesophytic deciduous forest dominated by *F. sylvatica* on nutrient-rich soils, with minor contributions of other tree species (*Fraxinus excelsior*, *Acer pseudoplatanus*, *Carpinus betulus*, *Tilia* sp., *Ulmus* sp.) in mid- and late successional stages (Ellenberg, 1988). In medieval and early modern periods the forests have been intensively used, but had never been converted to conifer stands, were used agriculturally or were affected by settlements; we can therefore consider all investigated forests as ancient deciduous forests (Wäldchen et al., 2013). Plots (100 m × 100 m) were located in large contiguous areas covered by the same management system while being separated from another management system by at least 3 km. Observations were thus not affected by fragmentation or edge effects. Climatic and edaphic gradients of plots were comparable between management systems (Table S1-1).

Plots largely resemble the tree species composition of natural vegetation with European beech dominating, contributing 87.3% to basal area (Tables S1-1 and S1-2). Among management systems, UNM showed lower proportions of European beech and higher proportions of other broadleaf hardwoods, which are legacies of the former coppice-with-standards forest management (Table S1-2). According to the habitat heterogeneity hypothesis (MacArthur & MacArthur, 1961), higher tree species diversity should positively affect biodiversity. Thus, our study may overestimate biodiversity of UNM in comparison to other natural beech forests on nutrient-rich soils with a higher share or total dominance of European beech (see for example Mölder, Streit, & Schmidt, 2014).

Even-aged forests have been traditionally managed for about two centuries in blocks of 8–18 ha ($M \pm SD$ 11.6 ± 2.6 ha) with a rotation period of about 140 years following natural regeneration from shelterwood trees that were kept for 20–40 years. Proportional to their share on rotation period, we selected plots from the following developmental phases: thicket (about 20 years old; three plots), pole wood (20–40 years; three plots), immature timber (40–80 years; four plots), mature timber (80–120 years; four plots) and thicket with shelterwood trees (120–140 years; three plots). Timber and deadwood volume were 350.8 ± 215.7 and 27.8 ± 12.1 m^3/ha. The density of large trees (dbh > 65 cm) was 4.5 ± 6.3 trees/ha.

Uneven-aged forests have been managed by single tree harvests and repeated thinnings of low intensity for about 140 years in Hainich and 250 years in Dün. They cover a total of 5,000 ha, which

is exceptional, both in length and spatial extent (Schütz, 2001). In these forests, deadwood volume was lower than in EA systems (17.7 ± 8.2 m^3/ha) but timber volume was higher (436.2 ± 82.2 m^3/ha), large trees were more frequent (17.9 ± 9.8 trees/ha) and of higher age (180–230 years) than in old EA stands. Size of management units was higher than in EA (26.9 ± 6.5 ha), due to lower intensity of single interventions.

Unmanaged forests are located in the Hainich National Park as part of the UNESCO World Heritage Site 'Ancient and Primeval Beech Forests of the Carpathians and other Regions of Europe'. In the 19th century, they were managed as coppice-with-standards for firewood and timber, and subsequently underwent a transformation to high forests for several decades. Time since management abandonment is 20 (five plots) to 70 (eight plots) years, which is at the upper range compared to other European beech forests set aside (Burrascano et al., 2018). Management units, which diluted in the meanwhile, were originally 24.1 ± 5.8 ha in size. UNM forests harboured highest timber volume (507.4 ± 96.2 m^3/ha) and number of large trees (20.2 ± 9.2 trees/ha), but only an intermediate amount of deadwood (21.6 ± 13.5 m^3/ha) compared to EA and UEA.

For more details, see Schall, Gossner, et al. (2018); further data on stand structure are given in Table S1-1.

The spatial arrangement of plots was comparable between EA and UEA, but UNM plots were aggregated within the Hainich National Park (Table S1-1), which might negatively affect β- and γ-diversity. By analysing the subset of plots located in Hainich separately, we show that the general findings were not driven by the spatial arrangement of UNM (Figure S1-2; Table S1-1).

2.2 | Taxonomic group sampling

Sampling methods were optimized for each taxon to achieve a representative sample of the communities occurring in each 1 ha plot. Arthropods, bryophytes and lichens were sampled in 2008, vascular plants in 2009 and ectomycorrhizal fungi and bacteria in 2011. Birds and bats were assessed in 2009 and 2010, deadwood fungi in 2010 and 2011. Two year collections were pooled per plot. For arthropod sampling, two pitfall traps and four flight-interception traps (two in the understorey and two in the canopy) per plot were used. Arthropods were separated into spiders, harvestmen and pseudoscorpions (henceforth 'harvestmen'), beetles, hymenopterans, lacewings and true bugs. Vascular plants, bryophytes, lichens and deadwood fungi were sampled in 20 m × 20 m quadrats located in the centre of each plot. For bryophytes and lichens we considered specimens found on soil, rocks, deadwood items and tree trunks and branches of shrubs up to 2.5 m height. Birds were monitored by the number of observed males, and bats by their flight activities. Assessment of below-ground taxa (ectomycorrhizal fungi DNA, bacterial RNA) was based on soil samples (for details see Schall, Gossner, et al., 2018).

