Contributed Paper

Current Near-to-Nature Forest Management Effects on Functional Trait Composition of Saproxylic Beetles in Beech Forests

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Abstract: *With the aim of wood production with negligible negative effects on biodiversity and ecosystem processes, a silvicultural practice of selective logging with natural regeneration has been implemented in European beech forests* (Fagus sylvatica) *during the last decades. Despite this near-to-nature strategy, species richness of various taxa is lower in these forests than in unmanaged forests. To develop guidelines to minimize the fundamental weaknesses in the current practice, we linked functional traits of saproxylic beetle species to ecosystem characteristics. We used continental-scale data from 8 European countries and regional-scale data from a large forest in southern Germany and forest-stand variables that represented a gradient of intensity of forest use to evaluate the effect of current near-to-nature management strategies on the functional diversity of saproxylic beetles. Forest-stand variables did not have a statistically significant effect on overall functional diversity, but they did significantly affect community mean and diversity of single functional traits. As the amount of dead wood increased the composition of assemblages shifted toward dominance of larger species and species preferring dead wood of large diameter and in advanced stages of decay. The mean amount of dead wood across plots in which most species occurred was from 20 to 60 m³/ha. Species occurring in plots with mean dead wood >60 m³/ha were consistently those inhabiting dead wood of large diameter and in advanced stages of decay. On the basis of our results, to make current wood-production practices in beech forests throughout Europe more conservation oriented (i.e., promoting biodiversity and ecosystem functioning), we recommend increasing the amount of dead wood to >20 m³/ha; not removing dead wood of large diameter (50 cm) and allowing more dead wood in advanced stages of decomposition to develop; and designating strict forest reserves, with their exceptionally high amounts of dead wood, that would serve as refuges for and sources of saproxylic habitat specialists.*

Keywords: biodiversity, body size, conservation, dead wood, ecosystem functions, functional diversity, niche position, phylogenetic diversity

Efectos Actuales del Manejo Casi Natural de Bosques sobre la Composición de Atributos Funcionales de Escarabajos Saproxílicos en Bosques de Haya

Resumen: *Con el objeto de producir madera con efectos negativos insignificantes sobre la biodiversidad y los procesos del ecosistema, durante las últimas décadas se ha implementado una práctica silvícola de tala selectiva con regeneración natural en bosques europeos de haya (Fagus sylvatica). No obstante esta estrategia casi natural, la riqueza de especies de varios taxa es menor en estos bosques que en bosques no manejados. Para desarrollar directrices para minimizar las debilidades fundamentales en la práctica actual, relacionamos atributos funcionales de especies de escarabajos saproxílicos con las características del ecosistema. Utilizamos datos a escala continental de 8 países europeos y datos a escala regional de un bosque extenso en el sur de Alemania y variables de bosques que representaron un gradiente de intensidad del uso de bosques para evaluar el efecto de las estrategias de manejo casi naturales sobre la diversidad funcional de los escarabajos saproxílicos. Las variables de bosques no tuvieron un efecto significativo sobre la diversidad funcional total, pero afectaron significativamente la media y diversidad de atributos funcionales individuales. A medida que incrementó la cantidad de madera muerta, la composición de los ensambles cambió hacia dominancia de especies mayores y de especies que prefieren madera muerta de mayor diámetro y con estadios avanzados de descomposición. La cantidad promedio de madera muerta en las parcelas en donde ocurrió la mayor parte de las especies fue de 20 – 60 m³/ha, Las especies que ocurrieron en parcelas con un promedio de madera muerta >60 m³/ha consistentemente fueron las que habitan en madera muerta de diámetro grande y con estadios avanzados de descomposición. Con base en nuestros resultados, para que las prácticas de producción de madera en bosques de haya en Europa están más orientadas a la conservación (i.e., promuevan el funcionamiento de la biodiversidad y del ecosistema), recomendamos incrementar la cantidad de madera muerta a >20 m³/ha; no remover la madera muerta de diámetro mayor a 50 cm y permitiendo más madera muerta en etapas de descomposición avanzadas; y diseñar reservas forestales estrictas, con sus cantidades de madera muerta excepcionalmente altas, que podrían funcionar como refugios para y como fuentes de especialistas de hábitats saproxílicos.*

Palabras Clave: Biodiversidad, conservación, diversidad filogenética, diversidad funcional, funciones del ecosistema, posición de nicho, tamaño corporal

Introduction

In Europe, modern forestry has substantially changed the species and age composition of forest fragments over the last 200 years, and extinctions of forest species have been documented (Speight 1989). To protect and promote biodiversity and ecosystem functions, forest authorities in Europe developed near-to-nature strategies to mitigate negative effects of logging, and these strategies are used widely throughout the world, although not necessarily commonly (Hunter & Schmiegelow 2010). One such strategy was established in the 1980s for the most widespread natural ecosystem type in Europe, beech (*Fagus sylvatica*) forest (Brunet et al. 2010). Near-to-nature forestry entails selective cutting, promoting native tree communities, and allowing natural regeneration (Johann 2006; Boncina 2011).

A combination of selective cutting in mature beech stands, with its shade tolerant trees, and natural regeneration is presumed to mimic the natural structure and regeneration process of old-growth beech forests. Despite such practices, forest authorities still must focus on wood production. Therefore, they regularly remove old and senescent trees (the so-called veteran trees), substantially reduce the amount of dead wood, and plant economically valuable conifers (Bauhus et al. 2009; Brunet et al. 2010) (Fig. 1). Logging generally reduces canopy cover and changes soil properties (Christensen et al. 2005; Durak 2010) (Fig. 1). These changes affect structural characteristics and key ecological processes in beech forests (Merino et al. 2008; Meyer & Schmidt 2011). Forest variables, such

as amount of dead wood and occurrence and age of old trees, effectively indicate intensity of forest use, which is more than a simple measure of the amount of wood removed (Bauhus et al. 2009) (Fig. 1).

