











RESEARCH ARTICLE

Animal Functional Traits

High-resolution 3D forest structure explains ecomorphological trait variation in assemblages of saproxylic beetles

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Abstract

1. Climate, topography and the 3D structure of forests are major drivers affecting local species communities. However, little is known about how the specific functional traits of saproxylic (wood-living) beetles, involved in the recycling of wood, might be affected by those environmental characteristics.
2. Here, we combine ecological and morphological traits available for saproxylic beetles and airborne laser scanning (ALS) data in Bayesian trait-based joint species distribution models to study how traits drive the distributions of more than 230 species in temperate forests of Europe.
3. We found that elevation (as a proxy for temperature and precipitation) and the proportion of conifers played important roles in species occurrences while variables related to habitat heterogeneity and forest complexity were less relevant. Furthermore, we showed that local communities were shaped by environmental variation primarily through their ecological traits whereas morphological traits were involved only marginally. As predicted, ecological traits influenced species' responses to forest structure, and to other environmental variation, with canopy niche, wood decay niche and host preference as the most important ecological traits. Conversely, no links between morphological traits and environmental

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characteristics were observed. Both models, however, revealed strong phylogenetic signal in species' response to environmental characteristics.

4. These findings imply that alterations of climate and tree species composition have the potential to alter saproxylic beetle communities in temperate forests. Additionally, ecological traits help explain species' responses to environmental characteristics and thus should prove useful in predicting their responses to future change. It remains challenging, however, to link simple morphological traits to species' complex ecological niches.

KEYWORDS

airborne laser scanning, Bayesian modelling, Coleoptera, environmental gradient, functional traits, HMSC, LiDAR, phylogeny

1 | INTRODUCTION

Climate, topography and the 3D structure of trees and shrubs are the main drivers of animal diversity across different taxa in forest ecosystems (Gouveia et al., 2014 for primates; Jung et al., 2012 for bats; Müller, Stadler, et al., 2010; Müller, Noss, et al., 2010 for birds; Rinker et al., 2001 for arthropods). The composition and distribution of species inhabiting the complex structures of forests can be determined both directly by specific structural features (e.g. host plants, deadwood, vertical biomass distribution) and indirectly by varying microclimatic conditions, such as radiation, temperature or humidity (Davies & Asner, 2014). Local climate conditions are further affected by the topography, with higher variation in rough terrain. Such local variation in micro- and topoclimate can even override macroclimatic gradients along elevation or latitude (Hodkinson, 2005). Species' responses to variation in forest structure and climate should be mediated by their traits (Burner, Stephan, Drag, et al., 2021). Consequently, changes in environment can alter the functional diversity of communities and this in turn can have strong impacts on community dynamics and stability, as well as ecosystem processes (de Bello et al., 2021). Yet, our understanding of the relationships between topographic, climatic and forest structure variables and specific functional traits in arthropods is still mostly lacking.

Saproxylic (wood-living) beetles are a taxonomically, phylogenetically and functionally diverse group of insects, accounting for roughly one-third of all forest-dwelling arthropod species (Kuuluvainen & Siitonen, 2013). By a common definition (Speight, 1989), saproxylic beetles are those that are closely associated with dead or decaying wood during at least some part of their life cycle. However, despite their important role as indicators of forest biodiversity (Bouget et al., 2013; Lachat et al., 2012), little is known about which functional traits directly influence the occurrences of beetles under different forest conditions.

In saproxylic beetles, most trait-based studies employed ecological (e.g. Gossner et al., 2013; Laaksonen et al., 2020), morphological (Hagge et al., 2021) or life-history traits (Gillespie et al., 2017) or their combinations (Wetherbee et al., 2020). Ecological traits can be considered as the intrinsic characteristics directly linking species with their specific resources (Seibold et al., 2015). Due to their

general character, they stand as surrogates of several more specific traits (e.g. morphological traits). As ecological traits cannot be measured on a single individual but rather represent experts' often subjective judgements about a given species (e.g. microhabitat preferences, trophic guilds or their feeding types; Freude et al., 1983; Köhler, 2000; Möller, 2009; Schmidl & Bussler, 2004), they should not be considered as traits in the strict sense (Violle et al., 2007). Nevertheless, they have been successfully used to assess the changes in functional diversity of saproxylic beetles along the forest gradients (Burner, Stephan, Drag, et al., 2021; Hagge et al., 2019; Janssen et al., 2017) and at sites affected by salvage logging (Thorn et al., 2014), or to estimate the extinction risk of species within this group (Seibold et al., 2015).

Unlike ecological traits, morphological traits are replicable, independent measurements of different body parts usually following a standardized protocol (Moretti et al., 2017). Except body size (e.g. Gossner et al., 2013; Laaksonen et al., 2020; Müller & Brandl, 2009), however, morphological traits have been employed only rarely in saproxylic beetles, mostly due to the complicated and labour-intensive trait collection process (Hagge et al., 2021). Nevertheless, theory suggests that they should be ecologically relevant, as species' morphological structures are linked to specific ecological functions that can directly respond to changing environmental conditions or land-use intensity (Barton et al., 2011). Moving from an understanding of species relationships along environmental gradients in forest to identifying the traits that underpin these relationships is thus a critical step in understanding community assembly and its underlying mechanisms (McGill et al., 2006).

In this study, we explore these trait-environment relationships by combining relevant morphological (Table 1) and ecological (Table 2) traits, information from airborne laser scanning (ALS) and field sampling. Based on previous publications and the proposed ecological functions of morphological traits (Hagge et al., 2021), we developed five predictions about how environmental characteristics measured in our study may influence the distribution of morphological traits of saproxylic beetle communities (Table 1). We apply a trait-based joint species distribution model (JSDM) to investigate how the occurrence probability of saproxylic beetle species changes

TABLE 1 Morphological traits (taken from Hagge et al., 2021) used to study beetle responses to environmental gradients including their presumed ecological functions

Trait	Range	Units	Predictions	Presumed ecological function and the mechanism
Colour	78–154	dark–pale index	Colour lightness will decrease at higher elevations	Thermoregulation—dark individuals can heat up faster than light individuals, so they should be favoured under conditions of low temperature (Trullas et al., 2007); UV protection—dark individuals have higher resistance to UV radiation, so they should be also favoured in higher elevations (True, 2003)
Body length	1.2–36.2	mm	Body size-related traits will increase with increasing amount of deadwood and with decreasing canopy density	Body size—larger species prefer dead wood of large diameter and of late decay stages (Gossner et al., 2013), or more robust beetles favour open habitats over structurally complex habitats (Barton et al., 2011)
Body width	0.4–16.1	mm		
Head length	0.2–5.9	mm		
Antenna length	0.2–19.4	mm	Eye length and antenna length will decrease with higher canopy density	Sensory—larger eyes and longer antennae were related to more open areas in carabid beetles (Talarico et al., 2007)
Eye length	0.1–4.2	mm		
Front femur length	0.2–7.1	mm	Wing length and front femur length will decrease with increasing deadwood amount and deadwood structure	Dispersal ability—ephemeral resource-related species have better dispersal ability than the species connected to more stable habitat (Komonen & Müller, 2018)
Wing length	1.1–31.4	mm		
Jaw length	0.1–4.1	mm	Jaw length will increase with increasing proportion of conifers	Wood processing—stronger mandibles can be related to harder wood that adult saproxylic beetles have to deal with (Hagge et al., 2021)

Trait	Range	Categories	Source
Canopy niche	1–3	open–closed	Seibold et al. (2015)
Decay niche	1–5	alive–decomposed	Seibold et al. (2015)
Flower visitor	2 categories	yes, no	Seibold et al. (2015)
Host tree	3 categories	conifer, broad-leaved, both	Seibold et al. (2015)
Habitat	4 categories	wood, mould, fungi, bark	Köhler (2000)

TABLE 2 Ecological traits used to study beetle responses to environmental gradients

along environmental gradients in Germany, and which traits predict variation in beetle responses.