Six taxa were classified into forest specialist and non-forest specialist species. Vascular plants were classified according to Schmidt, Kriebitzsch, and Ewald (2011), birds according to Glutz von Blotzheim and Bauer (1988), and bats, beetles, spiders and true bugs based on expert knowledge (see Acknowledgements). Bryophyte and lichen forest specialists comprised a high share of singletons and doubletons (53% for bryophytes and 67% for lichens) and were therefore not considered in the analyses.

2.3 | Statistical analysis

We used a conceptual framework to link the complementarity of species assemblages among management systems to the shape of the biodiversity response surface along different mixtures of management systems (Figure 1). We varied the share of EA, UEA and UNM forests at steps of 10% to create 66 compositionally distinct 'virtual' forest landscapes. Each landscape was represented by 10 randomly drawn plots and replicated 1,000 times (= 1,000 resamplings of plots per composition). The number of possible resampling combinations of plots per landscape composition by far exceeded the number of replications for (a) mixtures of all three forest management systems, for example, 284,427 unique combinations for a landscape composed of 1 EA, 1 UEA and 8 UNM (and e.g. 139,053,200 unique combinations for 3 EA, 3 UEA and 4 UNM), (b) mixtures of two forest management systems, for example, 9,295 unique combinations for a landscape composed of 1 UEA and 9 UNM and (c) pure EA forests (19,448 unique combinations for 10 out of 17 EA) but (d) was only 286 for pure UEA and UNM forests (10 out of 13 plots). We therefore used the 286 unique combinations of plots as resamplings for pure UEA and UNM forest landscapes, resampled the other cases (a–c) without replacement and accounted for the number of resamplings in all statistical analyses (by inversely weighting the number of resamplings 1/286 vs. 1/1000).

As response variables, we calculated (a) regional γ-diversity for Hill numbers 0, 1 and 2 accounting for species frequencies (Chao et al., 2014), that is, species richness ^{0}D, Shannon diversity ^{1}D and Simpson diversity ^{2}D. (b) Beta-diversity was calculated as share on γ-diversity measured as multiple-site Jaccard dissimilarity and its turnover and nestedness components (Baselga, 2010) and (c) α-diversity ^{0}D for all 64,572 individual replications of compositionally distinct landscapes. In contrast to real landscapes, decreasing shares of management systems will not lead to the extirpation of respective unique species, but will reduce their frequencies. This means that results of our method are more conservative compared to the real world, when the share of a forest management system decreases. Nevertheless, management systems with a high number of infrequent unique species will benefit disproportionately from an increasing number of management units (= an increasing area share) within the 'virtual' landscape. We tested the influence of species with different frequency by analysing the Hill numbers 0, 1 and 2. In addition, our approach is based on a constant size of forest management units and consequently a constant habitat availability for the occurring species within these units and assumes that the landscape configuration does not limit dispersal of species and thus

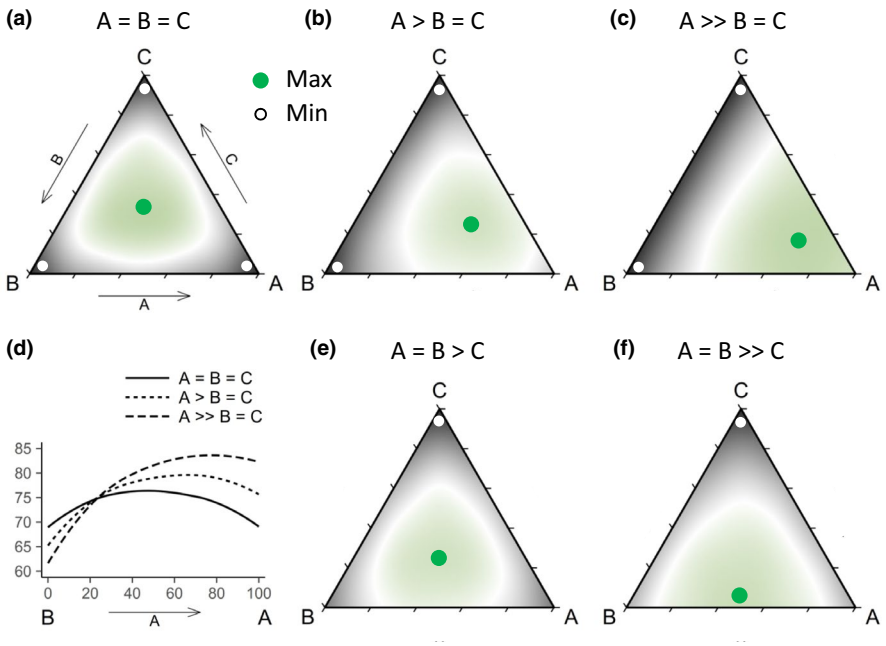

FIGURE 1 Conceptual framework of the effect of mixing communities on γ-diversity (regional species richness) conditional to the occurrence of unique species. Note that this is an example using constructed data to illustrate the effect of complementarity between communities on the shape of the response surface. We distinguish communities A, B and C sharing 60 common species and comprising 30 unique species in total. Each community was represented by plots consisting of 20 species (i.e. α-diversity), which were randomly drawn from the respective community species pools. Mixtures of communities A, B and C were generated along compositional gradients of communities (1/12 step width, i.e. 91 compositions) randomly sampling 12 plots per composition. We used 100 resamplings per composition to calculate mean γ-diversity. Note that in our empirical study we did not construct species assemblages by randomly assigning species of the community species pool to plots. Instead, we always kept the species assemblages sampled on a particular plot and just randomly drew plots from the pool of plots within one management system. (a) Gamma-diversity peaks at equal shares of communities (four plots for A, B and C) when communities comprise an equal number of unique species (10 unique species for A, B and C). With an increasing number of unique species in one community, here A (b, 18 unique species; c, 26 unique species), at cost of the other two communities γ-diversity gradually increases with the share of A. (d) Considering only the compositional gradient of A and B, γ-diversity turns from humped shaped to one-sided with increasingly uneven distribution of unique species. When the number of unique species increases in two communities, here A and B (e, 12 unique species each; f, 14 unique species each), at cost of the third community (C), then γ-diversity peaks at equal shares of communities A and B, while community C shows minimum γ-diversity

