

Specialisation and diversity of multiple trophic groups are promoted by different forest features

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57 **Abstract**

58 While forest management strongly influences biodiversity, it remains unclear how the structural and
59 compositional changes caused by management affect different community dimensions (e.g. richness,
60 specialisation, abundance or completeness) and how this differs between taxa. We assessed the effects
61 of nine forest features (representing stand structure, heterogeneity and tree composition) on thirteen
62 above- and belowground trophic groups of plants, animals, fungi and bacteria in 150 temperate forest
63 plots differing in their management type. Canopy cover decreased light resources, which increased
64 community specialisation but reduced overall diversity and abundance. Features increasing resource
65 types and diversifying microhabitats (admixing of oaks and conifers) were important and mostly
66 affected richness. Belowground groups responded differently to those aboveground and had weaker
67 responses to most forest features. Our results show that we need to consider forest features rather than
68 broad management types and highlight the importance of considering several groups and community
69 dimensions to better inform conservation.

70 **Introduction**

71 Land-use is among the strongest drivers of biodiversity loss (Foley *et al.* 2005; Flynn *et al.* 2009;
72 Newbold *et al.* 2015). In temperate forests, management can involve various elements, including
73 removal of timber and deadwood, the introduction of non-native trees and/or the promotion of a few
74 productive tree species (Bengtsson *et al.* 2000; McGrath *et al.* 2015; Chaudhary *et al.* 2016). Several
75 studies have examined management effects on forest communities, however they generally consider
76 only a limited number of taxa, mostly aboveground, and typically focus on species richness alone
77 (reviewed in Paillet *et al.* 2010; Chaudhary *et al.* 2016). However, different taxa, and community
78 dimensions other than richness, might show contrasting responses to management (Flynn *et al.* 2009;
79 Paillet *et al.* 2010; Aubin *et al.* 2013). It is important to quantify and understand this potential
80 variation in responses to determine the ecological mechanisms by which management affects
81 communities and to guide conservation decisions (Aubin *et al.* 2013; Simons *et al.* 2016). To achieve
82 a comprehensive understanding of the effects of forest management on biodiversity we need to
83 “unpack” communities by considering responses of a range of community dimensions and taxa,
84 including those belowground, which represent a large proportion of biodiversity and play
85 fundamental roles in ecosystem functioning.

86 Most studies examining the effects of forest management on biodiversity have compared
87 biodiversity between general management types (Paillet *et al.* 2010; Chaudhary *et al.* 2016). Whilst
88 this provides information about specific management regimes, it makes comparisons complicated, as
89 management varies substantially between countries and regions. It also makes it challenging to link
90 effects of management to ecological theory, which typically considers more general mechanisms such
91 as the role of resource availability and environmental heterogeneity in shaping communities (Stevens
92 & Carson 2002; Cadotte *et al.* 2017). To explore the mechanisms by which forest management affects
93 biodiversity, we therefore need to focus on how management changes various forest features.

94 To promote timber production, forest managers modify several features, such as tree species
95 composition, stand age and density, or deadwood amounts (Bengtsson *et al.* 2000; Seidl *et al.* 2011;
96 Schall & Ammer 2013). These modifications directly affect the amount, type and heterogeneity of
97 resources or microhabitats, as well as abiotic conditions, all of which can strongly affect forest
98 communities (Duguid & Ashton 2013; Chamagne *et al.* 2016; Zellweger *et al.* 2016, see detail in Table
99 1). The effects of some forest features on particular taxa are starting to be understood (Table 1),
100 however, a clear link with management is still lacking (but see Schall *et al.* 2018) and the mechanisms
101 behind many of these effects are unclear. For instance, positive effects of forest age on biodiversity
102 can be partly attributed to increased amounts of deadwood and partly to the provision of key micro-
103 habitats (Brunet *et al.* 2010; Vuidot *et al.* 2011; Paillet *et al.* 2017). It is therefore important that studies
104 consider a large set of management-driven forest features, to understand their distinct roles in shaping
105 communities.

106 Species richness is a key measure in both conservation and functional ecology research,
107 however, it does not fully characterise communities (Wilsey *et al.* 2005; Lyashevskaya & Farnsworth
108 2012). Another important community dimension is total abundance, which may respond differently to
109 environmental drivers (Table 1) (Haddad *et al.* 2001; Pärtel *et al.* 2011; Purschke *et al.* 2013).
110 Alongside the number and abundance of species, the characteristics of species present can vary
111 strongly with management (Devictor *et al.* 2008; Simons *et al.* 2016). Species which are restricted to
112 forest habitats, i.e., forest specialists, may be most sensitive to management changes (e.g. Fuller *et al.*
113 2008), and preserving forest specialists is likely to be of central concern for conservation (Paillet *et al.*
114 2010; Lange *et al.* 2014). A further relevant community dimension is the proportion of species that
115 could potentially be present, based on their environmental requirements, but are missing from a
116 community due to dispersal limitation (Lewis *et al.* 2017). This "dark diversity" can be used to estimate
117 how far a given community is from its potential diversity, i.e. its "completeness" (Pärtel *et al.* 2011).
118 In general, we would expect species richness to be mostly related to the heterogeneity of resources and

habitat, abundance to resource availability, forest specialisation to features defining the particular environmental conditions present in forests (e.g. light levels), and completeness to features linked to dispersal limitation (Table 1).