2 | MATERIALS AND METHODS

2.1 | Study area and species sampling

The data used for this study are from 384 plots covering five distinct regions in Germany (Figure 1; for more details, see Appendix S1). As many of these data have been previously used in other studies, additional methodological details for each of the projects are available

in the original publications (e.g. Bae et al., 2019; Heidrich et al., 2020). Briefly, the five regions represented diverse forest types in Central Europe, covering the whole gradient of forest management intensities (unmanaged old-growth forest–intensively managed forest), tree species composition (broadleaved–coniferous) and climate represented by elevation (lowland–mountains; 87–1420m a.s.l.). At each 1-ha plot, one pitfall trap and one flight interception trap (40×60cm, hung ca. 1.5m above the ground) were set from March to October during a single year (2007, 2008 or 2016, depending on the project), and emptied once a month. The beetles were pooled from the entire season at each plot and identified morphologically to the species level by experts. The dataset was then filtered to include only

FIGURE 1 Five regions in Germany where saproxylic beetles were collected. Biodiversity Exploratories Project (Fischer et al., 2010): SCH—Schorfheide-Chorin region (48 plots), HAI—Hainich region (49 plots), ALB—Schwäbische Alb region (50 plots); BIOKLIM project (Bässler et al., 2009): BAY—Bavarian Forest National Park (168 plots); Steigerwald project (Doerfler et al., 2018): STE—Steigerwald region (69 plots). Forest area data originate from Copernicus HRL Forest products data (www.eea.europa.eu/data-and-maps/).

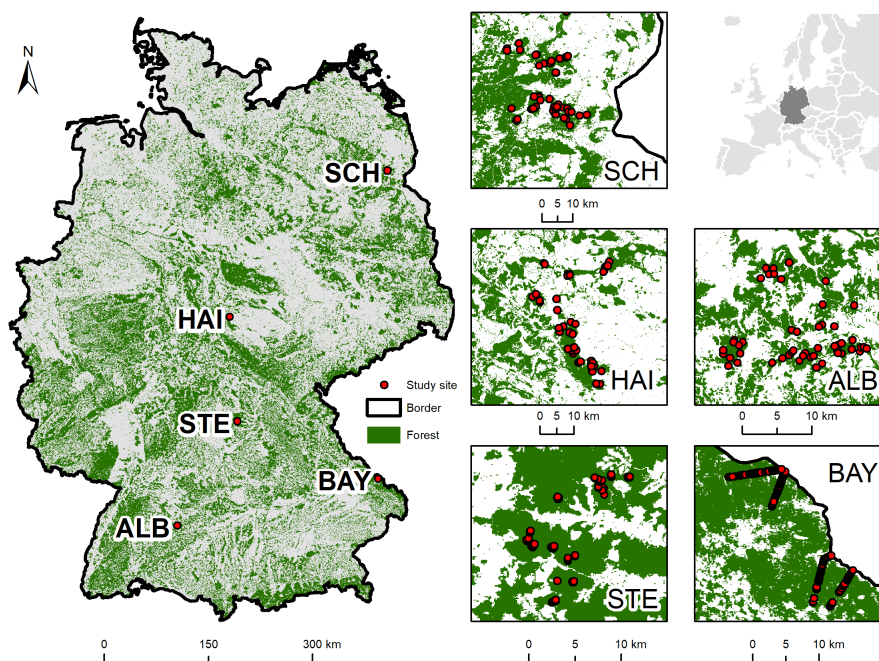


TABLE 3 Environmental characteristics including topographic, climatic and forest variables derived from airborne laser scanner (ALS; Bae et al., 2019) and field measurements (Heidrich et al., 2020). For canopy density, a canopy height model (CHM) with 1-m spatial resolution was derived from the ALS point cloud by assigning each CHM pixel the maximum z-value of all ALS points within. Similarly, for terrain roughness, a digital elevation model (DEM) with 1-m spatial resolution was derived from the z-values of all ALS ground returns

Variable	Description	Range	Units	Source
Canopy density	Proportion of CHM pixels >2 m	11–100	%	ALS
Vegetation density	Penetration rate $0\text{ m} < x < 2\text{ m}$	<1–42	%	ALS
Elevation	Mean of the z-values; proxy for climate (temperature and precipitation) variables	87–1420	m a.s.l.	ALS
Terrain roughness	Standard deviation of the slope values in the DEM	0.77–14.45	—	ALS
Vertical structure	Standard deviation of the z-values from the ALS point cloud	1.13–12.43	—	ALS
Proportion of conifers	Proportion of conifers by basal area	0–100	%	Measured
Deadwood amount	Deadwood volume (log-transformed)	0–2772	m^3/ha	Measured
Deadwood richness	Tree species richness of deadwood	1–9	Number of species	Measured
Deadwood structure	A combination of deadwood objects, decay classes and diameter classes	1–41	Number of types	Measured

saproxylic beetles ($n = 519$) based on the German reference list of saproxylic beetles (Köhler, 2000; Schmid & Bussler, 2004). Fieldwork permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen and Brandenburg (Table S1).

2.2 | Environmental characteristics

To cover a wide range of topographic, climatic and forest structure characteristics, five ALS-based variables (canopy density, vegetation density, elevation, terrain roughness and vertical structure) further supplemented by four forest inventory variables measured on-site (proportion of conifers, deadwood amount, deadwood richness and

deadwood structure) were included (Table 3). As many environmental characteristics are highly correlated with each other, we selected only those that have been shown to be the most influential for saproxylic beetles (Heidrich et al., 2020; Müller et al., 2020) and which were not strongly correlated with each other ($r < 0.62$; Figure S1). The maximum variance inflation factor (VIF) of the covariates was less than three, indicating low multicollinearity (Naimi et al., 2014). As elevation was closely negatively correlated with mean annual temperature and positively correlated with mean annual precipitation (Figure S2), only elevation was included in the models (as a proxy for climate). The ALS-based data were recorded under leaf-on conditions for each 1-ha plot in all five regions in Germany between 2007 and 2018 and processed following the methods described in

Bae et al. (2019). The individual measurements of deadwood (deadwood amount, deadwood richness and deadwood structure) were taken from Heidrich et al. (2020). Deadwood richness represented the number of tree species contributing to deadwood objects per plot, whereas the deadwood structure was calculated as the number of different deadwood types (a combination of deadwood objects, decay classes and diameter classes) per plot. The proportion of conifers (as opposed to broadleaf tree species) was calculated based on the basal area of individual tree species identified during a comprehensive forest inventory.