population sizes. However, we cannot exclude effects of changes in landscape configuration that may occur in real landscapes (e.g. effects of isolation on species dispersal; MacArthur & Wilson, 1963; Warren et al., 2015). As all three investigated management systems represent beech forests within an almost pure beech forest landscape, all systems are potentially suitable for most detected species and do not represent 'hostile' environments keeping potential dispersal limitations low. Recently, it has been proposed that the patch size and the patch isolation effect are driven mainly by the amount of habitats available in a landscape (Fahrig, 2013). As the habitat amount is comparable for the management systems studied (Table S1-1), this would also suggest a rather minor effect of habitat isolation and thus landscape configuration in our system.

We analysed the effect of landscape composition on response variables using general additive models with two factorial full tensor product spline smoothers (GAM: response ~ te (EA, UEA)). While β-and γ-diversity may show nonlinear response surfaces exceeding 3 (*df*; Figure 1), the α-diversity response surface is a simple inclined plane (two-factorial linear model with 3 *df*), when driven by landscape composition. We generally report R^2 and the *df* based on the 64,572 replications (weighting the number of replications). Ternary diagrams and bivariate plots were used to visualize response surfaces. As *p*-values are not informative for models of resamplings, we inferred for significant differences of response variables between landscape compositions by comparing the maximum and the minimum diversity. For γ-diversity, we used the one-sided 95% confidence interval of conditional variance (Chao et al., 2014). For α- and β-diversities, differences were inferred by pairwise comparison of resamplings (i.e. for one-sided $p < 0.05$ at least 950 of 1,000 comparisons showed larger values for the maximizing landscape composition).

To understand how α- and β-diversity control γ-diversity in different taxonomic groups, we calculated linear models with α-diversity, β-turnover and β-nestedness as predictors based on the means of the 66 compositions, and decomposed the explained variance to estimate variable importance. We compared importance metrics able to cope with variable correlations as given among α- and β-diversities, that is, LGM, PMVD and CAR scores, and selected CAR scores as being the most robust metric (Grömping, 2015). CAR scores measure the R^2 contribution of regressors based on game theory and sum up to the model R^2.

To summarize the effect of landscape composition across taxonomic groups, we quantified multidiversity (Allan et al., 2014) as the average relative diversity of taxa weighted by the species number of taxa (log weighting) to account for general differences in size of taxonomic groups. When a landscape composition shows multidiversity of 100%, then all taxa were equally supported close to the optimum. Landscape compositions of low multidiversity discriminate some taxonomic groups. We quantified strength (R^2) and significance of the effect of landscape composition on multidiversity using general additive models with two factorial spline smoothers, taking the relative diversity of the taxonomic groups as response variable and their species number as weight. Here the R^2 is a conservative estimate of effect strength on multidiversity, as least squares methods disproportionally weight larger deviations.

For quantifying γ-diversities the function 'estimateD' of package iNEXT version 2.0.12 (Chao et al., 2014), for β-diversities the package BETAPART version 1.4-1 (Baselga, 2010), for generalized additive modelling the package MGCV version 1.8-18 and for variance partitioning the package RELAIMPO version 2.2-2 (Grömping, 2015) were used in R version 3.4.1 (R Core Team, 2014).

3 | RESULTS

In the analysis, we considered 3,652 taxonomic units, including 52 vertebrate, 1,133 arthropod, 183 plant, 37 lichen and 271 deadwood fungi species as well as 823 ectomycorrhizal fungi and 1,153 bacterial operational taxonomic units. These species numbers were based on an extensive sampling, for example, 63,203 sampled specimens of arthropods.

Gamma-multidiversity across 14 taxonomic groups was significantly affected by forest landscape composition, but we hardly observed complementarity of species assemblages between forest management systems. The maximum multidiversity was found in a landscape composed of 100% EA and declined with increasing shares of UEA and UNM, independent of the weighting of species frequency (Figure 2; Figures S2-1). In 100% EA landscapes species richness (97.5% ^{0}D), exponential Shannon entropy (97.5% ^{1}D) and the inverse of Simpson diversity (97.1% ^{2}D) approached the optimum (i.e. 100%). Pure UEA (86.2% ^{0}D, 84.7% ^{1}D, 84.5% ^{2}D) and UNM (87.0% ^{0}D, 86.7% ^{1}D, 87.0% ^{2}D) landscapes consistently lost more than 10% of biodiversity compared to a landscape composed of pure EA. The current landscape composition in the Hainich-Dün region, comprising about 40% EA, 30% UEA and 30% UNM, fell below the maximum biodiversity by more than 4%. Mixed landscapes of 90% UEA and 10% UNM lost about 10% (87.7% ^{0}D, 87.2% ^{1}D, 87.3% ^{2}D).

