

Biodiversity along temperate forest succession

Torben Hilmers¹  | Nicolas Friess²  | Claus Bässler³ | Marco Heurich³ |
Roland Brandl² | Hans Pretzsch¹ | Rupert Seidl⁴ | Jörg Müller^{3,5} 

¹Chair of Forest Growth and Yield Science, Technical University of Munich, Freising, Germany

²Department of Ecology – Animal Ecology, Faculty of Biology, Philipps-Universität Marburg, Marburg, Germany

³Bavarian Forest National Park, Grafenau, Germany

⁴Department of Forest and Soil Sciences, Institute of Silviculture, University of Natural Resources and Life Sciences (BOKU) Vienna, Wien, Austria

⁵Department of Animal Ecology and Tropical Biology, University of Würzburg, Rauhenebrach, Germany

Correspondence

Nicolas Friess, Department of Ecology – Animal Ecology, Faculty of Biology, Philipps-Universität Marburg, Karl-von-Frisch Str. 8, 35032 Marburg, Germany.
Email: nico.friess@posteo.de

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Abstract

1. The successional dynamics of forests—from canopy openings to regeneration, maturation, and decay—influence the amount and heterogeneity of resources available for forest-dwelling organisms. Conservation has largely focused only on selected stages of forest succession (e.g., late-seral stages). However, to develop comprehensive conservation strategies and to understand the impact of forest management on biodiversity, a quantitative understanding of how different trophic groups vary over the course of succession is needed.
2. We classified mixed mountain forests in Central Europe into nine successional stages using airborne LiDAR. We analysed α - and β -diversity of six trophic groups encompassing approximately 3,000 species from three kingdoms. We quantified the effect of successional stage on the number of species with and without controlling for species abundances and tested whether the data fit the *more-individuals* hypothesis or the *habitat heterogeneity* hypothesis. Furthermore, we analysed the similarity of assemblages along successional development.
3. The abundance of producers, first-order consumers, and saprotrophic species showed a U-shaped response to forest succession. The number of species of producer and consumer groups generally followed this U-shaped pattern. In contrast to our expectation, the number of saprotrophic species did not change along succession. When we controlled for the effect of abundance, the number of producer and saproxylic beetle species increased linearly with forest succession, whereas the U-shaped response of the number of consumer species persisted. The analysis of assemblages indicated a large contribution of succession-mediated β -diversity to regional γ -diversity.
4. *Synthesis and applications.* Depending on the species group, our data supported both the *more-individuals* hypothesis and the *habitat heterogeneity* hypothesis. Our results highlight the strong influence of forest succession on biodiversity and underline the importance of controlling for successional dynamics when assessing biodiversity change in response to external drivers such as climate change. The successional stages with highest diversity (early and late successional stages) are currently strongly underrepresented in the forests of Central Europe. We thus recommend that conservation strategies aim at a more balanced representation of all successional stages.

KEYWORDS

biodiversity, forest dynamics, forest succession, habitat heterogeneity, LiDAR, species density, temperate forests, β -diversity

1 | INTRODUCTION

After a severe disturbance with high tree mortality, forests undergo a series of successional stages. Following successful regeneration, forests canopies eventually close and subsequently diversify in both their vertical and horizontal structures. With ongoing succession, forests accumulate biomass, and the initial cohort of trees gradually dies, which increases the amount of dead wood (Franklin et al., 2002; Oliver & Larson, 1990). Recent studies have revealed a dynamic and increasingly complex picture of forest succession that suggests the possibility of multiple successional pathways and nonlinear effects of varying disturbance severities (Donato, Campbell, & Franklin, 2012; Tepley, Swanson, & Spies, 2013). Nevertheless, key attributes of forests, such as carbon storage and biodiversity, are inherently linked to their successional stages (Seidl, Donato, Raffa, & Turner, 2016).

Despite the fundamentally dynamic nature of forests, accounting for successional dynamics remains a challenge for the development of conservation concepts (Tikkanen, Heinonen, Kouki, & Matero, 2007). Based on a limited number of focal species and their habitat preferences, conservation efforts often focus on one or a few successional stages (Swanson et al., 2011). For instance, it has been shown that late stages of forest succession, including plenter (mixture of trees of different ages, sizes, and heights), terminal, and decay stages, are the preferred habitat for species considered as typical “forest dwellers”, e.g., white-backed woodpecker in Central Europe (*Dendrocopos leucotos*; Carlson, 2000). Late successional stages are often prioritized in conservation due to their high diversity in taxa, including birds, bats, saproxylic organisms (Avila-Cabadilla, Stoner, Henry, & Añorve, 2009; de la Peña-Cuellar, Stoner, Avila-Cabadilla, Martínez-Ramos, & Estrada, 2012; Jacobs, Spence, & Langor, 2007), lichen (Kuusinen & Siitonen, 1998), and fungi (Redecker, Szaro, Bowman, & Bruns, 2001).