The recycling of detritus is a key process in forest ecosystems, and it drives element cycling and productivity. Both the quantity and quality of detritus affect the diversity of decomposers and decomposition (Moore et al. 2004); thus, knowledge of the structural diversity of dead wood is needed to understand the effects of forest use on wood decomposition. However, it is difficult to measure the complex diversity of dead wood. Saproxylic beetles are, along with fungi, reliable indicators of many aspects of dead-wood ecology (Stokland et al. 2012). These beetles promote decomposition through mutualisms with fungi or microorganisms and by creating entry ports (Stokland et al. 2012). As bioengineers, some of them generate resources for other organisms and thus promote biodiversity and influence ecosystem functions (Zhou et al. 2006; Buse et al. 2008; Müller et al. 2008*a*). For the most part, however, these important functional roles of saproxylic beetles have been ignored and research has focused on the correlation of their species richness to intensity of forest use.

If the focus were to shift from single species to species assemblages, functional diversity would become a critical parameter to evaluate (Pielou 1966) because it can be used to study the functional role of assemblages, functional redundancy, and the consequences of species loss in ecosystems (Petchey & Gaston 2006). Functional diversity is linked to phenotype and therefore species' traits
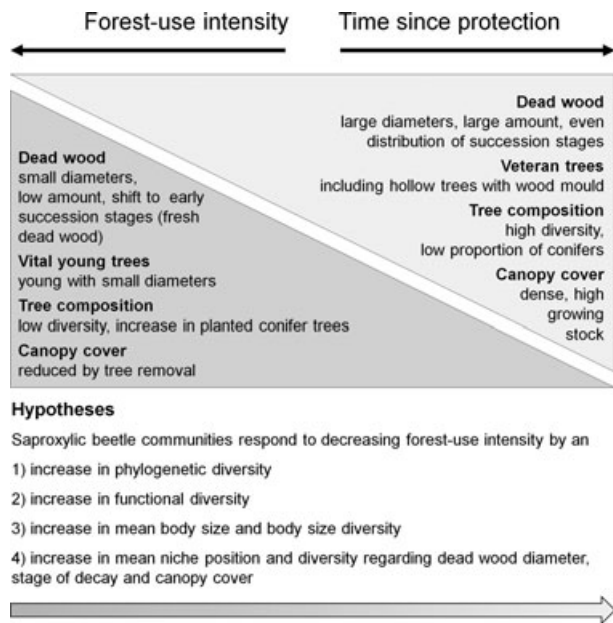
Figure 1. Conceptual framework showing the assumption of how intensity of logging with near-to-nature silvicultural practices in European beech forests may affect forest stand structures and the predicted shifts in functional trait composition of saproxylic beetle assemblages.

(Tilman 2001). One can analyze the change in functional diversity along climate or land-use gradients and correlate functional diversity to ecosystem processes (Cadotte et al. 2011; Ding et al. 2012). In the context of exploring the effects of land use, analyzing functional diversity may provide information on the suitability of saproxylic beetles as bioindicators, a possibility almost unmentioned in the existing literature. Most traits do not vary randomly across species; rather, they are correlated to evolutionary relatedness. Therefore, phylogenetic diversity is often used as a surrogate of functional diversity (Ding et al. 2012).

In managed beech forests, various taxonomic groups, particularly saproxylics, are lower in species richness and diversity and undergo considerable species turnover relative to species in unmanaged forests (Müller et al. 2008*b*; Brunet et al. 2010; Lassauce et al. 2011). Even the near-to-nature forestry practices applied in beech forests reduce the amount and diameter of dead wood, amount of dead wood in later stages of decay, and number of veteran trees (Fig. 1). These structural changes may lead to shifts in the trait composition of saproxylic species assemblages, in particular traits associated with species' preferred diameter and decay stage of dead wood. These traits are linked to feeding strategies, life-cycle duration, and contribution of assemblages to wood decay (Stokland et al. 2012). Reduced habitat availability and diversity may shift the mean trait composition of assemblages toward species that prefer dead wood of smaller diameter and earlier decay stages and reduce single-trait diversity (i.e., habitat

niche positions: dead-wood diameter, decay stage, and sun exposure). Body size is another functionally meaningful trait. The life cycle, especially the duration of larval development, of large-bodied beetles is relatively long; thus, these species rely on large pieces of dead wood because they provide a more stable environment (Foit 2010). Overall, reduced structural diversity of dead wood and increased intensity of forest use may lead to a decrease in functional and phylogenetic diversity (Bishop et al. 2009).

We investigated the effects of forest-use intensity on the occurrence of saproxylic beetle species and the composition of their assemblages with respect to their traits (body size and habitat niche positions). We used data from both a continental and a regional scale to test our hypotheses that less intense forestry practices result in higher phylogenetic and functional diversity; larger mean body size and body-size diversity; higher occurrence of species that prefer dead wood of large diameter and in advanced stages of decomposition and forests with closed canopies; and higher single-trait diversity with regard to habitat preferences (Fig. 1).

Methods

Study Areas and Sites

We used 2 data sets in our study: a European-wide data set of standardized trap samples (Müller et al. 2012) and regional data from intensive sampling in one beech forest of the Steigerwald in southern Germany. The latter data set was collected within a 15×15 km^2 forest area that spanned a gradient of forest use from intensively managed forests to strict forest reserves (Müller et al. 2008*b*) (Table 1). The data set from 8 European countries covered 75% of the distributional range of European Beech, from the Carpathians in the east to the Pyrenees in the west and north up to Sweden. We expanded the data set described by Müller et al. (2012) by 17 stands (41 sampling traps) in 3 regions of Germany, Schwäbische Alb, the Hainich-Dün, and the Schorfheide-Chorin.