Considering forest specialists of bats, birds, spiders, beetles, true bugs and vascular plants, the finding that γ-multidiversity peaks in landscapes dominated by EA (pure EA: 98.2% ^{0}D, 98.9% ^{1}D, 98.5% ^{2}D) and shows the minimum in pure UEA (83.4 ^{0}D, 83.7 ^{1}D), or UNM (84.2 ^{2}D) landscapes was even more pronounced (Figures S2-2 and S2-3). However, in contrast to all species, forest specialists showed some degree of complementarity of species assemblages between EA and UNM for higher Hill numbers, which is indicated by an edge-peaked maximum of abundant species (99.0% ^{1}D, 98.7% ^{2}D) in landscapes composed of 90% EA and 10% UNM (Figure S2-3).

Gamma-diversity (^{0}D, ^{1}D or ^{2}D) of 10 of the 14 taxonomic groups significantly responded to forest landscape composition (Table 1; Figure 2b,d; Figures S2-4, S2-5 and S2-6). In accordance with γ-multidiversity, γ-diversity showed no complementarity of species assemblages between forest management systems for most investigated groups. With R^2 values between 40% and 70%, the response was strongest for spiders, beetles, vascular plants, birds, harvestmen and true bugs, which all showed their maximum diversity in pure and close-to-pure (birds and true bugs) EA landscapes. For spiders, beetles and vascular plants, the finding of highest diversity in 100% EA and lowest diversity in 100% UNM was independent of the frequency weighting. Deadwood fungi were the only group in our study with a maximum diversity in 100% UNM landscapes, while lacewings and bacteria peaked in 100% UEA. The response of these three groups to landscape composition is the main reason that multidiversity was 2.5% lower than the potential maximum (i.e. 100%) in pure EA landscapes. Taxa that reached their diversity maximum in mixed landscapes were birds, which peaked at 80% EA and 20% UNM for ^{0}D and ^{1}D, true bugs (^{1}D peak at 90% EA and 10% UEA), and ectomycorrhizal fungi (^{2}D peak at 80% EA and 20% UEA).

Landscape composition affected mean α-diversity ^{0}D of 11 (Figure S2-7), β-turnover ^{0}D of 9 (Figure S2-8), and β-nestedness ^{0}D of 6 (Figure S2-9) taxonomic groups (see summary in Table S2-1). Maximum α-diversity was observed in pure UEA for one taxon and in pure UNM and EA landscapes for five taxa each, while six taxa showed minimum α-diversity in pure UNM, three taxa in pure UEA and two taxa in landscapes dominated by EA (Table S2-1). Thus, for α-diversity UNM either reduces or promotes local biodiversity, depending on the taxon. Beta-turnover peaked in landscapes of pure or dominating EA for six taxonomic groups, and for one group each in mixed EA/UNM, pure UNM and pure UEA landscapes, while minimum turnover was found in pure UEA for six groups and in pure UNM for three groups. Complementarity in species assemblages was therefore mainly higher within the EA management system than between systems and lowest within the UEA system. Beta-nestedness showed no directed trend across taxonomic groups.

Linear models showed that γ-diversity is well explained by α-diversity, β-turnover and β-nestedness. We observed a high goodness of fit with R^2 between 85% and 98% for 12 of the 14 taxonomic groups and R^2 > 59% for bats and harvestmen (Figure S2-10). However, only α-diversity and β-turnover (and not β-nestedness) turned out to drive γ-diversity. The contribution of α-diversity and β-turnover to model R^2 depended on taxonomic groups. In birds and ectomycorrhizal fungi γ-diversity was mainly driven by β-turnover and in deadwood fungi and beetles by α-diversity. In all other groups, γ-diversity was driven by both components.

There were no consistent responses of α-diversity and β-turnover to landscape composition (Table S2-1). Spiders (Figure 3a) and vascular plants were the only taxa comprising the maxima (but not minima) of α-diversity and β-turnover at an identical landscape