2.3 | Beetle traits

To test how traits influence the responses of saproxylic species to the environmental covariates, we used several ecological and morphological traits available in the literature. Specifically, we took five ecological traits from Seibold et al. (2015) and Köhler (2000) (Table 2). Although these traits represent complex responses of multiple functional traits (Violle et al., 2007), some of them have direct links to our environmental characteristics, which makes them a valuable addition in our understanding of beetle functional ecology (Fountain-Jones et al., 2015). Three categorical traits (flower visitor, preferred host tree and habitat type) were based on expert estimates, whereas two continuous traits (canopy niche and decay niche) were estimated as the mean niche position of individual species weighted by their occurrence probabilities (for more details, see Gossner et al., 2013). Additionally, we included nine morphological traits (taken from Hagge et al., 2021), characterizing five important aspects of ecological function in beetles (colour, body shape, locomotion, sensory and foraging; Table 1). Each of these traits was measured using a standardized protocol of trait measurements (Moretti et al., 2017). All the morphological measurements had strong phylogenetic signal (Pagel's lambda ranging from 0.53 to 0.97; Hagge et al., 2021) and, except for colour, were highly correlated with body length. Therefore, they were log-transformed and then standardized for body length by fitting a phylogenetic generalized least squares regression following Hagge et al. (2021). The traits within both sets (ecological and morphological) were only weakly correlated ($r < 0.67$; VIF < 2.7 ; Figures S3 and S4).

For species missing one or more ecological or morphological traits, different approaches were used to estimate those values (see Appendix S2). To check the robustness of the results with the estimated missing trait values, we repeated the analyses excluding the species containing any missing values and compared the results (Appendix S3).

2.4 | Data analyses

We used Bayesian joint species distribution models (JSDMs) from the Hierarchical Model of Species Communities (HMSC; Tikhonov et al., 2020) R-package (R Core Team, 2020) to estimate the role

of traits in species' responses to the environment. We excluded species present in five or fewer traps because they were too rare to reliably estimate niches (Ovaskainen & Abrego, 2020). We fitted presence/absence models with a probit link function, including nine environmental characteristics as fixed effects. To account for the hierarchical structure of the study design (plots clustered within five regions in Germany and regions sampled in different years), we included region as a random effect. To account for the spatial autocorrelation of the plots within each region, we also included a spatially explicit random effect on the level of individual plots using their GPS coordinates. To avoid overly complex models by combining many continuous and categorical traits in the same model, we analysed ecological and morphological traits separately in two independent models. In both models, we included traits as a hierarchical level to estimate how species traits influence their responses to environmental variation. To account for possible phylogenetic correlations in the species' responses to the environmental variables, beyond that explained by traits included in the analyses (Ovaskainen & Abrego, 2020), a saproxylic beetle phylogeny derived from Hagge et al. (2021) was included in both models.

We fitted the models with Bayesian inference using the default prior distributions of Tikhonov et al. (2020) except that the prior distribution of spatial random effect was modified to span only the range of distances (up to 40 km) which was well represented within each of the regions. For each model, we sampled the posterior distribution with eight Markov chain Monte Carlo (MCMC) chains, each of which was run for 20,000 iterations, out of which the first 15,000 were removed as burn-in. The iterations were thinned by 40 to yield 125 posterior samples per chain, and thus 1000 posterior samples in total. We assessed effective sample size (ESS) to assure adequate independence of samples, and potential scale reduction factors (Gelman & Rubin, 1992) to assure model convergence. Model fitting was conducted with high-performance computational resources provided by Würzburg University.

We explored the explanatory power of the model by computing the species-specific AUCs (area under the curves), measuring how well the models distinguished between the presences and absences of the species. To assess the extent of overfitting of the fixed effects, we performed a two-fold cross-validation, in which the sampling units were assigned randomly to two folds and predictions for each fold were based on a model fitted to data on the other fold. The proportion of total variation explained by fixed effect covariates and the random effect was assessed by variance partitioning (Ovaskainen & Abrego, 2020).

For each species, HMSC models include beta (β) parameters which reflect how environmental covariates (e.g. topographic, climatic and forest structure) influence that species' occurrence probability (i.e. that species' niche; Ovaskainen & Abrego, 2020). Niches of each species are not estimated entirely independently from each other but rather may depend on species traits via a hierarchical level in the models. These relationships between traits and niches are estimated by gamma (γ) parameters. At this level, the phylogenetic

signal of residual variation in the effect of measured traits on species niches (i.e. the effect of missing species traits) is captured by the rho (ρ) parameter. In other words, rho ($0 < \rho < 1$) measures the phylogenetic signal in species niches after accounting for the measured traits. High signal suggests that some missing but phylogenetically structured traits explain variation in species niches (β), whereas low signal means that any relevant but unmeasured traits are randomly distributed in the phylogeny.

For both models, we estimated the beta, gamma and rho parameters. To understand the species–environment relationships, we extracted the signs of beta parameters and compared the percentage of all species showing positive or negative responses to each environmental covariate with at least 95% posterior probability. To address the trait–environment relationships, we extracted the signs of gamma parameters (positive, negative or no response) with at least 95% posterior probability. We also provided the relaxed level of statistical support (85% posterior probability) to observe even the less supported trait–environmental relationships. Finally, we extracted the median value of rho parameter with its 95% credible interval (i.e. the Bayesian 95% confidence interval).

To examine the effects of environmental gradients on community-weighted mean traits, we made model predictions across a gradient of each of five ALS-based characteristics (focal variables) in our fitted model. Across each focal variable gradient, all other environmental covariates were fixed to their mean value.

3 | RESULTS

In 384 plots, we detected 519 saproxylic beetle species. Of these, we selected 233 species that were present in more than five plots for inclusion in two JSDMs containing ecological traits and morphological traits respectively. The mean explanatory power of each model (mean AUC over species) was 0.90 and 0.91 respectively. The mean predictive power of both models (based on the cross-validation) was

expectedly smaller than the explanatory powers (AUC = 0.78 and 0.76 respectively).

Out of the explained variance, fixed effects explained 76% and 82% in the ecological and morphological model respectively (Figure 2). The most important covariate was elevation (26%) in the ecological model, followed by proportion of conifers and canopy/vegetation density (8%–13%). In the morphological model, the most important covariates were vegetation density (34%) and elevation (24%).

3.1 | Species niches

Individual species responses were mainly influenced by elevation and proportion of conifers in both models (β parameter; Figure 3). Specifically, 41% of species ($n = 95$) in the ecological trait model and 28% of species ($n = 65$) in the morphological trait model responded negatively to elevation, whereas a positive response was recorded for only 6% ($n = 14$) and 9% ($n = 20$) of species respectively. Regarding proportion of conifers, 12% of species ($n = 28$) responded negatively and 31% ($n = 72$) positively in the ecological model, while 15% ($n = 35$) responded negatively and 9% ($n = 22$) positively in the morphological model. Deadwood characteristics (deadwood richness and deadwood structure) and terrain roughness affected occurrences of the fewest saproxylic beetle species.

3.2 | Species traits

We found that a rather large part of the variation among species niches was explained by traits in the ecological model (with the proportion of conifers and elevation as the most dominant ones), while the traits in the morphological model explained much less (Table S2).