To achieve a comprehensive understanding of the drivers of forest diversity we need to consider a whole range of trophic groups (Seibold *et al.* 2018), which might respond differently to particular forest features. For instance, autotrophs should mostly respond to features affecting light levels and saproxylic species to deadwood (see detailed hypotheses in Table 1). Our knowledge of belowground responses is particularly limited. Where studied, it appears that these groups are mainly affected by soil conditions (Goldmann *et al.* 2015; Kaiser *et al.* 2016) and their responses to management may not necessarily mirror those of aboveground groups (Allan *et al.* 2014). However, we can hypothesize that belowground groups could respond to tree species identity and diversity if they form specialised, symbiotic or parasitic relationships with trees (e.g. fungi), or if trees differ in their litter chemistry and effects on soil properties (Gömöryová *et al.* 2013; Goldmann *et al.* 2015, 2016, Table 1).

We investigated the effects of forest features on multiple community dimensions, using a unique dataset that includes 13 above- and below-ground trophic groups of organisms in 150 German temperate forest plots. We examined the effects of forest features related to stand composition (percentage of dominant species), structure (mean tree size, canopy cover and deadwood volume) and heterogeneity (vertical and horizontal heterogeneity, tree and deadwood diversity) on four community dimensions: species richness, abundance, specialisation and completeness. Our main hypotheses are that, i) community dimensions respond differently to forest management, with richness and specialisation being most sensitive to heterogeneity and abundance to resources, ii) aboveground organisms respond strongly to management while belowground ones respond mainly to soil factors, and iii) forest features associated with an increase in the availability and heterogeneity of resources generally enhance all community dimensions.

Methods

We studied 150 forest sites located in three regions in the southwest, centre and northeast of Germany, which form part of the large-scale Biodiversity Exploratories project (Fischer *et al.* 2010). The three regions differ in climatic, geological and topographical conditions, with mean annual temperatures ranging from 6-8.5°C and mean annual precipitation from 500-1,000 mm (Fischer *et al.* 2010).

In each region, fifty 100×100 m forest plots were installed within larger management units. Plots were selected from a larger number of candidate plots to minimise variation in environmental characteristics, whilst covering a representative range of forest management types and intensities (see details in Fischer *et al.* 2010). The dominant tree species were European beech (*Fagus sylvatica*, present in 69.3% of plots), and to a lesser extent, Norway spruce (*Picea abies*; 10.6%), Scots pine (*Pinus sylvestris*; 10.0%) and two oak species (*Quercus robur* and *Q. petraea*; 4.6%). These forests represent common lowland forest types in western and central Europe, which are dominated by a few broadleaf species (mostly beech). The two conifers are native to Central Europe but would not grow in the study regions under natural conditions (spruce) or would be less frequent (pine). However, they have been cultivated in the study regions for approximately 250 years. Oaks would also be less frequent under natural conditions. The studied forests can be classified into three broad management types: (i) unmanaged broadleaf (16% of the 150 plots); (ii), managed broadleaf (even-aged: 50%, uneven-aged 8%); and (iii) managed conifer (even-aged: 26%).

Forest features

Forest features were measured during a comprehensive forest inventory between 2008 and 2010. In each plot, all trees with a diameter at breast height (DBH)>7 cm were surveyed and plots were scanned using terrestrial LIDAR (Appendix SA2 in Supporting Information). From this inventory, we calculated three measures of stand properties (canopy cover, mean DBH, and deadwood volume), four of stand heterogeneity (tree diversity, horizontal and vertical heterogeneity in stand structure and

diversity in deadwood decay stage and origin) and two of stand composition (proportion of conifers and oaks in the plot). All features were weakly correlated with each other (Spearman $\rho < |0.6|$, Appendix Fig. S1).

To account for differences in soil characteristics, we used the first two principal components (PC) of an analysis combining soil information across the three regions: pH, texture, moisture, nutrients (nitrogen, phosphorus and sulphur) and organic and inorganic carbon (Appendix Fig. S2, Table S1).

Species richness and abundance

We measured richness (of species or operational taxonomical units, OTUs) and abundance for multiple taxa using established methods for each taxon (Appendix SA2). Aboveground groups were assessed between 2007-2009 and included understorey vascular plants and shrubs (hereafter “plants”), bryophytes, lichens, fungi on deadwood, arthropods (Araneae, Coleoptera, Hemiptera, Hymenoptera, Neuroptera, Orthoptera, Opiliones), birds and bats. Belowground groups (bacteria and soil fungi) were sampled in 2011 and analysed using pyrosequencing (richness) and soil phospholipid fatty acids (abundance) (Goldmann *et al.* 2016; Richter *et al.* 2018). In total, we had complete information for all taxa, environmental and forest features for 142 of the 150 plots.