Beetle-Assemblage Data

Beetles were sampled with flight-interception traps placed 1.5 m above the ground during the growing season (mountains, May–September; lowlands, April–October) (Müller et al. 2012). The European data set consisted of samples of 1156 traps from 242 forest stands in 79 forest sites. The regional data were gathered from 69 circular plots of 0.1 ha that were separated by at least 100 m. There, an entomologist also used beating, sieving, and bark-peeling techniques on dead wood structures and visual inspection of trees and inflorescences to sample

Table 1. Predictor variables and information on the measurement units used in models of the Europe-wide and regional data sets of saproxylic beetles (details in Supporting Information).

Variable type	Variable	Europe	Regional (Steigerwald)
Geographical	Latitude	Northing (ETRS. 1989[a] LAEA projection[b])	–
	Longitude	Easting (ETRS. 1989[a] LAEA projection[b])	–
Landscape (3-km radius)	Forest area	CORINE[c] types 311, 312, 313 (%)	–
	Broad-leaf trees	CORINE[c] types 311 + 50% of 313, relative to total forest area (%)	–
	Urban area	Proportion of traffic and settlements (CORINE[c] types: 111,112, 141,142) (%)	–
Local climate (1-km radius)	Temperature	WorldClim Bio10, mean temperature of the warmest quarter (°C)	–
	Precipitation	WorldClim Bio18; precipitation of the warmest quarter (mm)	–
Forest stand (1-ha surrounding)	Protection	Time since protection (years)	Yes/no
	Veteran trees	Occurrence of trees > 250 years (yes/no)	Age of oldest tree
	Dead wood	Amount in 3 categories: low (0–29 m^3 ha^{-1}), medium (30–70 m^3 ha^{-1}), high (>70 m^3 ha^{-1})	Amount log(m^3 ha^{-1})
	Tree diversity	Number of tree genera	Number of tree genera
	Conifers	Occurrence (yes/no)	(%)

Abbreviations: [a]ERTS, European Terrestrial Reference System; [b]LAEA, Lambert azimuthal equal-area projection; [c]CORINE, Pan-European project CORINE Land Cover (CLC) (CORINE 2006).

beetles in each plot. This additional sampling was performed in spring, summer, and fall over 2 weeks in each season for 1 h on each plot. All sampled individuals in both data sets were identified to species, except Staphylinidae and Pselaphidae in France. We omitted these families from analyses on the European scale. We classified beetles as saproxylic following reference lists from Germany cited in Müller et al. (2012).

Environmental Data

For the European-wide data set, we used variables that characterized geography, landscape, local climate, and forest stands as predictors of certain characteristics of the beetle assemblages (Table 1). For the regional data set, we used only forest-stand variables because the climate and landscape were similar among all plots.

We selected the forest-stand variables to represent a gradient of intensity of forest use (Fig. 1). On the basis of differences in the structure of the 2 data sets, it was not always possible to extract data on the same forest-stand variables for subsequent analyses. Nevertheless, we attempted to use variables that had at least the same ecological meaning. As a descriptor of the protection status on the European-wide scale, we used time since protection because the protected areas were set aside up to 80 years ago. On the regional scale, all protected areas were set aside about 40 years ago; thus, we considered protection on a nominal scale (yes or no). For European data, the variable veteran trees describe the presence or absence of trees older than 250 years. For regional scale, we used the age of the oldest tree in a particular stand. We classified the amount of dead wood

as low (0–29 m^3/ha), medium (30–70 m^3/ha), and high (>70 m^3/ha) for European data and as an absolute amount of dead wood for regional data. For both data sets, we measured tree diversity as the number of tree genera in a particular stand. Data on the proportion of conifers were not available for all forests. Therefore, we used the presence or absence of conifers as a categorical variable for the European data and the percentage of conifers as a continuous variable for the regional data (Table 1).

We used latitude and longitude as geographic variables. We estimated landscape characteristics in 3-km radius around the center of each stand primarily on the basis of data provided by CORINE (2006), a European-wide project mapping land use across most European countries. We extracted climate variables from WorldClim (resolution of 30 s) and calculated mean values in a 1-km radius to minimize bias introduced by rough terrain.

Trait Characterization

We compiled information on 4 ecological traits for each species (Supporting Information): mean body size, diameter of dead wood in which a species was recorded, decay stage of the dead wood, and canopy cover of forests in which the species is known to occur. In his compilation, Möller (2009) provides semiquantitative information on diameter, decay stage, and canopy cover across categories. We first extracted the occurrence of species across the following categories (axes): (1) diameter: <15 cm, 15–35 cm, >35 cm, and >70 cm; (2) decay stage: 0, alive; 1, freshly dead (1–2 years); 2, initiated decomposition (loose bark, tough sapwood); 3, advanced

decomposition (soft sapwood, partly tough hardwood); and 4, extremely decomposed and moldered; and (3) canopy cover: open, semiopen, and closed. Then, we estimated niche positions for each beetle species along these 3 axes on the basis of occurrence of species across these categories and weighting scores (0.5, very rarely used; 1, rarely used; 2, commonly used; 3, preferred; see Supporting Information for an example.

Phylogeny

We constructed an approximate phylogeny of all sampled beetles to control for the relation between species in trait–environment correlations and to calculate phylogenetic diversity of assemblages. The current phylogeny of beetles is still under debate (Lawrence et al. 2011). Therefore, we used the genetic phylogeny provided by Hunt et al. (2007) as our base topology. We expanded this tree on the basis of phylogenetic relations of several subgroups and additional information from taxonomic classifications (for more details, see S4 and Fig. S4-1) to construct the tree topology. The final tree was calibrated with 24 calibration points from fossil records (Supporting Information) with the function bladj in the program phylocom. The resulting tree had branch lengths of millions of years (Webb et al. 2008).