In the ecological trait model, we recorded 12 relationships between species traits and responses to environmental characteristics

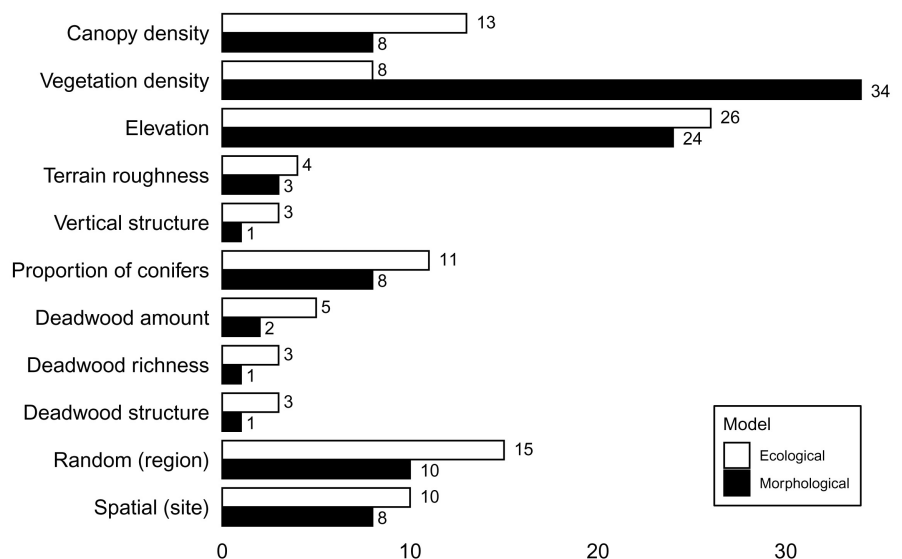


FIGURE 2 The % of variance explained by nine fixed effect covariates and two random effects (region and site). Based on the results of variance partitioning on models that included ecological traits (white) and morphological traits (black) of saproxylic beetle species (package HMSC; Tikhonov et al., 2020).

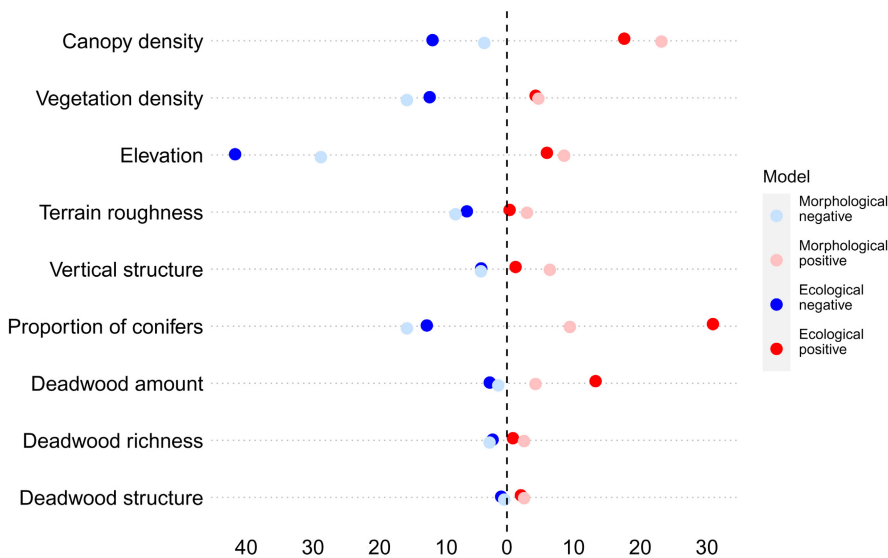


FIGURE 3 Percentage of all beetle species showing positive (red) and negative (blue) responses to the environmental covariates with at least 95% posterior probability. Light and dark colours represent models based on the morphological and ecological traits respectively ($N_{\text{species}} = 233$).

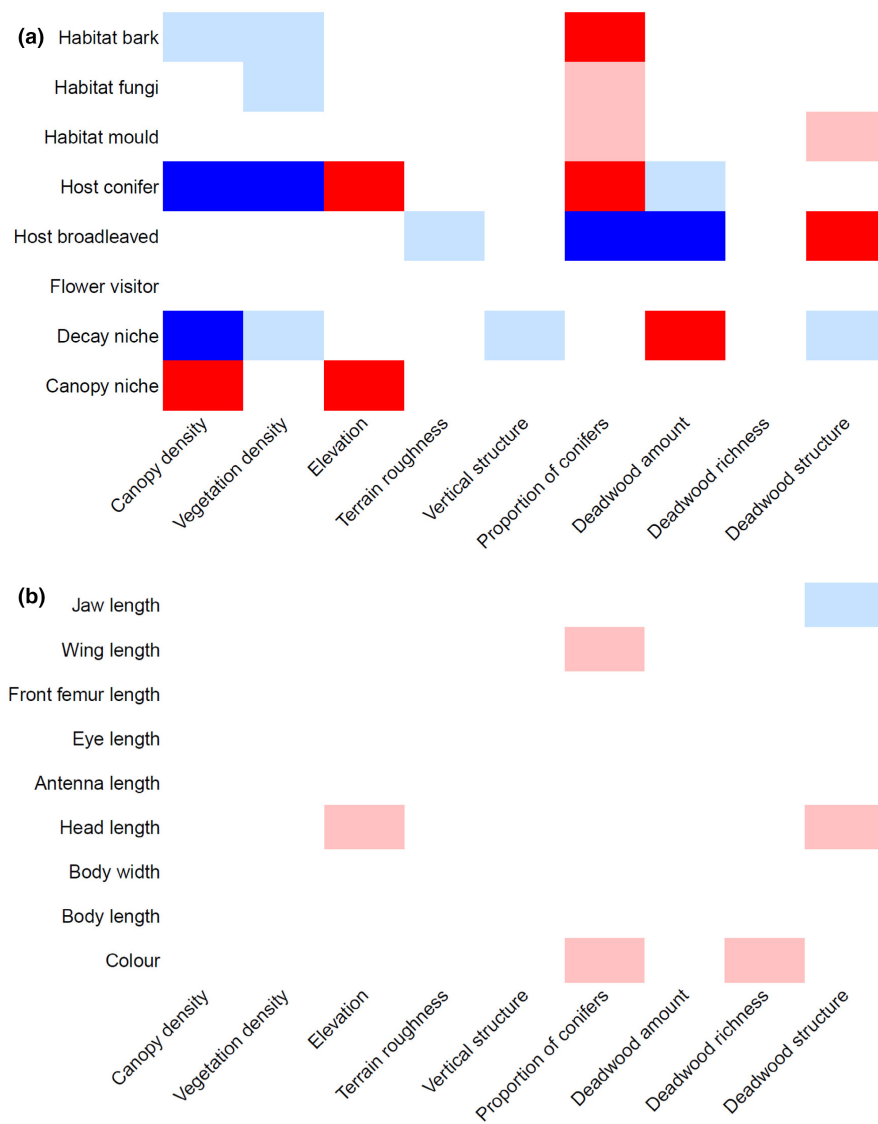


FIGURE 4 Heat map of the gamma (γ) parameter, representing the effects of species traits on species niches (responses to environmental characteristics). Based on models that included (a) ecological traits and (b) morphological traits. The direction of each response is given by the colour (positive: red, negative: blue, no response: white) while the colour intensity represents 95% (dark) and 85% (light) posterior probability. Mean values of γ parameter are given in the supplementary (Tables S3 and S4).