To consider the functional role of the organisms in the ecosystem, we classified the taxa into 13 trophic/functional groups (*sensu* Seibold *et al.* 2018). Arthropods were classified into decomposers, herbivores, omnivores and carnivores. Insectivorous birds and bats were classed as vertebrate carnivores. Soil fungi were separated into three groups (mycorrhizal symbionts, saprotrophs and pathogens) using FunGuild (Nguyen *et al.* 2016). Plants, bryophytes and lichens were considered as separate groups as they all can respond differently to forest features. We kept bacteria as a single group because we did not have information on bacterial functions. We then calculated richness and abundance for each of the 13 trophic groups.

A measure of overall ecosystem richness can be useful for addressing general trends (e.g. for conservation purposes) in addition to studying individual responses of the various trophic groups. We therefore calculated overall ecosystem richness (multidiversity *sensu*, Allan *et al.* 2014), by scaling richness values of each trophic group to the maximum observed across all plots and calculating the average across groups. In this metric all groups are weighted equally, thus preventing the measure from being driven by speciose groups such as bacteria (Allan *et al.* 2014). We also calculated multiabundance in an analogous manner to multidiversity. We computed multidiversity and multiabundance for above- and belowground groups, separately and combined.

Forest specialisation

Literature data on forest specialisation is only available for a small subset of organisms. To obtain a comparable metric of forest specialisation for all species recorded in our study, we calculated the extent to which each species was a forest specialist (i.e. occurring primarily in forests) versus a habitat generalist (occurring equally in grasslands and forests). We did this by matching our forest data with data on the same groups, measured in 150 grasslands in the same regions (Fischer *et al.* 2010; Gossner *et al.* 2016; Soliveres *et al.* 2016). We used the forest and grassland datasets to calculate an index of forest specialisation (FS_i) for each species i based on its frequency in forests and grasslands: $FS_i = (nF_i / nF_{plots}) / ((nF_i / nF_{plots}) + (nG_i / nG_{plots}))$. Where nF_i and nG_i are the number of forest and grassland plots respectively, where species i occurred. nF_{plots} and nG_{plots} are the total number of forest and grassland plots, respectively. The index of forest specialisation ranges between 1 for complete forest specialists and 0 for complete grassland specialists, it is 0.5 for habitat generalists. For lichens, bryophytes and vascular plants we used information from a total of 654, 1816 and 3000 plots, respectively, in forests and grasslands in the same study regions (Boch *et al.* 2013a, 2016; Socher *et al.* 2013).

We then calculated the community mean forest specialisation (hereafter “specialisation”) for each plot by averaging the individual species specialisation values (FS_i). Because mean specialisation is scaled between 0 and 1, and thus comparable between groups, we calculated overall community specialisation (multispecialisation) for each plot by simply averaging the specialisation values of multiple trophic groups. Deadwood fungi were excluded from this analysis as we did not have any information for this group from grasslands.

A comparison of FS_i with literature data for plants, birds, beetles, spiders and hymenopterans confirmed that our measure reflects species specialisation to forests (Appendix Fig. S3,S4). However, note that FS_i might describe specialisation to managed beech forests, as this is the dominant forest type in our dataset. In addition, while forests and grasslands represent important land cover types in the three regions (Fischer *et al.* 2010), our measure does not include other habitats such as hedgerows, urban areas, croplands or wetlands, and therefore should not be considered as an absolute, but rather a relative, measure of species specialisation to forests. Finally, we tested whether increases in community specialisation were linked to species richness and if they were due to an increase in the proportion of specialists or a decrease in generalists (Appendix Fig.S5, S6).

Dark diversity and community completeness

We considered as missing, i.e. belonging to dark diversity, all the species that were absent from a given plot but had a probability of occurrence in the plot that exceeded a threshold value. We estimated the probability that a given species occurs in a given plot by calculating Beals’ probabilities (Beals 1984). As this method is considered unreliable for species that do not show strong associations with any others, we filtered out such species using the randomisation approach of De Cáceres & Legendre (2008) with 500 permutations. This process also removed most of the rare species (final $n=2690$, i.e. 26% of all species) for which there is insufficient information to calculate occurrence probabilities (De Cáceres & Legendre 2008). We calculated Beals’ probabilities separately for each group and each

region and we only tested for co-occurrences between species from the same group, e.g. only between plants, but not between plants and herbivores. We then defined a threshold probability of occurrence separately for each group, as the 5% quantile of probabilities of occurrence across all plots (Lewis *et al.* 2016).

We calculated community completeness as the log-ratio of richness and dark diversity (as defined in Pärtel 2014; Lewis *et al.* 2016, 2017). It has only been shown that plant communities dominated by species with low dispersal ability had higher dark diversity (Riibak *et al.* 2017). We also checked whether this relationship held for arthropods, using data on dispersal abilities from literature (Gossner *et al.* 2015). Communities that had more species with good dispersal abilities were more complete (Pearson $r=0.77$, $p<0.001$, Appendix Fig. S7) and had lower dark diversity ($r=-0.31$ $p<0.001$), thus confirming that for arthropods too, dark diversity is related to dispersal limitation. Results based on completeness calculated with a broad (0%) and narrow (10%) threshold, as suggested by Lewis *et al.* (2016), were also consistent with the ones reported here (Appendix Fig. S8).