Data Analyses

To visualize the occurrence of saproxylic beetle species along gradients characterizing forest-use intensity in beech forests, we considered the first 2 axes of a canonical correspondence analysis (CCA) with the variables veteran trees, dead wood, tree diversity, and conifers available for both data sets. All these variables characterize aspects of forest-use intensity (Fig. 1). To evaluate which particular trait makes species susceptible to forest-use intensity, we modeled the positions of species along the axes versus their body size and their niche positions (regarding dead-wood diameter and decay stage, and canopy cover). In such an analysis, data points (species) may not be independent, which inflates the degrees of freedom (Garland et al. 1992). Therefore, we constructed a linear generalized least-squares model (GLS) with a correlation structure derived from our phylogenetic tree constructed using Pagel's λ (Pagel 1999). Pagel's λ is the degree of phylogenetic constraints from 0 (not constrained) to 1 (fully constrained) and was estimated by maximizing the likelihood of the model (Freckleton et al. 2002).

In a second approach, we characterized assemblages of saproxylic beetles to test our predictions (Fig. 1). We calculated the following characteristics on the basis of presence and absence data because the mass occurrence of a single species in some traps may bias the results. The phylogenetic diversity, based on the patristic distances extracted from the phylogeny, was calculated as the effect size of the mean phylogenetic distance between co-occurring saproxylic species within each assemblage with the function ses.mpd in the add-on package picante. We calculated effect size on the basis of a null model with 999 randomizations by reshuffling the tip labels to achieve independence from species numbers (Webb et al. 2002). This null model retained the structure of the assemblage matrix of beetles and tested whether the phylogenetic composition of species within assemblages was random with respect to the phylogeny. Values >0 indicated overdispersion; values <0 indicated clumping (Pausas & Verdu 2010). Following the same procedure, we calculated the functional diversity as effect size on the basis of an Euclidian distance matrix created with standardized values of the 4 selected ecological traits. Additionally, we calculated the diversity values for each of these traits (hereafter body-size diversity, diameter diversity, decay diversity, and canopy diversity) and the mean values of all 4 traits of the assemblages (hereafter mean body size, etc.). The latter characterize the average of the trait space of the assemblages; the former characterize the dispersion around the average.

To test for effects of environmental variables on characteristics of saproxylic beetle assemblages, we used generalized linear mixed-effect models (lmer) with forest stand as a random factor to account for pseudoreplications on the European scale. On the regional scale, the residuals of multiple linear models were tested for spatial independence (Supporting Information).

Results

Across both data sets, we recorded 752 saproxylic species. The Europen data set contained records of 456,638 individuals of 709 saproxylic beetle species (excluding Staphylinidae and Pselaphidae). The range of species caught per trap was 1–111. The regional data set contained records of 9303 individuals of 284 saproxylic beetle species, and the range of species richness was 11–48 species/plot.

In both data sets, the composition of the saproxylic beetle assemblages was most associated with 2 main gradients: a conifer axis and a dead-wood and veteran-tree axis (Fig. 2). We modeled the position of species along these 2 axes. For European data, the dead-wood diameter niche was significantly correlated with both of these ordination axes (λ 0.1–0.2) (Table 2). For regional data, decay niche was significantly correlated with the dead wood and veteran tree axis. In both models, the phylogenetic constraint was low (Table 2). Although not significant in our GLS, the diameter niche was correlated in univariate models with the dead-wood axis for regional data (Supporting Information). Furthermore, diameter niche and decay niche were significantly correlated ($\lambda = 0.83$, $p < 0.001$, $R^2 = 0.246$).
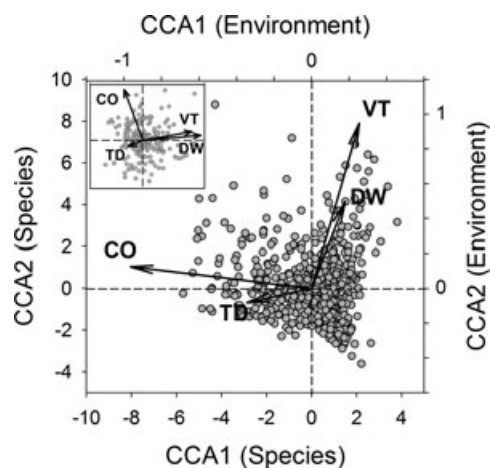
Figure 2. Ordination plot resulting from canonical correspondence analysis of saproxylic beetles caught in 1156 flight-interception traps throughout Europe (large plot) and on 69 plots in the Steigerwald (regional scale) (small plot). Circles show the position of saproxylic beetle species (Europe 709 species, regional 284 species) relative to 4 forest-stand variables (VT, occurrence of veteran trees; DW, amount of dead wood; CO, occurrence of conifers; TD, tree diversity). The figure indicates 2 axes: conifer axis (European scale, CCA1, eigenvalue 0.128; regional scale, CCA2, eigenvalue 0.156) and a dead-wood and veteran-tree axis (European scale, CCA2, eigenvalue 0.084; regional scale, CCA1, eigenvalue 0.209).

The large effect of dead wood on the functional composition of saproxylic beetle assemblages was further illustrated by the traits of species that were positively correlated with the dead wood and veteran tree axis of the CCA for both data sets (especially diameter and decay niches [Supporting Information]). For none of the species the mean amount of dead wood across

plots in which it occurred was <10 m^3/ha, although plots with such a low amount of dead wood were sampled (Fig. 3). The majority of species occurred on average in plots with an amount of dead wood of 20–60 m^3/ha. Most species occurring on average on plots with an amount of dead wood >60 m^3/ha required dead wood of large diameter (approximately 50 cm) (Fig. 3) and in the late stages of decay. These species were either small or large.

Variables that characterized geography, landscape, and local climate affected saproxylic beetle assemblages in the European data set (symbols outside the confidence interval in Fig. 4; see also Supporting Information). When we controlled for these variables and compared the European results with the regional results, we found no support for our prediction that a decreasing intensity of forest use, as represented by the stand variables, results in increasing phylogenetic and functional diversity (Fig. 4 & Supporting Information).