(γ parameter) that differed from zero with at least 95% posterior probability (Figure 4a). For example, as we expected, the occurrence probabilities of species associated with more shady conditions

increased with increasing canopy density, but also with elevation. Furthermore, the occurrence probabilities of species associated with more decomposed wood decreased with canopy density and

increased with increasing deadwood amount, whereas the occurrence probabilities of species associated with broadleaved trees decreased with the higher proportion of conifers and higher deadwood amount and increased with deadwood structure. All associations are listed in Figure 4a. Model predictions supported the above-mentioned relationships between species traits and responses to environmental characteristics, and additionally suggested the changes in the proportion of species occurring in different habitats along the elevation gradient (Figure S5).

In the morphological model, no association (95% posterior probability) between traits and niches was revealed (Figure 4b). Furthermore, the predicted community-weighted mean body size did not change along any of the five ALS-derived gradients (Figure S6).

3.3 | Phylogenetic signal

The residual phylogenetic signal in species niches (after accounting for the measured traits) was intermediate for both models. The median value of the posterior distribution of the ρ parameter was 0.57 (95% CI: 0.43–0.68) for the ecological model and 0.21 (0.04–0.52) for the morphological model. Therefore, more phylogenetically correlated niche-determining traits were missing from the ecological model than from the morphological.

4 | DISCUSSION

Recently, much ecological research has shifted in perspective from taxonomy to function, with successful application of trait-based approaches (Cernansky, 2017). Whereas ecological traits have proven to be useful in studying beetles' responses to the environments (Fountain-Jones et al., 2015), morphological traits have been employed very rarely (e.g. Barton et al., 2011; Burner, Stephan, Drag, et al., 2021). In this study, we thus linked for the first-time detailed ALS- and field-derived topographic, climatic and forest variables with the independent effects of multiple ecological and morphological traits on saproxylic beetle community assembly.

4.1 | Occurrence probability along the environmental gradients

Environmental heterogeneity increases the number of unique habitat types, amounts of resources and overall structural complexity of forests. Therefore, with increasing environmental heterogeneity, there is often an increase in species richness across different taxa (Stein et al., 2014). Accordingly, it has been shown that species richness of saproxylic beetles increases with deadwood, as well as with vertical, horizontal and topographic heterogeneity (Heidrich et al., 2020). Our results, however, indicate that many of these variables had only marginal effects on the occurrences of saproxylic species. For example, deadwood heterogeneity (represented by

the taxonomic and structural richness of deadwood) increased occurrence for fewer than 3% of the species. Similarly, vertical and topographic heterogeneity (represented by vertical structure and terrain roughness respectively) increased occurrence for only 7% and 3% of the species respectively. It seems that whereas variables characterizing environmental heterogeneity often increase the species richness of local beetle assemblages, only a few species respond strongly to that increase and their occurrences are mostly driven by other environmental characteristics such as temperature, host tree diversity or canopy density. This may be because of often-specific local habitat requirements such as species' close relationship with specific host fungi species (Thorn et al., 2015); host tree species (Burner, Birkemoe, Stephan, et al., 2021); tree hollow microenvironmental characteristics (Quinto et al., 2014); and decay stage, diameter and tree species of deadwood (Speight, 1989).

4.2 | Scale dependency of ALS variables

Our study was novel in its inclusion of several ALS-derived environmental covariates as well as those based on ground measurements. As the effects of many environmental characteristics are scale dependent (Levin, 1992), an advantage of ALS technology is that it provides the opportunity for researchers to summarize values at the scale of choice from the tree to the landscape level. For example, using the ALS data, it has been shown that arthropod diversity increased with canopy density at the tree scale, but decreased with increasing canopy density at the stand scale (Müller et al., 2014). Similarly, the effects on functional diversity might be also scale dependent. On the one hand, it has been shown that the functional diversity of saproxylic beetles is driven mainly on the regional level, whereas local diversity simply mirrors those patterns (Hagge et al., 2019). In that case, large-scale forest characteristics could be more relevant, as observed for example in naturally disturbed forests (Cours et al., 2021). On the other hand, the importance of variables directly characterizing the beetle species occurrences and their relationship to specific microhabitats has also been emphasized (Dolek et al., 2009; Micó et al., 2020). Such variables, however, cannot be observed directly with ALS, so ALS must be combined with local measurements. This combined approach has proved valuable in assessing habitat for birds (Hinsley et al., 2002), mammals (Melin et al., 2013) and insects (Müller & Brandl, 2009) and is likely to continue to be a fruitful method in the search for trait–environment relationships.

4.3 | Ecological traits

Despite the theoretical link between species' traits and their response to the environment (Winemiller et al., 2015), studies quantifying such links across taxa have had mixed success (Burner, Stephan, Drag, et al., 2021; Raine et al., 2018; Yates et al., 2014). Our model including ecological traits showed a rather high number

of non-random associations between species traits and individual forest, climatic and topographic characteristics. This is not so surprising as ecological traits are 'emergent' traits resulting from complex combinations of phenotypic characteristics that reflect required resources and thus link species mechanistically to potential habitats (Violle et al., 2007). Therefore, ecological traits, when available, seem to represent a good option with their high ability to predict future species responses to environmental changes (Gossner et al., 2013; Laaksonen et al., 2020). As such, they have been used to study the changes of functional diversity under different habitat conditions (Hagge et al., 2019; Thorn et al., 2014) or to predict species' extinction risk (Seibold et al., 2015).

Despite their usefulness in predictions, however, ecological traits do little to advance our understanding of the link between the functional traits and species niches, one of the primary goals of trait-informed ecology (de Bello et al., 2021). Most of our revealed relationships between species' ecological traits and environmental characteristics were in line with forest variables that can for simplicity be characterized as a gradient between low elevation broadleaved forest with high canopy density and relatively low amounts of deadwood, and high elevation conifer-dominated forest with open canopy and more deadwood (often caused by bark beetle disturbances; Müller, Stadler, et al., 2010; Müller, Noss, et al., 2010). For example, species preferring more decomposed wood (high decay niche) increased in occurrence in forests with large amounts of deadwood but decreased in occurrence under high canopy density. Similarly, species associated with conifers (host conifer) increased at higher elevations and with increased proportion of conifers and decreased in forests with high vegetation and canopy density. Although somewhat trivial, these trait–niche associations represent an empirical validation of the reliability of our JSDM methods and of these beetle trait classifications based on the expert opinion. Similar results considering beetle–host tree association estimates were also obtained from Nordic forests (Burner, Birkemoe, Stephan, et al., 2021), further validating the expert estimates for saproxylic beetle traits.

4.4 | Morphological traits

The lack of associations between morphological traits and species niches in our dataset was in spite of our use of the most complete and diverse database for saproxylic beetles (Hagge et al., 2021). This highlights the difficulty in discovering the direct trait–niche links in beetles. In bird and bat assemblages, however, morphological measurements (particularly body mass and wing and beak/mouth-related characteristics) have been good predictors of various habitats (e.g. Byamungu et al., 2021; Conenna et al., 2021; Neate-Clegg et al., 2021). Body size is generally considered to be a fundamental trait in species biology potentially related to many environmental characteristics (Peters, 1983). In saproxylic beetles, mean body length increased with increasing amounts of deadwood (Gossner et al., 2013; Janssen et al., 2017). Larger species are known to be at an increased risk of extinction in birds, fish

and mammals (Chichorro et al., 2019) as well as in beetles (Hagge et al., 2021), although smaller species appear to be more susceptible to certain threats. Therefore, further investigations into morphological traits and their relationships to species niches are needed to advance trait-based ecology. The growing number of trait databases available for a variety of vertebrate and invertebrate taxa (Moretti et al., 2017; Tobias, 2022) promises further developments in this field.