Understanding the inherent changes in species diversity as forests develop provides an important baseline for assessing the effects of external drivers such as climate change (Thom et al., 2017). In the absence of such a dynamic baseline, observed changes in biodiversity that are simply the effect of forest dynamics could be easily misattributed to effects of climate change. Furthermore, understanding the variation in biodiversity over the entire course of succession could also provide a more comprehensive perspective on the effects of different management strategies on biodiversity. In Europe, for instance, the majority of forests are currently of intermediate age, as a result of heavy exploitation during and after the first half of the 20th century (Vilén et al., 2012). Late stages of forest succession, such as the terminal and decay stages, are largely absent, as most forests are harvested before trees reach old age (Faustmann, 1995). Similarly, early successional stages are kept as short as possible by planting

trees (Parker et al., 2000) or employing silvicultural techniques that accelerate stand development (Dale et al., 2001).

Variation in biodiversity along the stages of succession can also help to better understand the underlying drivers of diversity in forests. For instance, resources that are relevant for different species groups, such as light on the forest floor and dead wood, distinctly vary with successional stage. The *more-individuals hypothesis*—a variant of the *species-energy hypothesis* (Wright, 1983)—suggests that an increase in resource availability leads to more individuals (Hurlbert, 2004). In individual-rich communities, more species reach viable population sizes, which increases the observed number of species. Another factor is the diversity of resources (Cramer & Willig, 2005). If particular stages of forest succession offer more resource types than others, these stages could harbour a larger number of species. This variant of the *habitat heterogeneity hypothesis* predicts an increase in the number of species independent of abundance (MacArthur & MacArthur, 1961).

To assess changes in α - and β -diversity over forest succession, we quantified the abundance and diversity of 23 taxonomic lineages representing six trophic groups across nine successional stages of forest succession (Figure 1a). Based on theoretical considerations and the expected changes in the amount and heterogeneity of resources along the stages of succession (Figure 1a), we hypothesized that:

- (H1) patterns of abundance and number of species of primary producers along the course of forest succession would be U-shaped, dependent on light reaching the forest floor; patterns of consumers would be U-shaped, if they depend on the primary producers; patterns of saproxylic organisms would be U-shaped, if they are dependent on the accumulation of dead wood along succession; and patterns of saprotrophs would be hump-shaped, following the pattern of biomass accumulation;
- (H2) the stage of forest succession would have no effect on the number of species when abundance is accounted for, if these responses are driven by an increase in individuals, as predicted by the *more-individual hypothesis*; and
- (H3) species compositions in the early and late successional stages, which are characterized by open canopies, would be similar as many insects respond to the openness of the habitat.

2 | MATERIALS AND METHODS**2.1 | Study area**

We used data from a survey of biodiversity and forest structure in the Bavarian Forest National Park in south-eastern Germany

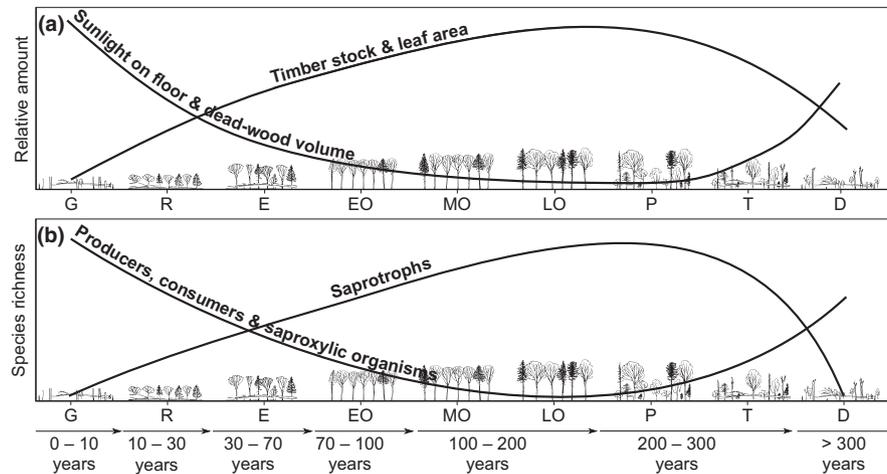


FIGURE 1 (a) Changes in resource availability with forest succession and (b) hypothesized response of saprotrophs, saproxylic organisms, producers, and consumers. The successional stages considered here follow Tabaku (2000), Drössler and Meyer (2006), and Zenner et al. (2016). Arrows represent an approximate timeline of the successional stages following Moning and Müller (2009). Note that the decay stage can occur already after 120 years due to forest disturbances, such as storms and bark beetle infestations. Stages: G, gap; R, regeneration; E, establishment; EO, early optimum; MO, mid-optimum; LO, late optimum; P, plenter; T, terminal; D, decay