In contrast, the analyses of single traits (Fig. 4 & Supporting Information) showed that the amount of dead wood was the forest-stand variable with the greatest effect on functional composition of saproxylic beetles independent of species richness. This result was highly consistent in both data sets. In line with our predictions, for both data sets, the mean body size (which did not increase with sample size [Supporting Information]), body-size diversity, and mean diameter increased significantly as the amount of dead wood increased. For the regional data set, the mean decay increased significantly as the amount of dead wood increased. In contrast to our predictions, for both data sets diameter diversity decreased as the amount of dead wood increased (Fig. 4 & Supporting Information). The increase in mean body size, body-size diversity, and mean diameter indicated that both large and small species preferring dead wood of large diameter occurred on plots with a large amount of dead wood (Supporting

Table 2. Results of a linear model of the relation of the canonical correspondence analysis (CCA) axis positions to body size, and the niche positions (dead-wood diameter, dead-wood decay stage, and canopy cover).[a]

	Europe-wide scale				Regional scale				
	conifer axis CCA1 $R^2 = 0.023$, $\lambda = 0.182$		dead wood/veteran tree axis CCA2 $R^2 = 0.067$, $\lambda = 0.099$		dead wood/veteran tree axis CCA1 $R^2 = 0.118$, $\lambda = -0.030$		conifer axis CCA2 $R^2 = 0.002$, $\lambda = 0.011$		Trait mean
Trait	estimate	P	estimate	p	estimate	p	estimate	p	(range)
Intercept	−0.302	0.303	−0.034	0.898	0.089	< 0.001	0.149	0.275	
Body size	−0.100	0.273	0.133	0.191	−0.117	0.172	−0.043	0.706	4.97 (0.5–50 mm)
Diameter	0.262	0.004[b]	0.541	<0.001[b]	0.127	0.222	−0.059	0.652	2.35 (1–4)
Decay	0.116	0.263	0.131	0.265	0.462	<0.001[b]	0.011	0.938	2.99 (1–5)
Canopy cover	−0.014	0.846	0.012	0.892	< −0.001	0.998	−0.004	0.976	1.71 (1–3)

[a]*Generalized least squares with a correlation structure derived from the phylogenetic tree of all sampled beetle species (752 species, see Supporting Information). We used Pagel's λ (Pagel 1999) to correct for phylogenetic relatedness. Pagel's λ was optimized by selecting the model maximizing the likelihood (Freckleton et al. 2002). Pagel's λ indicates the degree of phylogenetic constraints from 0 (not constrained) to 1 (fully constrained).*
[b]*Significant at p < 0.05.*
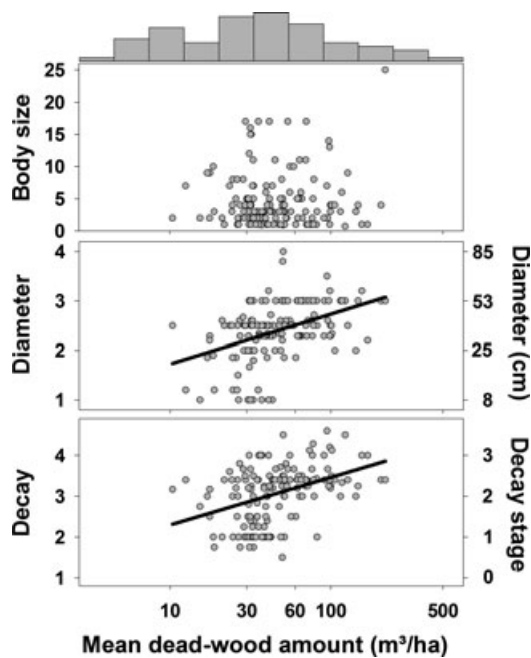
Figure 3. Correlation between traits of saproxylic beetle species and the position of a single species on an axis of the amount of dead wood (measured with high resolution) on the regional scale (Steigerwald) (gray bars, frequency distribution of dead-wood amount). This axis was calculated as the mean value of log-transformed values of dead-wood amount across the plots on which a species occurred. We estimated niche positions for each beetle species along the diameter and decay stage axes (left-hand axis) on the basis of occurrence of species across categories known from literature (diameter: <15 cm, 15–35 cm, >35 cm, and >70 cm; decay stage: 0, alive; 1, freshly dead [1–2 years]; 2, initiated decomposition [loose bark, tough sapwood]; 3, advanced decomposition [soft sapwood, partly tough hardwood]; and 4 [extremely decomposed and moldered]) and weighting scores (0.5, very rarely used; 1, rarely used; 2, commonly used; 3, preferred). For illustration, the scales of the original classification of dead-wood diameter niche and dead-wood decay-stage niche are on the right-hand axis. All species that were sampled on at least 3 plots were included (n = 149 species).

Information). Thus, along the gradient of decreasing intensity of forest use, the number of large species increased and turnover of smaller species occurred.

Discussion

Results of previous studies show that the amount of dead wood affects species richness of saproxylic beetles (Grove 2002; Müller & Bütler 2010; Lassauce et al. 2011). We demonstrated for the first time that irrespective of the geographic scale and species richness, the amount of

dead wood (particularly of large diameter and in a late stage of decay stages) is an important biological legacy (i.e., a feature left after harvest, also, for example, large trees [Franklin et al. 2007]) that influence the functional composition of saproxylic beetles in beech forests. Therefore, the current strategy of wood production in beech forests, which avoids clearcutting and relies on natural regeneration processes but depresses dead wood to low amounts, is insufficient as a conservation-oriented management strategy.