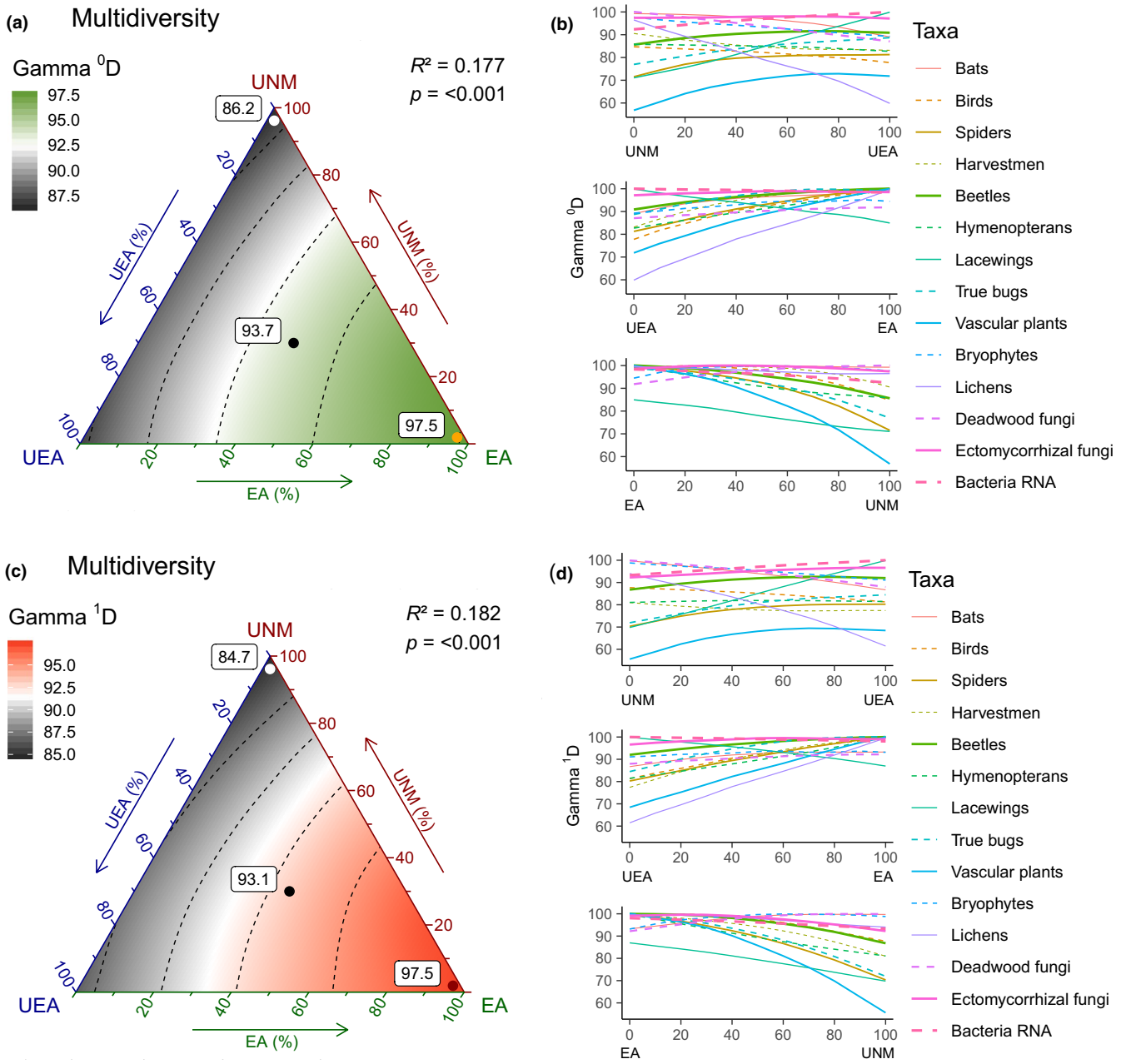

FIGURE 2 Gamma-multidiversity in % and relative γ-diversity for Hill-numbers 0 (a, b) and 1 (c, d) of 14 taxonomic groups along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1,000 resamplings of 10 plots per step (66 unique landscape compositions). Originating from median diversity (white) the colour saturation increases towards minimum (white dot) and maximum multidiversity (orange/red dot). The black dot marks the multidiversity of the actual landscape composition (40% EA, 30% UEA and 30% UNM). Relative γ-diversity along bivariate gradients of forest composition (b, d) show how taxonomic groups drive γ-multidiversity (line thickness resembles weighting of taxonomic groups). For ternary gradients of forest composition for each taxonomic group see Figures S2-4 and S2-5

composition (100% EA). All other groups showed either contrasting responses such as birds (Figure 3b), deadwood fungi (Figure 3c) and ectomycorrhizal fungi or overlapping responses such as beetles and lichens (Figures S2-4, S2-7 and S2-8). In case of contrasting responses of α-diversity and β-turnover, their effects on γ-diversity levelled off (ectomycorrhizal fungi) or were controlled by the stronger driver, that is, β-turnover in birds and α-diversity in deadwood fungi.

4 | DISCUSSION

Our study revealed no overall positive effect of mixing different forest management systems at the landscape scale on biodiversity. Instead, we found a maximum multidiversity across 14 taxa in pure EA landscapes. Among individual taxa, only deadwood-fungi (maximized in UNM landscapes), bacteria and lacewings (maximized in

TABLE 1 Explained variance R^2 of γ-diversity response (for Hill numbers 0, 1 and 2) to forest landscape composition and landscape composition comprising maximum and minimum diversity of 14 taxonomic groups and six forest specialist subgroups. Biodiversity minimizing and maximizing landscape compositions were only given for significant differences (bold printing of either EA, UEA or UNM means pure forest landscapes of that type; for mixed landscapes the dominating forest management system was printed bold). Results are based on 66 compositionally distinct forest landscapes characterized by resamplings (N = 64,572). *p < 0.05 significant difference between the minimum and maximum diversity. For the respective ternary diagrams, see Figures S2-4, S2-5 and S2-6