All the community dimensions contributed complementary information. Richness and completeness were the most closely related dimensions (Spearman ρ : 0.6), all other pairwise correlations between dimensions were lower than $|0.45|$ (Appendix Fig. S9).

Effects of forest features on forest communities

We fitted linear models and checked model assumptions for each group and community dimension separately. We standardized all variables (mean=0 and sd=1), to be able to compare effect sizes between the predictors. We accounted for soil characteristics by including the first two axes of the PCA as covariates in all models. To account for regional differences, we calculated residuals for all our variables (soil PC, forest features and community dimensions) from linear models including region, and we used these residual values in all analyses. To assess which trophic groups were most strongly affected by forest features, we calculated the average of absolute total effects for each group

268 across all forest features, inverse weighted by their standard errors (i.e. variables with higher standard
269 errors had less influence on the average).

270 The effects of forest features on richness might be mediated by changes in abundance.
271 Therefore, we also ran the same models with the residuals of richness as the response variable, i.e.
272 after correcting richness for abundance. Given that the proportion of conifers included both pines and
273 spruces, we also analysed their effects separately.

274 Variance inflation factors (VIF) showed that all our variables had $VIF < 3$, hence there was no
275 multicollinearity in the models (Fox & Weisberg 2011). Using generalised additive models (GAM;
276 Wood 2011), we did not find evidence for potential non-linear relationships. We tested for residual
277 spatial autocorrelation using Moran's I tests. To reduce potential type I errors associated with multiple
278 testing while minimising type II errors, we controlled for false discovery rates (FDR) using a
279 Benjamini-Hochberg procedure with a threshold of 0.2 (Verhoeven *et al.* 2005). To assess whether our
280 results were influenced by differences in detectability between groups, we calculated sampling
281 coverage using the iNEXT package in R (Hsieh *et al.* 2016) and verified if sampling coverage was
282 related to the forest features using the same linear models as described above.

283 We also performed a parallel analysis using broad forest management types (conifer managed,
284 broadleaf managed and broadleaf unmanaged) instead of forest features (Appendix SA5). We
285 performed all analyses using R v.3.4.3 (R Core Team 2017).

286

287 **Results**

288 *Response of the community dimensions to forest features*

289 While the effects of the different forest features were generally similar for multidiversity, -
290 abundance and -completeness (grey panels, Fig. 1), they were often in the opposite direction for
291 multispecialisation (white panels, Fig. 1). In particular, higher canopy cover reduced richness,
292 abundance and completeness, but increased specialisation (Fig. 1, Fig.2, Appendix Table S2). Richness

293 was the dimension that responded most frequently to the forest features (23% of significant
294 relationships out of 117 tests across all groups, or 16% when corrected by abundance, Fig. 1 and
295 Appendix Fig. S10), followed by completeness (17% of 117 tests), specialisation (14% of 108 tests)
296 and abundance (13% of 90 tests). There were few effects on the specialisation of arthropod carnivores,
297 omnivores and decomposers, bryophytes and symbionts because almost all species in these groups
298 were specialist (specialisation index close to 1, Appendix Fig. S3). For most groups, an increase of the
299 community specialisation is linked to an increase in the proportion of specialists in the community.
300 However, for soil fungi saprotrophs and pathogens it might be due to a decrease in generalists
301 (Appendix Fig.S5).

302

303 *Response of the trophic groups to forest features*

304 Every trophic group was significantly associated with several forest features (mean: 2.1 ± 1.1 sd.
305 features) with an absolute weighted mean effect of $0.11 (\pm 0.03)$ across all community dimensions and
306 forest features (“mean effect” column in Fig. 2). The groups that responded significantly to most forest
307 features were deadwood fungi (mean across all dimensions: 3.5 ± 0.7), vertebrate carnivores (3.3 ± 1.5),
308 bryophytes (3.0 ± 1.0) and plants (3.0 ± 1.2). The least affected group were bacteria, for which only
309 conifer cover was significant. However, this group includes different trophic groups having potentially
310 contrasting responses. Our models generally explained more variation for above than for belowground
311 groups (Appendix SA5).

312

313 *Relative importance of forest features*

314 The two measures of stand composition (proportion of conifers and oaks) and canopy cover had the
315 strongest and most contrasting effects across all dimensions and trophic groups (Fig. 2). Most other
316 forest features had consistent trends across the 13 groups but had fewer significant effects (all blue or
317 all red columns in Fig. 2, Appendix Fig.S11).

318 Among the heterogeneity measures, vertical and horizontal heterogeneity generally increased
319 the four community dimensions aboveground. However, we only found one significant effect of tree
320 diversity on richness (of saprotrophic fungi) and just a few positive effects of deadwood diversity (e.g.
321 on deadwood fungi or vertebrates).