(Bässler, Förster, Moning, & Müller, 2008). The study area covers 24,000 ha and comprises a wide range of stages of forest succession that resulted from considerable variation in disturbance history and stand age. We utilize this variation in a space-for-time substitution approach in our analysis. The total annual precipitation is between 1,300 and 1,900 mm and increases with elevation (Supporting Information Figure S1a), which ranges from 655 to 1,420 m a.s.l. Annual mean air temperature varies between 3.5°C at high elevations and 7.0°C at low elevations (Bässler, 2004). The national park is dominated by mixed mountain forests of Norway spruce (*Picea abies* (L.) Karst.), silver fir (*Abies alba* Mill.), and European beech (*Fagus sylvatica* L.).

2.2 | Data

Forest structure was characterized from field measurements and airborne light detection and ranging (LiDAR) on 287 plots, each with a circular area of 1,000 m². The plots include stands that were managed until a few decades ago and also remnants of old-growth forests. All measurements were conducted in the years 2006–2008 (Bässler et al., 2008). For each study plot, GPS coordinates were used to extract information on elevation from a digital terrain model (DTM 25) of the national park.

In a space-for-time substitution approach, differences in the environmental conditions of sites often bias the analysis. Therefore, we collected data on both soil characteristics and macro-climate for each plot (for details, see Supporting Information Appendix S1). By using elevation and the first PCA axis of soil parameter, we were able to control for potential differences.

The vegetation in the herbaceous layer (up to 1 m height), shrub layer (up to 5 m height), tree layer 1 (>5 to 15 m height), and tree layer 2 (>15 m) were estimated on 200 m² circular plots. Standing and downed woody debris were recorded in the field on each plot.

Full-waveform LiDAR data were collected across our plots using a Riegl LMS-Q560 under leaf-on conditions in 2007 (nominal sensor altitude: 400 m, average point density: 25 points m⁻²). Single trees in an area of 1,000 m² around the centre of each plot were detected using 3D segmentation (for details, see Supporting Information Appendix S1).

2.3 | Stages of forest succession

In our study, plots were classified to successional stages by combining the decision trees of Zenner, Peck, Hobi, and Commarmot (2016) and Tabaku (2000) (Supporting Information Figure S2). These decision trees incorporate information on canopy projection area, maximum diameter at breast height (DBH), proportion of dead wood, normalized quartile of the DBH, and the cover and height of the regeneration layer (Supporting Information Figure S2). The combination of these two protocols was necessary as Zenner et al. (2016) only considered trees with DBH >7 cm, and Tabaku (2000) explicitly also included regeneration and establishment stages. The combined decision tree was used to identify nine successional stages on 287 plots, i.e., gap, regeneration, establishment, early-optimum, mid-optimum, late-optimum, plenter, terminal, and decay stages (Figure 1).

2.4 | Taxonomic groups

We analysed the variation in biodiversity with forest succession considering 2,956 species from 23 taxonomic lineages. The species were group-specifically sampled in a standardized way and covered six trophic groups: producers (higher plants, lichen, mosses), consumers I (phytophagous and pollinating arthropods), consumers II (invertebrates feeding on animal tissue), consumers III (vertebrates feeding on animal tissue), saprotrophs *sensu lato* (species feeding on

dead tissue), and the special case of saproxylic saprotrophs (species depending on dead wood during their life cycle). Overall, this distinction of the 23 lineages into trophic groups yielded 33 functional groups; each of these functional groups were analysed on 29–287 plots (for details, see Supporting Information Appendix S1 and Table S1).

2.5 | Statistical analysis

All analyses were conducted in R (version 3.3.2; R Core Team, 2016). To test the influence of successional stage on the diversity of the 33 functional groups in the six trophic levels (Supporting Information Table S1), we calculated generalized linear mixed models with a Poisson distribution. We modelled either the number of species sampled on each plot (Gotelli & Colwell, 2001) or abundances (i.e., the number of all sampled individuals of a taxon) as response variables, with successional stage as the predictor. To test for regular trends across successional stages using linear and quadratic contrasts, we coded the factor forest successional stage as ordered. Elevation and soil characteristics were included as additional predictor to control for confounding effects of the local conditions. To account for the overdispersion frequently observed in models of count data, we included an observation-level random effect (i.e., the plot) in all models (Harrison, 2014). First, we calculated the overall effect (U- or hump-shaped response) of the forest successional stage modelled with linear and quadratic contrasts on the number of species or abundances of all 33 functional groups. We tested whether differences in the number of species are in accordance with the predictions of the *more-individuals hypothesis* or the *habitat heterogeneity hypothesis* by controlling for abundances in a subsequent model using the number of species as response variable, while accounting for abundances (note that with the exception of plants, all abundance values were square-root transformed). Second, we used the models to predict the number of species in each group while keeping elevation and soil parameters constant. Since forest successional stages do not always proceed in an orderly manner in reality (e.g., due to storms or bark beetle infestation), the successional stage was incorporated as an unordered factor in this case. Predictors were tested for significance using a general linear hypothesis testing framework as implemented in the multcomp R package version 1.4-6 (Hothorn et al., 2016).