4.5 | Study limitations

Despite the lack of signal in morphological traits in our dataset, our results support the theoretical expectation that morphology can help predict species niches (de Bello et al., 2021). We found intermediate residual phylogenetic signal in species niches in both of our models implying that some phylogenetically correlated traits influencing species' responses to environmental characteristics were missing from both analyses (Ovaskainen & Abrego, 2020). For example, additional traits related to species physiology, such as ability to perceive various chemical compounds (Elgar et al., 2018), the gut microbial assemblages (Birkemoe et al., 2018) or thermal tolerance (Hof, 2021), could perhaps better predict niches. Further research would thus be useful to better identify these relevant traits. In the meantime, ecological investigations that include both species traits and their phylogenetic relationships are likely to be more informative than studies based on traits alone.

Ecological studies often strive to understand the distributions and habitat requirements of rare species because such species are often of the highest conservation concern and risk of extinction (Lennon et al., 2011; Säterberg et al., 2019). One limitation of our study, as in any study of diverse organisms, was that rare species were by their nature poorly represented (Burner, Birkemoe, Åström, et al., 2021), and our JSDM required exclusion of those present in only a few traps (Ovaskainen & Abrego, 2020). Therefore, limitations of our sampling strategy make it difficult to know if our findings hold for the rarest species, which often possess unique combinations of traits (Burner et al., 2022).

5 | CONCLUSIONS

Although species traits can provide valuable insights into the niches and ecology of forest taxa, linking simple morphological traits to species' complex ecological requirements remains a challenge. Moreover, the rather strong phylogenetic signal in species niches implies that additional relevant traits can be identified, and that phylogenies may serve as suitable proxies in the meantime (Hof et al., 2010; Liu et al., 2015). Additional work could clarify the extent to which trait–niche relationships detected in well-sampled species can be used to make informed estimates of the ecology of rare and poorly known species. Combining niche-based approaches with remote sensing methods across a variety of taxa could increase our

ability to understand the factors driving species distributions, and to better predict the impacts of future climate and land use changes.

AUTHOR CONTRIBUTIONS

Jörg Müller supervised the project; Lukas Drag and Jörg Müller designed methodology; Jörg Müller, Peter Schall and Wolfgang Weisser collected the data; Paul Magdon processed the ALS data; Lukas Drag analysed the data; Lukas Drag and Mária Potterf visualized the data; Lukas Drag and Jörg Müller wrote the manuscript—original draft; Ryan C. Burner, Jörg G. Stephan, Tone Birkemoe, Inken Doerfler, Martin M. Gossner, Paul Magdon, Otso Ovaskainen, Mária Potterf, Peter Schall, Jörg G. Stephan, Tord Snäll, Anne Sverdrup-Thygeson and Wolfgang Weisser reviewed and edited the later versions. All the authors contributed substantially to the final version and gave final approval for publications.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data deposited in the Dryad Digital Repository <https://doi.org/10.5061/dryad.f4qrj707> (Drag et al., 2022).

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REFERENCES

- Bae, S., Levick, S., Heidrich, L., Magdon, P., Leutner, B., Wöllauer, S., Serebryanyk, A., Nauss, T., Krzystek, P., Gossner, M., Schall, P., Heibl, C., Bässler, C., Doerfler, I., Schulze, E., Krah, F., Culumsee, H., Jung, K., Heurich, M., ... Müller, J. (2019). Radar vision in the mapping of forest biodiversity from space. *Nature Communications*, *10*, 4757.
- Barton, P. S., Gibb, H., Manning, A. D., Lindenmayer, D. B., & Cunningham, S. A. (2011). Morphological traits as predictors of diet and microhabitat use in a diverse beetle assemblage. *Biological Journal of the Linnean Society*, *102*, 301–310.
- Bässler, C., Förster, B., Moning, C., & Müller, J. (2009). The BIOKLIM project: Biodiversity research between climate change and wilding in a temperate montane forest—The conceptual framework. *Waldökologie Landschaftsforschung und Naturschutz*, *7*, 21–23.
- Birkemoe, T., Jacobsen, R. M., Sverdrup-Thygeson, A., & Biedermann, P. H. W. (2018). Insect-fungus interactions in dead Wood Systems. In M. Ulyshen (Ed.), *Saproxylis insects*. *Zoological monographs* (Vol. 1). Springer.
- Bouget, C., Larrieu, L., Nusillard, B., & Parmain, G. (2013). In search of the best local habitat drivers for saproxylis beetle diversity in temperate deciduous forests. *Biodiversity and Conservation*, *22*, 2111–2130.
- Burner, R. C., Birkemoe, T., Åström, J., & Sverdrup-Thygeson, A. (2021). Flattening the curve: Approaching complete sampling for diverse beetle communities. *Insect Conservation and Diversity*, *15*, 157–167.
- Burner, R. C., Birkemoe, T., Stephan, J. G., Drag, L., Muller, J., Ovaskainen, O., Potterf, M., Skarpaas, O., Snäll, T., & Sverdrup-Thygeson, A. (2021). Choosy beetles: How host trees and southern boreal forest naturalness may determine dead wood beetle communities. *Forest Ecology and Management*, *487*, 119023.
- Burner, R. C., Drag, L., Stephan, J., Birkemoe, T., Wetherbee, R., Muller, J., Siitonen, J., Snäll, T., Skarpaas, O., Potterf, M., Doerfler, I., Gossner, M., Schall, P., Weisser, W., & Sverdrup-Thygeson, A. (2022). Functional structure of European forest beetle communities is enhanced by rare species. *Biological Conservation*, *267*, 109491.
- Burner, R. C., Stephan, J. G., Drag, L., Birkemoe, T., Muller, J., Snäll, T., Ovaskainen, O., Potterf, M., Siitonen, J., Skarpaas, O., Doerfler, I., Gossner, M., Schall, P., Weisser, W., & Sverdrup-Thygeson, A. (2021). Traits mediate niches and co-occurrences of forest beetles in ways that differ among bioclimatic regions. *Journal of Biogeography*, *48*, 3145–3157.
- Byamungu, R. M., Schleuning, M., Ferger, S. W., Helbig-Bonitz, M., Hemp, A., Neu, A., Vogeler, A., Böhning-Gaese, K., Tschapka, M., & Albrecht, J. (2021). Abiotic and biotic drivers of functional diversity and functional composition of bird and bat assemblages along a tropical elevation gradient. *Diversity and Distributions*, *27*, 2344–2356.
- Cernansky, R. (2017). The biodiversity revolution. *Nature*, *546*, 22–24.
- Chichorro, F., Juslén, A., & Cardoso, P. (2019). A review of the relation between species traits and extinction risk. *Biological Conservation*, *237*, 220–229.
- Conenna, I., Santini, L., Rocha, R., Monadjem, A., Cabeza, M., & Russo, D. (2021). Global patterns of functional trait variation along aridity gradients in bats. *Global Ecology and Biogeography*, *30*, 1014–1029.
- Cours, J., Sire, L., Ladet, S., Martin, H., Parmain, G., Larrieu, L., Moliard, C., Lopez-Vaamonde, C., & Bouget, C. (2021). Drought-induced