	^0D			^1D			^2D		
Taxon	**Min**	**R^2**	**Max**	**Min**	**R^2**	**Max**	**Min**	**R^2**	**Max**
Spiders	**UNM**	**0.588***	**EA**	**UNM**	**0.696***	**EA**	**UNM**	**0.730***	**EA**
Beetles	**UNM**	**0.599***	**EA**	**UNM**	**0.569***	**EA**	**UNM**	**0.550***	**EA**
Vascular plants	**UNM**	**0.521***	**EA**	**UNM**	**0.569***	**EA**	**UNM**	**0.587***	**EA**
Birds	**UEA**	**0.454***	**EA**-UNM	**UEA**	**0.536***	**EA**-UNM		0.446	
Harvestmen		0.212			0.446		**UEA**-UNM	**0.580***	**EA**
True bugs		0.294		**UNM**	**0.404***	**EA**-UEA	**UNM**	**0.489***	**EA**
Deadwood fungi	**UEA**	**0.368***	**UNM**		0.362		**UEA**	**0.424***	**UNM**
Lacewings		0.323		**UNM**	**0.321***	**UEA**	**UNM**	**0.329***	**UEA**
Bacteria	**UNM**	**0.358***	**UEA**	**UNM**	**0.305***	**UEA**	**UNM**	**0.230***	**UEA**
Lichens		0.210			0.226			0.253	
Hymenopterans		0.169			0.216			0.178	
Bats		0.103			0.173			0.175	
Ectomycorrhizal fungi		0.033			0.139		**UNM**	**0.275***	**EA**-UNM
Bryophytes		0.059			0.055			0.091	
Forest specialists									
Spiders	**UNM**	**0.525***	**EA**	**UNM**	**0.631***	**EA**	**UNM**	**0.666***	**EA**
Vascular plants	**UNM**	**0.515***	**EA**	**UNM**	**0.598***	**EA**	**UNM**	**0.621***	**EA**
Beetles	**UEA**	**0.459***	**EA**	**UEA**	**0.484***	**EA**-UNM	**UEA**	**0.506***	**EA**-UNM
Birds		0.267			0.291			0.262	
Bats		0.076			0.194			0.201	
True bugs		0.030			0.058			0.114	

UEA landscapes) showed different responses. These findings were independent of species frequency or forest specialization. The high γ-diversity in the EA system was taxon specifically driven by high local diversity (beetles), species turnover among stands (birds) or both (spiders, true bugs and vascular plants).'Effective complementarity' with highest γ-diversity in a mixed landscape was observed in a few cases only.

Thus, in contrast to our expectations, the results show that a single, relatively coarse-grained management system can yield maximum landscape level multidiversity, while fine-grained UEA or UNM forests with complex canopy and stand structures do not significantly add to this diversity. To understand this result it may be worth to recap the EA system in European beech stands, which differs strongly from EA management approaches in other parts of the world. The studied EA forests result from shelterwood cuttings which span between 20 and 40 years from the seeding cut in a mast year to final tree harvests removing 20%–30% of the growing stock at each harvest (Röhrig et al., 2006). This differs from approaches such as clearcutting which are also classified as 'even-aged forest management' (Laiho, Lähde, & Pukkala, 2011). Applied on large areas, the clearcut system was shown to have negative effects on biodiversity because it differs strongly from the spatio-temporal scales of natural disturbances even in boreal forests (Kuuluvainen & Grenfell, 2012). The shelterwood system under study, though, maintains a continuous canopy cover, but is characterized by regular thinning interventions, which prevent a complete closure of the canopy starting from the late pole wood phase. Therefore, sufficient light for an abundant and diverse herb layer can reach the forest floor in later developmental phases (Figure S2-11). In contrast, UEA and UNM provide less light due to closed canopies (UNM) or due to canopy layering (UEA; Boch, Prati, Müller, et al., 2013; Ehbrecht, Schall, Ammer, Fischer, & Seidel, 2019). The abundance and diversity of primary producers is likely to cascade up to higher trophic levels as indicated by an α-diversity response of true bugs, beetles, harvestmen and spiders similar to vascular plants (Leidinger et al., 2019; Figure S2-7). In fact, canopy openness was found to be the most important structural feature that drives above-ground α-diversity in forests (Penone et al., 2019) indicating that beside resource availability also favourable microclimatic conditions are of general importance for local biodiversity. For regional biodiversity, our study provides evidence for the importance of resource (habitat) heterogeneity between stands (Hilmers et al., 2018). Even though birds