At the community level, we calculated multiple-site dissimilarities for taxonomic groups using the Sørensen dissimilarity index and partitioned the thus derived β -diversity into its additive turnover and nestedness components as implemented in the betapart R package version 1.4-1 (Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017). To quantify the contribution of β -diversity among plots and among stages of forest succession to the γ -diversity in our study system, we used additive diversity partitioning as implemented in the R package vegan, version 2.4-3 (Oksanen et al., 2017). For a statistical test of the potential effects of forest succession on assemblages, we performed multivariate analyses of variance using distance matrices based on presence-absence data, applying the adonis function with 999 permutations as implemented in the vegan package.

These analyses considered taxonomic groups with sufficiently high numbers of species not separated into trophic levels (i.e., excluding taxonomic groups with ≤ 30 species). Changes in species composition of these taxa along forest succession were illustrated using partial correspondence analyses conditioned on the effects of elevation and soil. Furthermore, we calculated the number of unique species for early (gap, regeneration, and establishment), mid (early, mid, and late optimum), and late (plenter, terminal, and decay) stages of forest succession to evaluate the importance of individual stages for certain species of the taxa under study. In this case, we resampled a fixed number of plots in the early, mid, and late stages, respectively, for each taxon in our study and calculated the number of species unique to these forest successional stages. The fixed number of plots was defined as half the number of plots of the rarest stage for each taxon. The resampling procedure was randomly repeated 1,000 times, and the mean number of unique species per forest succession phase was calculated.

3 | RESULTS

3.1 | Stages of forest succession

Plots were not equally distributed across successional stages (Supporting Information Figure S3). The most prevalent stage (29% of 287 plots) was the mid-optimum stage, and the least prevalent stages (3%) were regeneration and plenter stages. Nevertheless, the distribution of plots across stages was representative for the Bavarian Forest National Park (Supporting Information Figure S3; Spearman's $\rho = 0.67$, $p < 0.05$). The successional stages differed in both elevation and soil characteristics (Supporting Information Figures S4 and S5; ANOVA: elevation $F_{8,278} = 19.8$, $p < 0.001$; soil $F_{8,278} = 5.06$, $p < 0.001$). Therefore, we used elevation and soil characteristics as control variables in the models of the number of species and abundance.

3.2 | Abundance and number of species

The response of the abundance of several taxa of producers, first-order consumers, saprotrophs, and saproxylic saprotrophs to forest succession yielded a U-shaped pattern. However, especially for taxa with low abundances or sample sizes, this response was not significant. We found no consistent response of higher order consumers to forest succession (Supporting Information Table S2). Nevertheless, the effect of the quadratic term of stages of forest succession was predominantly positive, which indicated a U-shaped response of most taxa (27 of 33 functional groups).

We found a positive quadratic term for forest successional stage for the number of species of producers and the majority of consumer taxa, which indicated a U-shaped response to forest succession. However, the number of species of most of the saprotrophic taxa did not strongly change along forest succession. Furthermore, the response patterns of saproxylic beetles and fungi were equally strong but opposing, with a U-shaped response of beetles to