Cross-species analyses are often characterized by large scatter (see R^2 values in Table 2). Therefore, we used an assembly-based approach for testing our predictions (Fig. 1). Assembly-based approaches are much more sensitive because they average across minor signals of species (Olalla-Tárraga et al. 2010). Our assembly-based approach based on functional traits revealed that as amount of dead wood increased, large and small species specialized on dead wood of large diameter entered the assemblages. This translated into an increase in body-size diversity. In contrast, the diversity of the diameter niche decreased as the amount of dead wood increased, which indicates a dominance of species preferring dead wood of large diameter when there is a large amount of dead wood. Body size correlates well with life-history traits (Sibly et al. 2012). Larger species in particular are characterized by a long developmental phase and slow growth rates (Haack & Slansky 1987), which make them dependent on large pieces of dead wood (Brin et al. 2011). Although the volume of branches seems to be sufficient even for large-bodied beetles, the microhabitat requirements of these species may restrict them to large pieces (Stokland et al. 2012). The sensitivity of a few large species to increasing intensity of forest use has been documented (e.g., long-horned beetle [*Cerambyx cerdo*], a species discussed as an important ecosystem engineer because it produces large galleries) (Buse et al. 2007, 2008).

Our finding of an additional turnover of small-bodied species as the amount of dead wood increased showed that some small species are also specialists on dead wood of large diameter (e.g., *Ropalodontus perforatus, Stenichnus godarti*). This finding was highlighted by the results of our cross-species analyses, in which species occurring in stands with large amounts of dead wood had high demand for dead wood of large diameters and in late stages of decay (Fig. 3). One may argue that having very high amounts of dead wood would overlook the requirements of species that prefer dead wood of small diameter. However, such species are less susceptible to effects of intensity of forest use and benefit when dead wood is >20 m³/ha (Fig. 3).

Although the traits we studied are currently the best available for examining functional links between assemblages and the environment, our analyses were constrained because these variables are at best surrogates.
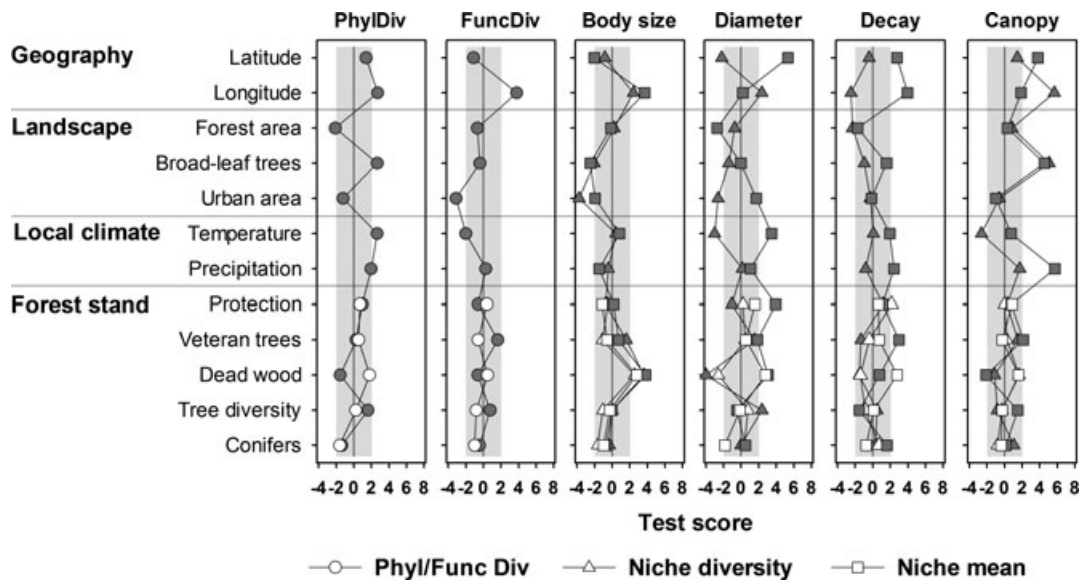
Figure 4. Results of linear regression analyses of effects of predictor variables (geographic, landscape, regional climate [Europe-wide scale only], forest stand variables) on the functional composition of saproxylic beetle assemblages (effect sizes of phylogenetic diversity [PhylDiv] and functional diversity [FuncDiv], and single traits) fitted by the linear model function (lm) (regional scale, white symbols) and a linear mixed-effect model (lmer) with forest stand as a random factor (European scale, grey symbols). Single traits are the mean values and effect sizes of diversity (measured as dispersion with null models with 999 randomizations) of body size and dead-wood niche characteristics (diameter, decay, canopy cover). Analysis on the regional scale is based on the complete data set. Shaded areas indicate range of nonsignificant values (t values: European ±1.998; regional ±1.960). For detailed values, see Supporting Information.

One major future challenge is to collect more information on the biology of these species. For example, in a recent study, gut analysis of well-known species presumed to be predators revealed that fungi are a major food (Prikryl et al. 2012). Gut or stable-isotope analyses are promising tools for estimating the trophic niche of saproxylics more precisely (Blüthgen et al. 2003).

In our analysis, phylogenetic diversity was not affected by forest-stand variables, which we used as surrogates for intensity of forest use. As species richness decreased with increasing intensity of forest use, species losses along this gradient occurred randomly across the phylogeny. Therefore, analyses of phylogenetic diversity do not seem to be a promising method for studying the assemblages of saproxylic beetles. Similarly, functional diversity seemed unaffected by forest-stand variables, even though single traits were affected. These results suggest that measures of functional diversity that combine several traits may mask important ecological effects, just as a pure diversity index may neglect the identity of species (Fleishman et al. 2006).

Veteran trees provided a higher diversity of decay niches only for the European data. On the one hand, this is consistent with previous findings that such trees provide resources for species of a broad range of successional stages (Speight 1989). On the other hand, in our assembly approach, one must keep in mind that only a

few of the species within the hyperdiverse community of saproxylic beetles are restricted to hollow veteran trees. Most of the saproxylic beetles living in veteran trees also develop in logs or snags (Speight 1989). In addition, the resolution of our measurement of veteran trees was low.