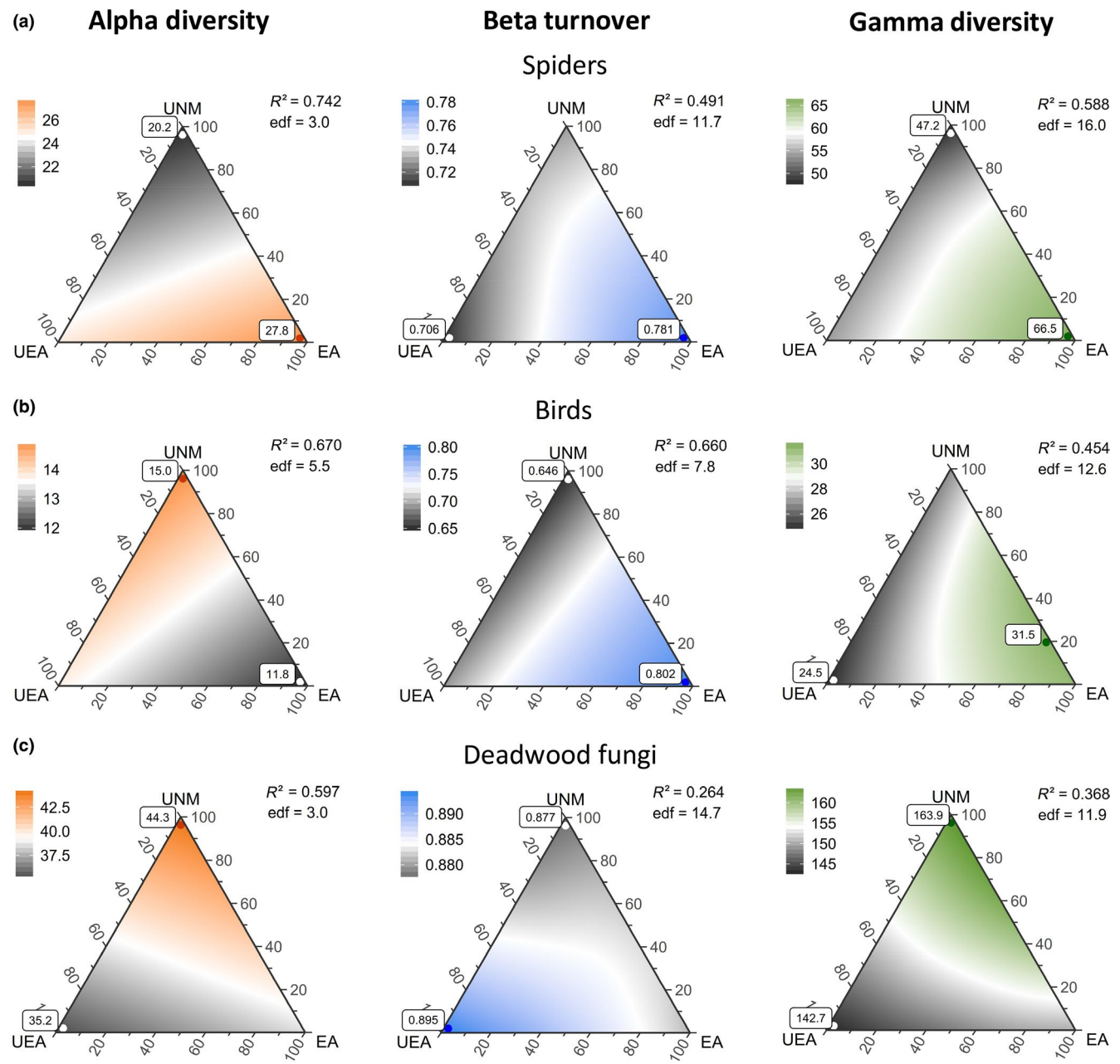

FIGURE 3 Alpha-diversity, β-turnover and γ-diversity ^{0}D of spiders (a), birds (b) and deadwood fungi (c) along compositional gradients of even-aged (EA), uneven-aged (UEA) and unmanaged (UNM) forests. The composition of forest landscapes was varied in steps of 10% using 1,000 resamplings of 10 plots per step (66 unique landscape compositions). With higher estimated *df* (edf) the shape of the diversity response surface becomes more complex. White represents the median diversity. Labelled dots show minimum and maximum diversity

showed higher α-diversity in UNM due to a higher availability of microhabitats (Paillet et al., 2018), their γ-diversity was mainly driven by the heterogeneity between the different developmental phases of EA with species such as common chiffchaff (*Phylloscopus collybita*), Eurasian bullfinch (*Pyrrhula pyrrhula*) and the garden warbler (*Sylvia borin*) preferring early developmental phases with low canopies, while the Eurasian treecreeper (*Certhia familiaris*) preferred the old ones. Species turnover between EA stands also contributed to γ-diversity patterns of vascular plants and spiders (Figure S2-8), which already comprised highest local diversity within EA (Table S2-1). In these two groups local resource availability and between stand environmental heterogeneity most likely interact. For vascular plants, it was shown that shade-tolerant forest specialists can persist after natural and anthropogenic disturbance within stands. The coexistence with more light-demanding species that benefit from disturbance increases α-diversity (Heinrichs & Schmidt, 2009; Kompa & Schmidt, 2005). For spiders, Oxbrough, Gittings, O'Halloran, Giller, and Smith (2005) underlined the importance of an open canopy for α-diversity and of a mosaic of stand ages to maintain both open and forest specialists in plantation forests. In a similar way, several studies showed that community composition of deadwood-dependent species largely differs between sunny and shady conditions (Müller

et al., 2015; Seibold et al., 2016) as well as between standing deadwood and deadwood on the ground (Boch, Prati, Hessenmöller, et al., 2013; Humphrey, Davey, Peace, Ferris, & Harding, 2002; Moning et al., 2009). A combination of deadwood exposed to different environmental conditions, as realised in the EA system, in combination with actively enhancing deadwood diversity (Gossner et al., 2016) might thus promote γ-diversity in this functional guild. While the potential high diversity of microhabitats in UNM enhanced the landscape level diversity of birds in an EA matrix when UNM contributes up to 20% area share, the higher structural diversity of UNM and also of UEA compared to EA at the stand level (Schall, Schulze, Fischer, Ayasse, & Ammer, 2018) provided no additional habitats to those provided by the different EA phases for the other taxa.