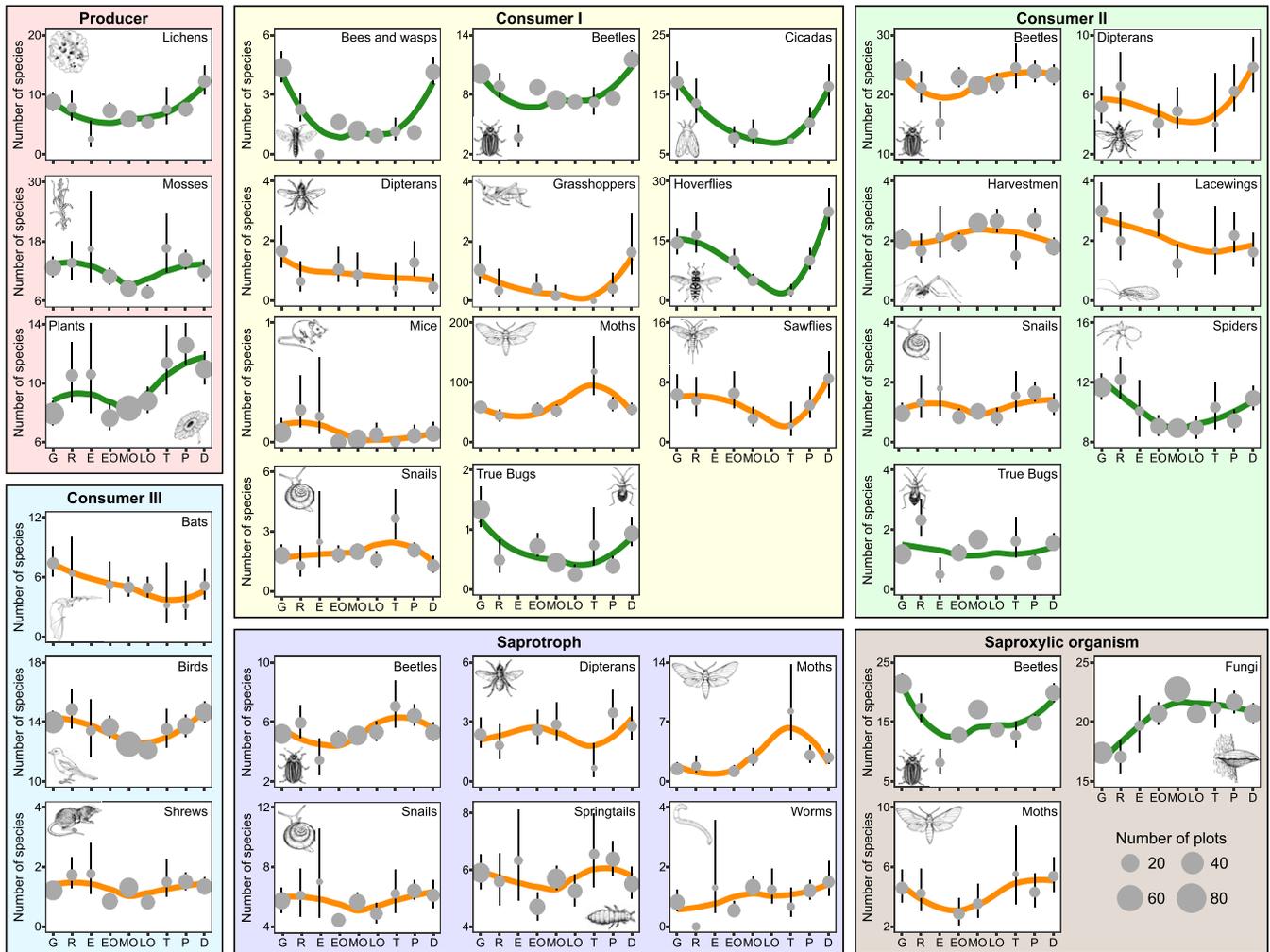


FIGURE 2 Variation in the number of species of 33 functional groups with stages of forest succession. The number of species was predicted using a generalized linear mixed model with Poisson error and an observation-level random effect. Predictor variables were the forest successional stage as an unordered factor, elevation, and soil parameters. For the predictions, elevation (800 m. a.s.l.) and soil parameters (mean value of the soil characteristics; PC1) were kept constant. Lines were generated by fitting a loess curve. Green lines indicate taxonomic groups whose number of species is significantly affected by the forest successional stage; orange lines indicate taxonomic groups whose number of species is not significantly affected by forest successional stage. Black bars indicate the SE within each successional stage. Note that data were not available for some taxonomic groups in some successional stages. Abbreviations are explained in Figure 1

forest succession and a hump-shaped response of fungi (Supporting Information Table S3, Figure 2).

When we controlled for abundances of each group in the models of the number of species, we found that abundances were the strongest predictor for every taxon analysed (Supporting Information Tables S3 and S4). However, a few taxa showed significant responses to forest succession even after we controlled for effects of abundance. Here, forest succession had a positive linear effect on plants and saproxylic beetles, i.e., over the course of forest succession, the number of species increased. The positive quadratic term in the model indicated a U-shaped response of the number of species of phytophagous beetles, true bugs, cicadas, predatory spiders, and dipterans to forest succession. By contrast, we found a negative quadratic relationship of the number of species of saprotrophic beetles and saproxylic fungi with forest succession, i.e., a hump-shaped response.