322 Among other structure measures, mean DBH, representing stand age (Fig. S1), had only a few
323 positive effects on higher trophic levels and deadwood volume had almost no effects on community
324 dimensions (Fig.2). Finally, soil properties affected belowground groups more strongly than
325 aboveground ones (Fig.2). The second component of the soil PCA (expressing variation in carbon,
326 phosphorus, and texture) was an important predictor of soil groups. Variation in the first component
327 had mostly been accounted for when correcting for regional differences.

328 Sensitivity analyses showed that the effects of the proportions of pine and spruce were
329 generally consistent, they were opposed to each other in only one case (arthropod herbivore
330 completeness, Appendix Fig.S12). The effects of the various forest features also remained unchanged
331 when multidiversity was calculated using different methods (Appendix Fig.S13). Spatial
332 autocorrelation did not affect our results (Appendix Tables S3,S4) and so we present the results of the
333 simpler models. Only in four of 99 cases could the results of richness and completeness have been
334 driven by higher sampling coverage (richness: effect of conifer cover on decomposers and bryophytes
335 and effect of oak cover on vascular plants; completeness: effect of conifer cover on arthropod
336 decomposers, Appendix Fig. S14).

337 Our parallel analysis using broad management types instead of forest features showed that
338 forest communities did not differ between management types when considering all dimensions and
339 groups together (Appendix Fig. S15,S16). In general, models using forest features explained more
340 variation than models using management types for all dimensions and trophic groups (except bacteria,
341 Appendix Fig.S17). Furthermore, different management types can lead to similar levels of forest
342 features (e.g. deadwood volume, Appendix Fig. S16).

Discussion

Differences between community dimensions

Despite the large effort devoted to understanding how forest management affects biodiversity, few studies have compared effects across taxa and community dimensions to gain a comprehensive understanding of how different forest features affect communities (Table 1). Our analysis of 13 above- and belowground trophic groups showed that different community dimensions varied in their response to a range of forest features. Richness was most sensitive to changes in forest features but some of these effects were driven by abundance. Abundance and completeness responded similarly but to fewer features. In contrast, forest specialisation generally had opposing responses to the other three dimensions (Fig. 1). While our forest specialisation measure may have its limitations (see methods section), this result is of major importance for understanding biodiversity change because it implies that measures targeting overall richness may fail to protect communities that depend upon particular forest habitats (Devictor & Robert 2009; Pellissier *et al.* 2017).

Differences between above and belowground groups

Generally, aboveground trophic groups responded similarly to the forest features. However, in most cases, responses of belowground groups did not mirror those aboveground, as also found in grasslands (Allan *et al.* 2014). For instance, we found stronger effects of canopy cover on aboveground than on belowground groups, perhaps because aboveground groups are directly affected by understorey light levels while soil organisms respond to other factors. Indeed, as predicted, belowground groups were mainly affected by soil conditions and tree identity (Goldmann *et al.* 2016; Kaiser *et al.* 2016; Richter *et al.* 2018). Increasing belowground diversity through changing forest management might therefore be more challenging than for aboveground organisms. However, our results show that admixing with oaks, would benefit both above- and belowground groups in beech-dominated stands.

368 *Effects of stand composition on community dimensions*

369 Forest features explained community patterns better than broad management types, as suggested before
370 (Duguid & Ashton 2013; Gossner *et al.* 2014). Species composition of the stand was the most
371 important predictor across community dimensions. Increasing oak cover had generally positive effects
372 across community dimensions and trophic groups: particularly on richness but surprisingly not on
373 abundance. The presence of unique microhabitats in oak stands might increase richness by favouring
374 species with specialised niches (Vuidot *et al.* 2011, Table 1), and oaks are generally known to support
375 high richness of several arthropod taxa (Brändle & Brandl 2001; Müller & Gossner 2007). Mixing oak
376 litter with beech litter could also have beneficial effects on belowground groups, as it reduces litter
377 packing and neutralises soil acidity (Godefroid *et al.* 2005). Increasing the proportion of oaks in the
378 stand is therefore beneficial for diversity as it increases richness without reducing specialisation, likely
379 by enhancing both generalist and specialist species. In beech-dominated forests, admixture of other
380 trees increases the number and amount of resources and microhabitats for certain species, suggesting
381 that shifting away from pure beech stands to mixed broadleaf stands might increase biodiversity.

382 Increasing conifer cover generally promoted species richness but decreased community
383 specialisation across most trophic groups (Fig.2). Coniferous stands therefore contained communities
384 with large proportions of generalists, with broad habitat niches, which may be of low conservation
385 interest (Julliard *et al.* 2004; Colles *et al.* 2009). In beech-dominated landscapes, increasing conifer
386 cover might increase species richness because conifers add unique resource types and microhabitats
387 (Table 1). We did not find evidence for non-linear effects of conifer cover but in forests dominated by
388 broadleaf trees other than beech, there is evidence that mixed conifer/broadleaf forests have higher
389 diversity than pure conifer stands (Felton *et al.* 2010). In contrast, and conifer cover increased the
390 specialisation of lichens, bacteria and symbionts but reduced their richness, suggesting that species
391 associated with conifers are rarely found in non-forest habitats (Király *et al.* 2013; Tedersoo *et al.*
392 2014). The completeness of belowground groups tended to decline with conifer cover while richness

393 was unaffected. Certain species may therefore be excluded from conifer stands due to increased
394 competition, loss of particular niches, or growth limitation by allelopathic compounds (Fahrig &
395 Triantis 2013; Moeslund *et al.* 2017). Our results clearly show that changes in tree species composition
396 have major effects on forest communities, with effects on most groups and all different dimensions.