- forest dieback increases taxonomic and functional diversity but not phylogenetic diversity of saproxylic beetles at both local and landscape scales. *Landscape Ecology*, 37, 2025–2043.
- Davies, A. B., & Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology & Evolution*, 29, 681–691.
- de Bello, F., Carmona, C. P., Dias, A. T., Götzenberger, L., Moretti, M., & Berg, M. P. (2021). *Handbook of trait-based ecology*. Cambridge University Press.
- Doerfler, I., Gossner, M. M., Müller, J., Seibold, S., & Weisser, W. W. (2018). Deadwood enrichment combining integrative and segregative conservation elements enhances biodiversity of multiple taxa in managed forests. *Biological Conservation*, 228, 70–78.
- Dolek, M., Freese-Hager, A., Bussler, H., Floren, A., Liegl, A., & Schmidl, J. (2009). Ants on oaks: Effects of forest structure on species composition. *Journal of Insect Conservation*, 13, 367–375.
- Drag, L., Burner, R. C., Stephan, J., Birkemoe, T., Doerfler, I., Gossner, M. M., Magdon, P., Ovaskainen, O., Potterf, M., Schall, P., Snäll, T., Weisser, W., Sverdrup-Thygeson, A., & Müller, J. (2022). High resolution 3D forest structure explains ecomorphological trait variation in assemblages of saproxylic beetles. *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.f4qrj707>
- Elgar, M., Zhang, D., Wang, Q., Wittwer, B., Pham, H. T., Johnson, T. L., Freelance, C. B., & Coquilleau, M. P. (2018). Insect antennal morphology: The evolution of diverse solutions to odorant perception. *The Yale Journal of Biology and Medicine*, 91, 457–469.
- Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., Hessenmöller, D., Korte, G., Nieschulze, J., Pfeiffer, S., Prati, D., Renner, S. C., Schöning, I., Schumacher, U., Wells, K., Buscot, F., Kalko, E. K., Linsenmair, K. E., Schulze, E., & Weisser, W. W. (2010). Implementing large-scale and long-term functional biodiversity research: The biodiversity Exploratories. *Basic and Applied Ecology*, 11, 473–485.
- Fountain-Jones, N., Baker, S. C., & Jordan, G. J. (2015). Moving beyond the guild concept: Developing a practical functional trait framework for terrestrial beetles. *Ecological Entomology*, 40, 1–13.
- Freude, H., Harde, K., & Lohse, G. A. (1983). *Die Käfer Mitteleuropas*. Goecke and Evers.
- Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical Science*, 7, 457–472.
- Gillespie, M., Birkemoe, T., & Sverdrup-Thygeson, A. (2017). Interactions between body size, abundance, seasonality, and phenology in forest beetles. *Ecology and Evolution*, 7, 1091–1100.
- Gossner, M., Lachat, T., Brunet, J., Isacsson, G., Bouget, C., Brustel, H., Brandl, R., Weisser, W., & Müller, J. (2013). Current near-to-nature forest management effects on functional trait composition of saproxylic beetles in beech forests. *Conservation Biology: The journal of the Society for Conservation Biology*, 27(3), 605–614.
- Gouveia, S. F., Villalobos, F., Dobrovolski, R., Beltrao-Mendes, R., & Ferrari, S. F. (2014). Forest structure drives global diversity of primates. *Journal of Animal Ecology*, 83, 1523–1530.
- Hagge, J., Abrego, N., Bässler, C., Bouget, C., Brin, A., Brustel, H., Christensen, M., Gossner, M. M., Heilmann-Clausen, J., Horák, J., Gruppe, A., Isacsson, G., Köhler, F., Lachat, T., Larrieu, L., Schlaghamersky, J., Thorn, S., Zapponi, L., & Müller, J. (2019). Congruent patterns of functional diversity in saproxylic beetles and fungi across European beech forests. *Journal of Biogeography*, 46(5), 1054–1065.
- Hagge, J., Müller, J., Birkemoe, T., Buse, J., Christensen, R. H., Gossner, M., Gruppe, A., Heibl, C., Jarzabek-Müller, A., Seibold, S., Siitonen, J., Soutinho, J. G., Sverdrup-Thygeson, A., Thorn, S., & Drag, L. (2021). What does a threatened saproxylic beetle look like? Modelling extinction risk using a new morphological trait database. *The Journal of Animal Ecology*, 90, 1934–1947.
- Heidrich, L., Bae, S., Levick, S., Seibold, S., Weisser, W., Krzystek, P., Magdon, P., Nauss, T., Schall, P., Serebryanyk, A., Wöllauer, S., Ammer, C., Bässler, C., Doerfler, I., Fischer, M., Gossner, M., Heurich, M., Hothorn, T., Jung, K., ... Müller, J. (2020). Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests. *Nature Ecology & Evolution*, 4, 1–9.
- Hinsley, S. A., Hill, R. A., Gaveau, D. L., & Bellamy, P. E. (2002). Quantifying woodland structure and habitat quality for birds using airborne laser scanning. *Functional Ecology*, 16, 851–857.
- Hodkinson, I. (2005). Terrestrial insects along elevation gradients: Species and community responses to altitude. *Biological Reviews*, 80, 489–513.
- Hof, C. (2021). Towards more integration of physiology, dispersal and land-use change to understand the responses of species to climate change. *Journal of Experimental Biology*, 224, jeb238352.
- Hof, C., Rahbek, C., & Araújo, M. B. (2010). Phylogenetic signals in the climatic niches of the world's amphibians. *Ecography*, 33, 242–250.
- Janssen, P., Fuhr, M., Cateau, E., Nusillard, B., & Bouget, C. (2017). Forest continuity acts congruently with stand maturity in structuring the functional composition of saproxylic beetles. *Biological Conservation*, 205, 1–10.
- Jung, K., Kaiser, S., Böhm, S. M., Nieschulze, J., & Kalko, E. K. (2012). Moving in three dimensions: Effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. *Journal of Applied Ecology*, 49, 523–531.
- Köhler, F. (2000). *Totholzkäfer in Naturwaldzellen des nördlichen Rheinlands*. Schriftenreihe der Landesanstalt für Ökologie, Bodenordnung und Forsten/Landesamt für Agrarordnung Nordrhein-Westfalen.
- Komonen, A., & Müller, J. (2018). Dispersal ecology of deadwood organisms and connectivity conservation. *Conservation Biology*, 32, 535–545.
- Kuuluvainen, T., & Siitonen, J. (2013). Fennoscandian boreal forests as complex adaptive systems. Properties, management challenges and opportunities. In C. Messier, K. J. Puettman, & K. D. Coates (Eds.), *Managing forests as complex adaptive systems. Building resilience to the challenge of global change* (pp. 244–268). Routledge, Earthscan.
- Laaksonen, M., Punttila, P., Siitonen, J., & Ovaskainen, O. (2020). Saproxylic beetle assemblages in recently dead scots pines: How traits modulate species' response to forest management? *Forest Ecology and Management*, 473, 118300.
- Lachat, T., Wermelinger, B., Gossner, M. M., Bussler, H., Isacsson, G., & Müller, J. (2012). Saproxylic beetles as indicator species for dead-wood amount and temperature in European beech forests. *Ecological Indicators*, 23, 323–331.
- Lennon, J. J., Beale, C. M., Reid, C. L., Kent, M., & Pakeman, R. J. (2011). Are richness patterns of common and rare species equally well explained by environmental variables. *Ecography*, 34, 529–539.
- Levin, S. A. (1992). The problem of pattern and scale in ecology: The Robert H. MacArthur Award Lecture. *Ecology*, 73, 1943–1967.
- Liu, H., Xu, Q., He, P., Santiago, L. S., Yang, K., & Ye, Q. (2015). Strong phylogenetic signals and phylogenetic niche conservatism in ecophysiological traits across divergent lineages of Magnoliaceae. *Scientific Reports*, 5, 12246.
- McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.
- Melin, M., Packalen, P., Matala, J., Mehtätalo, L., & Puseenius, J. (2013). Assessing and modeling moose (*Alces alces*) habitats with airborne laser scanning data. *International Journal of Applied Earth Observation and Geoinformation*, 23, 389–396.
- Micó, E., Ramilo, P., Thorn, S., Müller, J., Galante, E., & Carmona, C. P. (2020). Contrasting functional structure of saproxylic beetle assemblages associated to different microhabitats. *Scientific Reports*, 10, 1520.
- Möller, G. (2009). *Struktur und Substratbindung holzbewohnender Insekten, Schwerpunkt Coleoptera -Käfer*. Freie Universität Berlin.
- Moretti, M., Dias, A. T. C., de Bello, F., Altermatt, F., Chown, S. L., Azcárate, F. M., Bell, J. R., Fournier, B., Hedde, M., Hortal, J., Ibanez, S., Öckinger, E., Sousa, J. P., Ellers, J., & Berg, M. P. (2017).

- Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, 31(3), 558–567.
- Müller, J., Bae, S., Röder, J., Chao, A., & Didham, R. K. (2014). Airborne LiDAR reveals context dependence in the effects of canopy architecture on arthropod diversity. *Forest Ecology and Management*, 312, 129–137.
- Müller, J., & Brandl, R. (2009). Assessing biodiversity by remote sensing in mountainous terrain: The potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology*, 46, 897–905.
- Müller, J., Noss, R., Bussler, H., & Brandl, R. (2010). Learning from a benign neglect strategy in a national park: Response of saproxylic beetles to dead wood accumulation. *Biological Conservation*, 143, 2559–2569.
- Müller, J., Stadler, J., & Brandl, R. (2010). Composition versus physiognomy of vegetation as predictors of bird assemblages: The role of lidar. *Remote Sensing of Environment*, 114(3), 490–495.
- Müller, J., Ulyshen, M., Seibold, S., Cadotte, M., Chao, A., Bässler, C., Vogel, S., Hagge, J., Weiss, I., Baldrian, P., Tláškal, V., & Thorn, S. (2020). Primary determinants of communities in deadwood vary among taxa but are regionally consistent. *Oikos*, 129, 1579–1588.
- Naimi, B., Hamm, N. A. S., Groen, T. A., Skidmore, A. K., & Toxopeus, A. G. (2014). Where is positional uncertainty a problem for species distribution modelling? *Ecography*, 37(2), 191–203.
- Neate-Clegg, M. H., Jones, S. E., Tobias, J. A., Newmark, W. D., & Şekercioğlu, Ç. H. (2021). Ecological correlates of elevational range shifts in tropical birds. *Frontiers in Ecology and Evolution*, 9, 621749.
- Ovaskainen, O., & Abrego, N. (2020). *Joint species distribution modelling: With applications in R*. Cambridge University Press.
- Peters, R. H. (1983). *The ecological implications of body size*. Cambridge University Press.
- Quinto, J., Micó, E., Martínez-Falcón, A., Galante, E., & Marcos-garcía, M. (2014). Influence of tree hollow characteristics on the diversity of saproxylic insect guilds in Iberian Mediterranean woodlands. *Journal of Insect Conservation*, 18, 981–992.
- R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-project.org>
- Raine, E. H., Gray, C. L., Mann, D. J., & Slade, E. M. (2018). Tropical dung beetle morphological traits predict functional traits and show intraspecific differences across land uses. *Ecology and Evolution*, 8, 8686–8696.
- Rinker, H. B., Lowman, M. D., Hunter, M. D., Schowalter, T. D., & Fonte, S. J. (2001). Literature review: Canopy herbivory and soil ecology, the top-down impact of forest processes. *Selbyana*, 22(2), 225–231.
- Säterberg, T., Jonsson, T., Yearsley, J., Berg, S., & Ebenman, B. (2019). A potential role for rare species in ecosystem dynamics. *Scientific Reports*, 9, 11107.
- Schmidl, J., & Bussler, H. (2004). Ökologisches Gilden xylobionter Käfer Deutschlands. *Naturschutz Und Landschaftsplanung*, 36(7), 202–218.
- Seibold, S., Brandl, R., Buse, J., Hothorn, T., Schmidl, J., Thorn, S., & Müller, J. (2015). Association of extinction risk of saproxylic beetles with ecological degradation of forests in Europe. *Conservation Biology*, 29(2), 382–390.
- Speight, M. C. D. (1989). Saproxylic invertebrates and their conservation. *Council of Europe, Nature and Environment Series*, 42, 1–79.
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17(7), 866–800.
- Talarico, F., Roméo, M., Massolo, A., Brandmayr, P., & Zetto, T. (2007). Morphometry and eye morphology in three species of *Carabus* (Coleoptera: Carabidae) in relation to habitat demands. *Journal of Zoological Systematics and Evolutionary Research*, 45, 33–38.
- Thorn, S., Bässler, C., Gottschalk, T., Hothorn, T., Bussler, H., Raffa, K., & Müller, J. (2014). New insights into the consequences of post-windthrow salvage logging revealed by functional structure of saproxylic beetles assemblages. *PLoS ONE*, 9(7), e101757.
- Thorn, S., Müller, J., Bässler, C., Gminder, A., Brandl, R., & Heibl, C. (2015). Host abundance, durability, basidiome form and phylogenetic isolation determine fungivore species richness. *Biological Journal of the Linnean Society*, 114, 699–708.
- Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehtikoinen, A., de Jonge, M. M. J., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the r-package Hmsc. *Methods in Ecology and Evolution*, 11(3), 442–447.
- Tobias, J. A. (2022). A bird in the hand: Global-scale morphological trait datasets open new frontiers of ecology, evolution and ecosystem science. *Ecology Letters*, 25(3), 573–580.
- True, J. R. (2003). Insect melanism: The molecules matter. *Trends in Ecology & Evolution*, 18, 640–647.
- Trullas, S. C., Wyk, J. H., & Spotila, J. R. (2007). Thermal melanism in ectotherms. *Journal of Thermal Biology*, 32, 235–245.
- Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional. *Oikos*, 116, 882–892.
- Wetherbee, R., Birkemoe, T., Skarpaas, O., & Sverdrup-Thygeson, A. (2020). Hollow oaks and beetle functional diversity: Significance of surroundings extends beyond taxonomy. *Ecology and Evolution*, 10, 819–831.
- Winemiller, K. O., Fitzgerald, D. B., Bower, L. M., & Pianka, E. R. (2015). Functional traits, convergent evolution, and periodic tables of niches. *Ecology Letters*, 18, 737–751.
- Yates, M., Andrew, N. R., Binns, M. R., & Gibb, H. (2014). Morphological traits: Predictable responses to macrohabitats across a 300 km scale. *PeerJ*, 2, e271.

SUPPORTING INFORMATION

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

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