Although we did not find a strong effect of time since protection, in contrast to the findings of recent European-wide meta-analyses (Paillet et al. 2010), our data showed that most biological legacies increased as time since protection increased (e.g., dead wood and protection, $r = 0.47$) (Fig. 1). This indicates that the availability of resources is more important than protection only or time since protection and high amounts of dead wood are found mostly in strictly protected forests (Paillet et al. 2010). Furthermore, we assumed that the distribution of species across the sampled plots was in equilibrium with respect to the environmental variables. The low importance of time since protection indicated that equilibrium with respect to trait composition was reached within a very short time.

To what extent are our results for saproxylic beetle species and beech forests transferable to other taxa or ecosystems? In European forests, species richness of saproxylic beetles is correlated with species richness of other taxonomic groups (Paillet et al. 2010), such as wood-inhabiting fungi, which exhibit a similar diversity in how they use dead wood as a habitat and nutrient source,

and carabid beetles, bryophytes, and lichens, which use dead wood for colonization or shelter. Due to the increase in habitat diversity as the amount of dead wood increases (Müller & Bütler 2010), we expect the functional-trait composition of these groups in temperate forests will also change as the amount of dead wood changes (Heilmann-Clausen & Christensen 2004; Stokland et al. 2012). The transferability of our results from European beech forests to other biomes or ecosystems may be more complicated. Beech forests are shady and characterized by gap regeneration. In forests characterized by more open canopies, the patterns of traits and forest-stand variables may differ, in particular in boreal forests, which are dominated by conifers and regularly suffer stand-replacing disturbances such as fire. Thus, species richness (Lassauce et al. 2011) and trait characteristics of saproxylic beetles may respond differently to intensity of forest use in boreal forests.

Our most important conclusion is that the composition of saproxylic beetle assemblages along a gradient of increasing amount of dead wood affected not only species richness, but also the functional composition of assemblages. What does this mean, other than more dead wood should be left in the forest? Analyses of the functional traits illuminated the qualitative weakness of current forestry practices—not only is a higher amount of dead wood needed, but more dead wood of large diameter and in advanced stages of decay is needed. This underlines the value of functional traits as indicators of structures or processes of ecosystems that are difficult to measure. Furthermore, our functional approach leads to useful recommendations for improving the cost-effectiveness and conservation value of current silvicultural practices in European beech forests: (1) increase the amount of dead wood in managed stands from the current 5–10 m^3/ha^{-1} to >20 m^3/ha^{-1}, (2) because economic pressures often preclude the accumulation of higher amounts of dead wood, forest managers should in particular conserve dead wood of large diameter (approximately 50 cm) and allow more dead wood in advanced stages of decomposition to develop, and (3) designate strict forest reserves—the only area in which high amounts of dead wood (>60 $m^3 ha^{-1}$) can accumulate to create refuges and source pools for habitat specialists. We suggest expansion of rules of thumb to more quantitative recommendations for deadwood management that balance the trade-off between economy and ecology in managed forests.

Acknowledgments

Supporting Information

Tests for spatial independence (Appendix S1), climate and landscape variables (Appendix S2), species list and traits (Appendix S3), species' phylogenies (Appendix S4), relation of body size and niche positions of species to intensity of forest use (Appendix S5), results of linear-regression analyses (Appendix S6), correlation of individuals and mean body size (Appendix S7), correlation of effect sizes of single traits (Appendix S8), correlation of amount of dead wood and mean body size and niche positions (Appendix S9), correlation of amount of dead wood and maximum diameter (Appendix S10), and Supporting Information references (Appendix S11) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

Literature Cited

Bauhus, J., K. Puettmann, and C. Messier. 2009. Silviculture for old-growth attributes. Forest Ecology and Management **258:**525–537.

Bishop, D. J., C. G. Majka, S. Bondrup-Nielsen, and S. B. Peck. 2009. Deadwood and saproxylic beetle diversity in naturally disturbed and managed spruce forests in Nova Scotia. Zookeys **22:** Special Issue 309–340.

Blüthgen, N., G. Gebauer, and K. Fiedler. 2003. Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community. Oecologia **137:**426–435.

Boncina, A. 2011. Conceptual approaches to integrate nature conservation into forest management: a Central European perspective. International Forestry Review **13:**13–22.

Brin, A., C. Bouget, H. Brustel, and H. Jactel. 2011. Diameter of downed woody debris does matter for saproxylic beetle assemblages in temperate oak and pine forests. Journal of Insect Conservation **15:**653–669.

Brunet, J., Ö. Fritz, and G. Richnau. 2010. Biodiversity in European beech forests—a review with recommendations for sustainable forest management. Ecological Bulletins **53:**77–94.

Buse, J., T. Ranius, and T. Assmann. 2008. An endangered longhorn beetle associated with old oaks and its possible role as an ecosystem engineer. Conservation Biology **22:**329–337.

Buse, J., B. Schröder, and T. Assmann. 2007. Modelling habitat and spatial distribution of an endangered longhorn beetle—a case study for saproxylic insect conservation. Biological Conservation **137:**372–381.

Cadotte, M. W., K. Carscadden, and N. Mirotchnick. 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology **48:**1079–1087.

Christensen, M., et al. 2005. Dead wood in European beech (*Fagus sylvatica*) forest reserves. Forest Ecology and Management **210**:267–282.

CORINE. 2006. Pan-European project CORINE land cover (CLC). Available from http://www.corine.dfd.dlr.de (accessed January 2012).

Ding, Y., R. G. Zang, S. G. Letcher, S. R. Liu, and F. L. He. 2012. Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. Oikos **121**:1263–1270.

Durak, T. 2010. Long-term trends in vegetation changes of managed versus unmanaged eastern Carpathian beech forests. Forest Ecology and Management **260**:1333–1344.

Fleishman, E., R. F. Noss, and B. R. Noon. 2006. Utility and limitations of species richness metrics for conservation planning. Ecological Indicators **6**:543–553.