At the kingdom level, the number of plant species in the regeneration and establishment stages was particularly high, with a minimum in the optimum stages, and a secondary maximum in the terminal and decay stages of succession. Animals benefited from canopy openness, and the number of animal species in the gap stage was high, followed by a decrease in the number of species until the mid- to late-optimum stages, and a subsequent increase towards the maximum number in the decay stage. The number of species of wood-inhabiting fungi and lichens steadily increased over the course of forest succession, saturating during the plenter stage (Figure 3).

3.3 | Species composition

Overall, we found high levels of species dissimilarity among plots for all taxa (Supporting Information Figure S6). The Sørensen index

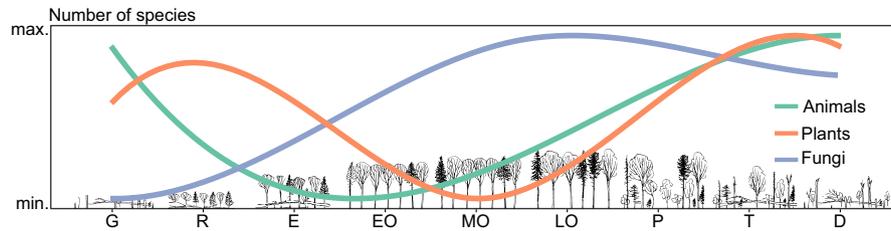


FIGURE 3 Normalized sum of predicted number of species along forest succession for the three kingdom animals, plants, and fungi. Lines were generated by fitting a loess curve. See Supporting Information Figure S9 for absolute values. Note that this figure is based on all plots, while Supporting Information Figure S9 is based on those plots that all taxa within the kingdom have in common. Abbreviations are explained in Figure 1

of dissimilarity exceeded 90% as a result of high spatial turnover; nestedness never accounted for more than 6% of the overall dissimilarity (Supporting Information Figure S6). Additive partitioning of the number of species showed that β -diversity among successional stages contributes most strongly to γ -diversity (Figure 4). Multivariate analysis of variance on distance matrices of taxonomic groups showed significant differences in species composition between successional stages for all taxa (Table 1). When we visualized the change in species composition along the course of forest succession by using partial correspondence analysis, a “circular” pattern emerged, i.e., early and late stages of succession had similar species compositions (Figure 5). Most unique species were found in the early and late stages of forest succession (Supporting Information Figure S7).

4 | DISCUSSION

Following our initial hypothesis (H1), our results showed that abundances and number of species of most taxa largely follow a U-shaped pattern along forest succession (Figure 2, Supporting Information Tables S2 and S3). However, counter to our expectations, saprotrophic organisms did not show a hump-shaped response to forest succession, and saproxylic fungi showed a hump-shaped response and not a U-shaped response to forest succession, which indicates that this latter species group does not closely track the accumulation of dead wood along forest succession. For most groups, the effect of forest succession was strongly affected by the abundances of the

respective groups, which provides strong support for the *more-individuals hypothesis* (H2; Supporting Information Table S4). However, we found a response of several taxa to forest succession even after we controlled for the effect of abundance (Supporting Information Table S4). Overall, the diversity of plants, animals, and fungi showed diverging patterns along forest succession, with peak diversity values in early and late stages (Figure 3). We found the highest rates of species turnover among successional stages (Figure 4 and Supporting Information Figure S7) and the most similar assemblages in early and late successional stages (open canopies; H3; Figure 5).

4.1 | Stages of forest succession

Although the youngest and oldest successional stages of our study would appear to be different, they actually are almost the same because succession is cyclic. The generation of old trees decays contemporarily with the growth of a new generation. According to Supporting Information Figure S2, the difference between the youngest and oldest stages in our study is in the 30% threshold of the canopy projection area. Nevertheless, the gap stage and the decay stage in our study differ markedly as the canopy projection area in the gap stage is considerably lower than in the decay stage (Supporting Information Figure S11). Dead wood volume is not included in our criteria for gaps and regeneration stages, although stands with low and high volumes of dead wood are dissimilar, especially for saproxylic species.

In our study, the forest successional stages establishment, late optimum, and plenter were underrepresented due to forest history