397

398 *Effects of stand structure on community dimensions*

399 The only measure of stand structure that had a large effect across groups was canopy cover, strongly
400 suggesting that light conditions are a major, general driver of forest communities. Aboveground groups
401 tended to decline in diversity, abundance and completeness with increasing canopy cover, while their
402 specialisation increased. These contrasting effects of canopy cover are largely responsible for the
403 differing responses of richness and specialisation and agree with previous studies showing that high
404 light levels increased understorey plant richness and abundance but decreased forest specialisation
405 (Table 1). High canopy cover also reduced arthropod carnivore diversity and herbivore diversity and
406 abundance. These negative trends could be related to direct effects of decreased solar radiation and
407 temperature (Salmon *et al.* 2008; Henneron *et al.* 2017), or to cascading effects due to the decline in
408 vascular plant species richness, abundance and composition (Henneron *et al.* 2017), although future
409 analyses would be needed to separate these potential mechanisms. Light conditions might also partially
410 underlie some of the effects of tree species composition since the canopies of oaks and some conifers
411 (e.g. Scots pines) are typically more open than those of beech stands, which could explain the decrease
412 of forest specialist plants in conifer stands (Canham *et al.* 1994; Boch *et al.* 2013b).

413 In contrast to canopy cover, mean tree size (or stand age; both captured by mean DBH) and
414 deadwood volume had very few effects on diversity. This was surprising as previous studies have
415 shown positive effects of stand age and deadwood on biodiversity (Table 1). It could be because we
416 did not measure very old stands, which are rare in Central European production forests, and which
417 would have higher levels of deadwood and tree cavities due to senescent trees, typical of primeval

418 forests (Christensen *et al.* 2005). However, stand age effects are thought to operate through greater
419 heterogeneity and dead wood availability in older stands (Lassauce *et al.* 2013) and, as it is likely that
420 these effect were captured by our composition and heterogeneity measures, stand age *per se* may not
421 a major driver of forest communities.

422

423 *Effects of stand heterogeneity on community dimensions*

424 We expected within-stand heterogeneity to increase richness because the increased niche
425 diversity should allow more species to coexist (Stein *et al.* 2014). However, heterogeneity-related
426 forest features had few effects on our forest communities, exceptions being an increase in deadwood
427 fungal richness and completeness with increasing deadwood diversity and some effects of horizontal
428 and vertical heterogeneity on bryophyte and lichen communities. The general lack of effects of vertical
429 or horizontal heterogeneity, or tree diversity, might be because species respond to heterogeneity at
430 larger scales, meaning that increasing heterogeneity at the plot scale would not affect communities if
431 the landscape remains homogeneous (Schall *et al.* 2018), or because there was not sufficient variation
432 in heterogeneity between our plots. For instance, tree diversity is relatively low, because all our forests
433 (including the unmanaged ones) have a history of management and because the main forest types in
434 Central Europe are dominated by one or two tree species (Fischer *et al.* 2010). The positive effects of
435 conifers and oaks suggest beneficial effects of mixing beech with other species. However, to further
436 test the role of heterogeneity, future studies should compare the effects of a larger gradient in diversity,
437 e.g. by doing similar studies in temperate regions with higher tree richness, or in highly diverse
438 subtropical or tropical forests.

439

440 *Conclusions*

441 Our study was able to identify the specific forest features that drive different dimensions of biodiversity
442 above and belowground. Consistent with our hypothesis, features that decreased light availability

443 (canopy cover) generally decreased abundance and diversity but favoured specialists. Features that
444 increased niche diversity by diversifying resources and microhabitats (oak and conifer cover) were
445 important drivers and mostly affected richness. Finally, aboveground organisms responded strongly to
446 the forest features while belowground ones were mainly driven by soil factors. Since these forest
447 features can be modified individually through management, our results open up the possibility of fine-
448 tuning forest management to maintain both species-rich forests and to conserve specialist-rich
449 communities. Our results suggest that it may not always be possible to realise this within a single stand,
450 given the contrasting responses of specialisation and richness to stand level features, which could argue
451 for increasing forest diversity at larger spatial scales (van der Plas *et al.* 2016; Schall *et al.* 2018). Our
452 results clearly show that it is essential to “unpack” both management and diversity while exploring the
453 relationships between biodiversity and complex forest management practices. Such approaches can
454 help to fine-tune management interventions to maintain and promote biodiversity in anthropogenic
455 landscapes.