Foit, J. 2010. Distribution of early-arriving saproxylic beetles on standing dead Scots pine trees. Agricultural and Forest Entomology **12**:133–141.

Franklin, J. F., R. J. Mitchell, and B. J. Palik. 2007. Natural disturbance and stand development principles for ecological forestry. General technical report NRS-19. U.S. Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

Freckleton, R. P., P. H. Harvey, and A. M. Pagel. 2002. Phylogenetic analysis and comparative data: a test and review of evidence. The American Naturalist **160**:712–726.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology **41**:18–32.

Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annual Review of Ecology and Systematics **33**:1–23.

Haack, R. A., and F. J. Slansky. 1987. Nutritional ecology of wood-feeding Coleoptera, Lepidoptera and Hymenoptera. Pages 449–486 in F. J. Slansky and J. G. Rodriguez, editors. Nutritional ecology of insects, mites, spiders and related invertebrates. John Wiley & Sons, London.

Heilmann-Clausen, J., and M. Christensen. 2004. Does size matter? On the importance of various dead wood fractions for fungal diversity in Danish beech forests. Forest Ecology and Management **201**:105–117.

Hunt, T., et al. 2007. A comprehensive phylogeny of beetles reveals the evolutionary origins of a superradiation. Science **318**:1913–1916.

Hunter, M.L., and F. Schmiegelow. 2010. Wildlife, forests and forestry: principles of managing forests for biological diversity. Prentice Hall, Englewood Cliffs, NJ.

Johann, E. 2006. Historical development of nature-based forestry in Central Europe. Pages 1–17 in J. Diaci, editor. Nature-based forestry in Central Europe: alternatives to industrial forestry and strict preservation, Ljubljana. Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, Ljubljana, Slovenia.

Lassauce, A., Y. Paillet, H. Jactel, and C. Bouget. 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. Ecological Indicators **11**:1027–1039.

Lawrence, J. F., A. Ślipiński, A. E. Seago, M. K. Thayer, A. F. Newton, and A. E. Marvaldi. 2011. Phylogeny of the Coleoptera based on morphological characters of adults and larvae. Annales Zoologici **61**:1–217.

Merino, A., C. Real, and M. A. Rodriguez-Guitian. 2008. Nutrient status of managed and natural forest fragments of *Fagus sylvatica* in southern Europe. Forest Ecology and Management **255**:3691–3699.

Meyer, P., and M. Schmidt. 2011. Accumulation of dead wood in abandoned beech (*Fagus sylvatica* L.) forests in northwestern Germany. Forest Ecology and Management **261**:342–352.

Möller, G. 2009. Struktur- und Substratbindung holzbewohnender Insekten, Schwerpunkt Coleoptera – Käfer. Dissertation zur Erlangung des akademischen Grades des Doktors der Naturwissenschaften (Dr. rer. nat.), Freie Universität, Berlin.

Moore, J. C., et al. 2004. Detritus, trophic dynamics and biodiversity. Ecology Letters **7**:584–600.

Müller, J., et al. 2012. Implications from large-scale spatial diversity patterns of saproxylic beetles for the conservation of European Beech forests. Insect Conservation and Diversity. doi: 10.1111/j.1752-4598.2012.00200.x

Müller, J., H. Bussler, M. M. Gossner, T. Rettelbach, and P. Duelli. 2008*a*. The European spruce bark beetle *Ips typographus* in a national park: from pest to keystone species. Biodiversity and Conservation **17**:2979–3001.

Müller, J., H. Bussler, and T. Kneib. 2008*b*. Saproxylic beetle assemblages related to silvicultural management intensity and stand structures in a beech forest in Southern Germany. Journal of Insect Conservation **12**:107–124.

Müller, J., and R. Bütler. 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. European Journal of Forest Research **129**:981–992.

Olalla-Tárraga, M. Á., L. M. Bini, J. A. F. Diniz-Filho, and M. Á. Rodríguez. 2010. Cross-species and assemblage-based approaches to Bergmann's rule and the biogeography of body size in Plethodon salamanders of eastern North America. Ecography **33**:362–368.

Pagel, M. 1999. Inferring the historical patterns of biological evolution. Nature **401**:877–884.

Paillet, Y., et al. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conservation Biology **24**:101–112.

Pausas, J. G., and M. Verdu. 2010. The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. BioScience **60**:614–625.

Petchey, O. L., and K. J. Gaston. 2006. Functional diversity: back to basics and looking forward. Ecology Letters **9**:741–758.

Pielou, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. Journal of Theoretical Biology **10**:370–383.

Prikryl, Z. B., M. Turcani, and J. Horak. 2012. Sharing the same space: foraging behaviour of saproxylic beetles in relation to dietary components of morphologically similar larvae. Ecological Entomology **37**:117–123.

Sibly, R., J. H. Brown, and A. Kodric-Brown. 2012. Metabolic ecology: a scaling approach. John Wiley & Sons, Oxford, United Kingdom.

Speight, M. C. D. 1989. Saproxylic invertebrates and their conservation. Council of Europe, Nature and Environment Series **42**:1–79.

Stokland, J., J. Siitonen, and B. G. Jonsson. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, United Kingdom.

Tilman, D. G. 2001. Functional diversity. Encyclopedia of Biodiversity **3**:109–120.

Webb, C. O., D. D. Ackerly, and S. W. Kembel. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. Bioinformatics **24**:2098–2100.

Webb, C. O., D. D. Ackerly, M. A. McPeek, and M. J. Donoghue. 2002. Phylogenies and community ecology. Annual Review of Ecology and Systematics **33**:475–505.

Zhou, G. Y., S. G. Liu, Z. Li, D. Q. Zhang, X. L. Tang, C. Y. Zhou, J. H. Yan, and J. M. Mo. 2006. Old-growth forests can accumulate carbon in soils. Science **314**:1417.