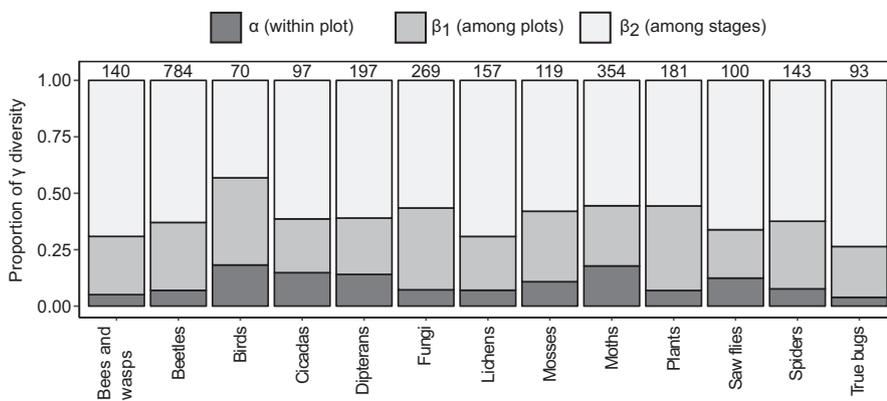


FIGURE 4 Proportion of γ -diversity due to α -diversity and β -diversity among plots and among stages of forest succession according to additive diversity partitioning. Results are based on presence-absence data for those taxonomic groups not separated into trophic levels with sufficiently high numbers of species (i.e., excluding taxonomic groups with ≤ 0 species). γ -Diversity for taxonomic groups is denoted above the respective bar

TABLE 1 Effects of forest successional stages on species composition. Results from a multivariate analyses of variance using distance matrices (Adonis) based on presence-absence data. Significance was tested using 999 permutations. Those taxonomic groups not separated into trophic levels and with sufficiently high numbers of species (i.e., excluding taxonomic groups with ≤ 30 species) were analysed. R^2 , coefficient of determination; soil, soil parameters of the plots. Significant effects are given in bold

Taxon	Plots (n)	Species (n)	R^2	p-value		
				Forest successional stage	Elevation	Soil
Lichen	109	157	0.25	<0.001	0.004	0.755
Mosses	109	119	0.20	<0.001	<0.001	<0.001
Plants	282	181	0.24	<0.001	<0.001	<0.001
Cicadas	36	95	0.36	0.009	0.003	0.120
Beetles	178	783	0.21	<0.001	<0.001	0.066
Birds	283	72	0.19	<0.001	<0.001	0.003
Moths	35	354	0.33	0.009	<0.001	0.524
Sawflies	35	100	0.33	0.003	0.066	0.084
Spiders	173	143	0.29	<0.001	<0.001	0.016
True bugs	150	93	0.14	<0.001	0.002	0.142
Dipterans	36	197	0.33	<0.001	0.005	0.059
Bees and wasps	142	140	0.14	<0.001	<0.001	0.638
Fungi	286	269	0.20	<0.001	<0.001	0.015

(Supporting Information Figure S5). This highlights an important limitation of a space-for-time approach as applied here, which *inter alia* assumes that the analysed stands have a consistent management and disturbance history (Dieler et al., 2017). Thus, particularly our results concerning these underrepresented stages should be interpreted with caution. Future analyses could supplement chronosequence data with simulation approaches to more explicitly study long-term trajectories of forest succession. In turn, the comprehensive dataset compiled here (Supporting Information Table S3) could be linked to simulation model output in future studies, quantifying how future forest development (influenced by changing climate and disturbance regime) impacts biodiversity (Thom et al., 2017). Our LiDAR approach revealed advantages and also limitations in the classification of successional stages, namely the ability to capture canopy closure across large spatial scales but the difficulty in characterizing the understorey and downed dead wood. In this context, our results quantify the changes in biodiversity across forest succession and present a dynamic baseline for the monitoring of biodiversity change in temperate forests. Future changes (e.g., driven by changes in climate or land use), whether observed or projected, need to be considered in the light of the natural dynamics of forest succession, acknowledging that there are no static reference conditions for the diversity in temperate forests.

4.2 | Ecology of taxa

Most taxa responded according to our predictions derived from the variation in critical resources across the stages of forest succession (cf. Figures 1 and 2). The high number of species of producers in both the early and late successional stages is most likely driven by shifts in primary production from trees to herbs, mosses, and lichens, which depends on sunlight reaching the forest floor (Zehetgruber et al., 2017). This U-shaped response increases the

resource availability for phytophagous insects (Bouget & Duelli, 2004). Previous analyses in our study region have shown that the number of species of several arthropod groups increases with forest development from closed forest to open canopies (Müller, Bußler, Goßner, Rettelbach, & Duelli, 2008). For arthropods, this is partly an effect of increased activity of ectotherms under the higher temperatures associated with open habitats. However, our results indicate that for consumer groups, the effect of forest succession on the number of species is not only driven by more individuals but also reflects an increase in habitat heterogeneity (Supporting Information Tables S2 and S4). An increase in the abundance and number of species controlled for abundance of first-order consumers is frequently followed by an increase in the abundance of predators, such as spiders, beetles, and birds, which results from bottom-up trophic interactions (Campbell & Donato, 2014). However, we found that although the amount of dead wood was high on our study plots in early stages of forest succession (Supporting Information Figure S11), this was not reflected in the number of species of wood-decaying (saproxylic) fungi. This is consistent with the more detailed analyses of Krah et al. (2018), which show that the mere amount of dead wood is a relatively poor predictor of the number of these fungal species. The number of fungal species might be driven more strongly by the host tree species, host size, dieback history, and canopy openness than by the amount and heterogeneity of dead wood (Abrego & Salcedo, 2013; Heilmann-Clausen et al., 2015; Krah et al., 2018).