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Table 1: Processes related to each forest feature and community dimension and expected relationships for the trophic groups. Only groups for which we have specific hypotheses or for which we found studies are shown. This table is not comprehensive but is a selection of studies to build up hypothesis for our groups and forest features. Note also that these hypotheses are formulated for anthropogenic stands and might vary when considering naturally disturbed forests. ↑↓: positive or negative effects (respectively) supported by literature, (↑↓): hypothesised effects or weak evidence. Bold type: result mostly supported in our analysis; italic: not supported or opposite of the hypothesis; plain: support for some taxa but not all; see Fig.1, 2 and discussion. The full list of references is provided in Appendix SA1. For further details on forest features, see Appendix SA2.

Forest feature	Process	Richness	Abundance	Forest specialisation	Completeness
		Mostly related to resource and habitat heterogeneity ¹⁻⁵	Mostly related to resource availability ¹⁻³	Mostly related to features defining the particular environmental conditions present in forests	Mostly related to dispersal limitation and features at larger spatial scale ⁶⁻⁸
Stand properties/structure	Change in resource or microhabitat amount				
Canopy cover (m ² /ha)	Decreases light/radiation, and temperature; increases air and soil moisture ⁹⁻¹³ . Increases temperature buffering ¹⁴ . Could reduce dispersal of wind-dispersed species ¹⁵	↓ Autotrophs ¹⁶⁻¹⁸ , <i>fungi</i> ^{19,20} ↓ ↑ Arthropods ^{13,21-25} , vertebrate carnivores ²⁶⁻²⁹ , soil fungi ^{30,31}	↓ Autotrophs ³² , <i>fungi</i> ²⁰ , ↓ ↑ Soil fungi ³⁰ , arthropods ^{23,33,34} , vertebrate carnivores ^{35,36}	↑ Autotrophs ^{16,37} , arthropods ³⁸ , birds ²⁹ (↑) <i>Belowground groups, fungi</i>	↓ Vascular plants, arthropods ¹⁵ (↓) <i>Bryophytes, lichens</i>
Mean DBH: mean diameter at breast height (cm)	Provides stable conditions and longer time for colonisation (reducing dispersal limitation), old trees increase the amount of microhabitats ³⁹⁻⁴²	↑ Aboveground groups ^{39,43,44} (↑) <i>Belowground groups</i> ⁴³	↑ Aboveground groups ³⁹ (↑) <i>Belowground groups</i>	↑ <i>Aboveground groups</i> ^{42,45,46} (↑) <i>Belowground groups</i>	(↑) Aboveground groups ^{42,47,48} (↑) <i>Belowground groups</i>
Deadwood volume (m ³ /ha)	Increases resource and habitat for saproxylic species ^{24,49-51} (arthropods, lichens and bryophytes on deadwood, deadwood fungi)	↑ <i>Saproxylic species</i> ^{23,24,33,44,50-55}	(↑) <i>Saproxylic species</i> ^{23,50,51}	(↑) <i>Saproxylic species</i>	
Stand heterogeneity	Increases the number of available niches				
Tree diversity	Alters resource composition and increases microhabitat diversity ^{56,57} . Could affect stand microclimate ⁵⁸ .	↑ All groups ^{25,29,31,59-63}		(↑) <i>All groups</i> ^{29,60,64,65}	

Vertical heterogeneity	Increases niche diversity for groups using the vertical space, a higher number of layers could also increase resource type for herbivores ⁶⁶ . Could decrease ground light/radiation and impact animal movement ^{66,67}	(↑↓) Aboveground groups ^{23,38,68–71}		(↑) Aboveground groups
Horizontal heterogeneity	Increases niche diversity. Could affect variation of stand microclimate ⁷²	(↑) All groups ^{26,68–71}		(↑) <i>All groups</i> ²⁹
Deadwood diversity	Increases resource diversity for saproxylic species (arthropods, lichens and bryophytes on deadwood, deadwood fungi)	↑ Saproxylic species ^{23,25,33,44,54,73}	(↑) <i>Saproxylic species</i> ⁵⁴	(↑) <i>Saproxylic species</i>
Stand composition	Changes and/or increases resource (wood, leaves, litter, light, soil nutrients) or microhabitat amounts, and number. Could affect stand microclimate⁵⁸.			
Proportion of conifers	Provides different resource types to broadleaves ⁷⁴ and specific microhabitats ⁷⁵ . Scots pine canopies are more open than beech ones and can change microclimatic conditions ⁷⁶ . Might provide shelter/structure in winter ⁷⁷	(↑) All groups ^{20,78–86}	(↑) All groups ^{80,83}	(↑) All groups ³⁸
Proportion of oaks	Provides different resource types and specific microhabitats ^{74,87,88} . Oak canopies are more open than beech ones and can change microclimatic conditions ⁷⁶ .	(↑) All groups ^{62,86,89–92}	(↑) All groups ^{57,92}	(↑) All groups

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690

691 **Figure 1:** Effects of forest features on all 13 trophic groups for each community dimension. Effect
 692 sizes are standardised regression coefficients extracted from linear models corrected for region and
 693 soil characteristics. Forest-feature effects on abundance, richness and completeness are concordant
 694 (most dots in grey quadrants for effect-size plots of pairs of these dimensions), while they are
 695 discordant between effects on specialisation and effects on the other dimensions (most dots in white
 696 quadrants). Thin error bars highlight p-values greater than 0.05 (non-corrected for False Discovery
 697 Rates), while bold ones are added to estimates that are significantly different from 0.