We found a different pattern for deadwood fungi, bacteria and lacewings with maximum (and minimum) diversity either in UNM or UEA. Bacteria and lacewings showed highest γ-diversity in UEA but with no significant difference to EA (Schall, Gossner, et al., 2018), while UNM was least diverse. This may indicate a general positive effect of forest management on these groups. In addition, aphids are the primary food resource for lacewings. Aphids might increase in population density in the canopy of the highly structured UEA forests and thus provide increased resource availability for the lacewings (Müller et al., 2017) compared to UNM closed canopy forests. In case of deadwood fungi, it is well known that fungal diversity increases with increasing availability of large deadwood and late decay stages (Heilmann-Clausen, 2001; Tomao, Bonet, Castaño, & de-Miguel, 2020). Large deadwood was most provided in the UNM forest stands (Schall, Gossner, et al., 2018), explaining a different diversity pattern for this taxonomic group. However, the effect size of these contrasting responses was too small to have an influence on the forest landscape composition driving maximum multidiversity.

Particularly surprising may be the fact that UNM forests do not complement managed forests until now. A likely reason may be that UNM forests are still developing old-growth stand structures as forest management ceased only 20 (five stands) to 70 (eight stands) years ago. With around 160 years they are far from senescence and still show impressive growth (Schall, Schulze, et al., 2018). This leads to closed canopies (Figure S2-11; Table S1-1) and low amounts of total deadwood (Schall, Gossner, et al., 2018). Habitat heterogeneity and deadwood availability of UNM forests were thus probably also not high enough yet to substantially contribute to higher multidiversity at the landscape scale. This is characteristic for most UNM forests in Central Europe set aside in optimum growth phase (Burrascano et al., 2018; Stiers et al., 2018). Natural or human disturbances that open the canopy and provide deadwood may be thus more effective than time in promoting biodiversity. However, the response of single taxa such as birds or deadwood fungi, hints towards the potential of UNM forests for specific organismic groups (Bässler et al., 2014; Paillet et al., 2010). Recent deadwood reinventories show an increase in total deadwood in UNM by 0.6 m^3/year (P. Schall & C. Ammer, unpubl. data) underlining the potential role of UNM forests in the future also for other deadwood-dependent taxa.

Though our study focuses on a specific beech forest landscape, we consider our results to be representative for beech forests in Central Europe with a well-developed understorey as an important resource and driver for higher trophic levels. Acidic beech forests, however, are relatively species poor (see Ellenberg, 1988). This fact may also result in lower biodiversity differences among forest management systems and combinations of management systems respectively. However, both for eutrophic and acidic beech forests similar trajectories in understorey development after different scales of natural disturbances (see Kompa & Schmidt, 2003, 2005) and in response to tree species composition (Heinrichs et al., 2019) have been observed.

Whether our results can be transferred to EA systems that operate at a finer spatial grain, like irregular shelterwood systems, or with much larger or smaller stand sizes than 8–18 ha (Table S1-1) or to UEA systems that operate with coarser graining such as group selection systems needs to be clarified by future studies. However, our results confirm a negative effect of homogenizing forest structures on biodiversity when fine-grained management is applied across temperate forest landscapes (Angers et al., 2005).

By keeping the size of management units constant, we factored out the effect of landscape configuration in our resampled 'virtual' landscapes. In real landscapes, a potential reduction of management units of a particular system in favour of another system may influence landscape configuration with potential consequences for species dispersal and therefore population sizes. We, however assume this effect to be negligible for our study area as the three investigated management systems represent beech forests within an almost pure beech forest landscape and are potentially suitable for most observed species. In fact, in 9 of 14 cases species turnover was higher within a management system than between management systems (Figure S2-8). In addition, species accumulation curves show similar shapes, showing that a reduction of habitat area reduces diversity irrespective of the management system (Figures S2-12 and S2-13). Our results are therefore valid for overall diversity, even though single species may show opposite responses.

5 | CONCLUSIONS

Our applied resampling approach provides novel insights on how biodiversity can be enhanced by combining management systems in forest landscapes. We found almost no complementarity of species assemblages between systems, even though they create different stand properties in terms of structural heterogeneity (Schall, Schulze, et al., 2018). Instead, multidiversity was maximized within a single management system that comprises different developmental phases and that can be characterized as the coarse-grained edge of continuous-cover forestry in Europe. The mixture of management abandonment and fine-grained management within forest landscapes, advocated by nature conservation and policy, rather reduced than enhanced multidiversity as well as the diversity of most

individual taxa. Thus, our study reveals potential consequences of creating forest landscapes exclusively aiming at high within-stand heterogeneity (UEA) and carbon accumulation in trees (using UNM as proxy) on biodiversity. This kind of management can favour certain groups of species but at the expense of many others (Neeson et al., 2018; Sabatini et al., 2019). For maintaining regional biodiversity in beech forests, forestry should promote the dissimilarity of environmental conditions and resources among forest stands as this was found to drive complementarity among species assemblages. Our results show that single management systems operating at intermediate spatial scales (management units sized 8–18 ha) and providing a matrix of different developmental phases can achieve this, even though some taxonomic groups would require certain shares of UEA or UNM. As our results are in contrast to the broad assumption that different management approaches including EA, UEA and UNM forests are needed at the landscape scale for biodiversity (Nolet et al., 2018), we encourage researchers to verify our results in forest landscapes of different composition and configuration across the temperate zone. Our applied resampling approach may be an effective tool to be used in future studies world-wide.

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AUTHORS' CONTRIBUTIONS

P.S., M.M.G. and C.A. designed the analysis; P.S., M.M.G. and S.H. analysed data; P.S., M.M.G., S.H. and C.A. wrote the draft of the manuscript. All other authors provided data and substantially contributed to revision. P.S. and M.M.G. contributed equally to this work.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4236t (Schall et al., 2017).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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