4.3 | Ecological mechanism: more-individual hypothesis and habitat heterogeneity hypothesis

With regard to the mechanisms driving biodiversity in temperate forests, our results suggest that the increase in the number

of species is largely based on higher abundances, as predicted by the *more-individuals hypothesis*. However, after controlling for abundances, the number of species of species-rich groups, such as beetles, true bugs, cicadas, spiders, and fungi, were still affected by the forest successional stages, which indicates variation in habitat heterogeneity in the form of host plants, microstructures or microclimates by facilitating coexistence, increasing niche space, and reducing local extinction risks (Stein & Kreft, 2015). Increased canopy openness in early and late successional stages (Supporting Information Figure S11) results in an increase in the number of species of vascular plants and mosses (Figure 3) owing to the occurrence of pioneer species with low shade tolerance. However, when we controlled for the effect of abundances, vascular plants showed a linear response to forest succession, which indicated that in early stages, the increase in the number of species is mainly driven by denser understorey vegetation and thus more individuals, rather than by habitat heterogeneity. The positive effect of forest succession on the abundance of vascular plants (Supporting Information Table S2) subsequently increases the diversity of herbivorous insects following the resource availability hypotheses. This increase in prey species might also support more predatory species. This interpretation is supported by the observed increase in the number of species of higher order consumers after we controlled for abundances.

High turnover rates between stands, as in our study (Supporting Information Figure S6), can be driven by sampling effort, with higher turnover rates with lower sampling effort locally, but also can occur because of ecological differences between stands. Our present study showed that species turnover along successional stages contributed most strongly to the overall γ -diversity (Figure 4). This indicates that for the promotion of forest diversity at the landscape scale, heterogeneity in forest successional stages is more important than within-stand heterogeneity, which is in accordance with the results of another recent multitaxon analysis of forest diversity in Europe's temperate forests (Schall et al., 2017).

4.4 | Implications for forest management

Based on our finding that both α -diversity and the number of unique species is highest in early and late stages of forest succession (Figures 2 and 3, Supporting Information Figures S7 and S10), we recommend that conservation efforts focus on these particular stages, which are currently underrepresented in Europe (Supporting Information Figure S8). Late successional stages cannot be produced artificially but have to develop naturally over long time periods (but see Speight, 1989 and Sebek, Altman, Platek, & Cizek, 2013 for techniques inducing premature senescence). α -diversity can be promoted in the short term by creating and maintaining early stages of succession, and this is an important option for ecosystem management (for experimental evidence, see Sebek et al., 2015). Canopy openings are a frequent result of logging activities, but these openings often lack the dead wood resources required by many saproxylic taxa (Heikkala,

Martikainen, & Kouki, 2016). Based on our findings, we recommend that in silviculture, the canopy should be opened by, e.g., creating gaps, to increase the photosynthetically active radiation at the forest floor, and some dead wood should be retained on site.

Because intermediate successional stages also support a wide variety of taxa and communities, especially plants, fungi, and lichen, a comprehensive conservation strategy has to maintain all successional stages on the landscape. However, for the conservation of regional biodiversity in multifunctional forests in Europe, this would mean that the proportion of stands in early and late successional stages should be increased.

All our implications only apply to the system we investigated, namely mixed mountain forests. However, more than half of Central Europe consists of mountain areas and most of the existing forests are concentrated there (CIPRA, 2007). Moreover, other studies have shown similar results on the uniqueness of, e.g., the early successional stages (e.g., Jacobs et al., 2007; Swanson et al., 2011; Tikkanen et al., 2007), which suggests a further transferability of our results to other forests systems across Europe or temperate mountain forests of other continents.

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AUTHORS' CONTRIBUTIONS

T.H., J.M., M.H., N.F., R.B. and H.P. conceived the idea and designed the methodology. T.H., C.B., and J.M. collected the data. T.H., N.F., R.B. and J.M. analysed and interpreted the data and led the writing of the manuscript with substantial input from all co-authors. All authors gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.213gk3r> (Hilmers et al., 2018).

ORCID

Torben Hilmers  <http://orcid.org/0000-0002-4982-8867>

Nicolas Friess  <http://orcid.org/0000-0003-0517-3798>

Jörg Müller  <http://orcid.org/0000-0002-1409-1586>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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