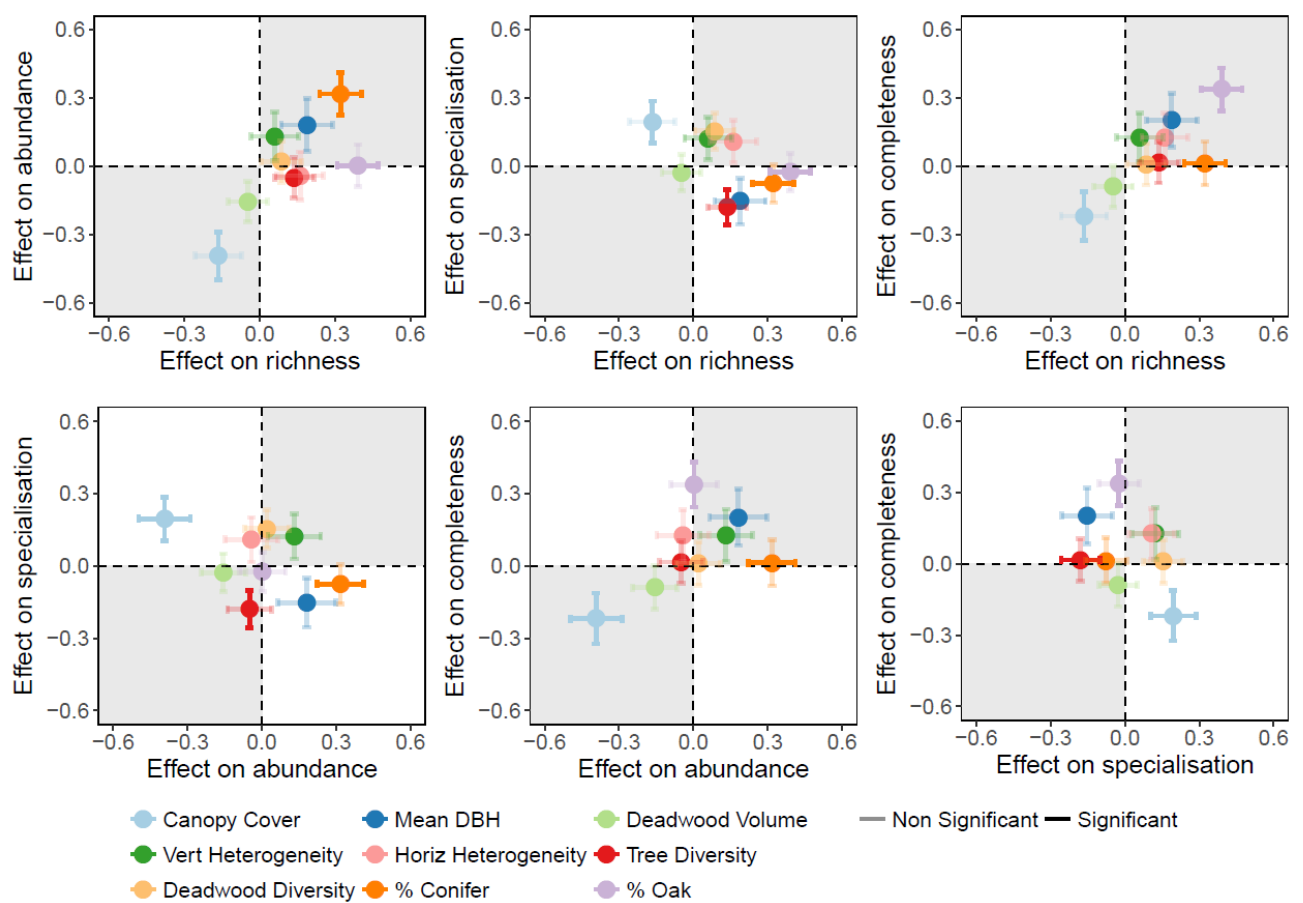


Figure 2: Effects (standardised regression coefficient estimates) of forest features on richness, abundance, forest specialisation, and completeness of 13 trophic groups. Blue indicates positive and red indicates negative effects. Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1. Symbols in grey indicate non-significant effects after controlling for false discovery rates (20% threshold). The last column of each panel indicates the average of absolute total effects for each group across all forest features, inverse weighted by their standard errors. “All-groups”, “Aboveground” and “Belowground” indicate multidiversity, -abundance, -specialisation and -completeness calculated for different sets of trophic groups (excluding the groups for which we had no information, white rows). We did not have abundance or specialisation for deadwood fungi. Soil fungal abundance includes all three trophic groups together.

