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RESEARCH ARTICLE

Traits mediate niches and co-occurrences of forest beetles in ways that differ among bioclimatic regions

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Abstract

Aim: The aim of this study was to investigate the role of traits in beetle community assembly and test for consistency in these effects among several bioclimatic regions. We asked (1) whether traits predicted species' responses to environmental gradients (i.e. their niches), (2) whether these same traits could predict co-occurrence patterns and (3) how consistent were niches and the role of traits among study regions.

Location: Boreal forests in Norway and Finland, temperate forests in Germany.

Taxon: Wood-living (saproxylic) beetles.

Methods: We compiled capture records of 468 wood-living beetle species from the three regions, along with nine morphological and ecological species traits. Eight climatic and forest covariates were also collected. We used Bayesian hierarchical joint species distribution models to estimate the influence of traits and phylogeny on species' niches. We also tested for correlations between species associations and trait similarity. Finally, we compared species niches and the effects of traits among study regions.

Results: Traits explained some of the variability in species' niches, but their effects differed among study regions. However, substantial phylogenetic signal in species

niches implies that unmeasured but phylogenetically structured traits have a stronger effect. Degree of trait similarity was correlated with species associations but depended idiosyncratically on the trait and region. Species niches were much more consistent—widespread taxa often responded similarly to an environmental gradient in each region.

Main conclusions: The inconsistent effects of traits among regions limit their current use in understanding beetle community assembly. Phylogenetic signal in niches, however, implies that better predictive traits can eventually be identified. Consistency of species niches among regions means niches may remain relatively stable under future climate and land use changes; this lends credibility to predictive distribution models based on future climate projections but may imply that species' scope for short-term adaptation is limited.

KEYWORDS
Bayesian joint species distribution models (JSDMs), climate change, Coleoptera, ecological traits, environmental gradients, HMSC, morphological traits, phylogeny, saproxylic beetles, species associations

1 | INTRODUCTION

Ecologist have been relatively successful in describing patterns of species distributions, but often struggle to identify mechanisms behind these patterns (Araújo & Guisan, 2006; Norberg et al., 2019). Theory suggests that these mechanisms consist both of species' responses to the environment (abiotic factors, via species' fundamental niches) and of their interactions with other species (biotic factors, contributing to realized niches; D'Amen et al., 2018; Staniczenko et al., 2017).

One promising avenue for better understanding these complex processes is the study of species traits. If a species' morphological and behavioural characteristics can help predict its response to the environment and interactions with other species, this can provide insights into the mechanisms behind the community assembly process (A. M. Brown et al., 2014; Vandewalle et al., 2010). Additionally, understanding the relationship between species traits and niches can allow us to make inferences about the ecology of rare species, for which detailed ecological information is seldom available (Ovaskainen et al., 2017).

Yet one challenge in examining the relationship between traits, environmental gradients and species co-occurrence patterns is that it is difficult to know if correlations observed in a single system are generalizable (Ovaskainen et al., 2019). If so, they may provide important insights into the assembly process. If not, perhaps these processes are more idiosyncratic, or at least dependent on other external factors (Norberg et al., 2019). Therefore, several replicated study systems, i.e. similar taxa in varied environments, are needed to test for generalizability of the relationships between traits, environmental gradients and species co-occurrence patterns.

Testing for consistency among several study systems can increase confidence in the generalizability of the results (Warton et al., 2015), but it also has implications for predicting species distributions under future climate and land use change scenarios (Araújo & Luoto, 2007; C. J. Brown et al., 2016). If most species respond similarly to environmental gradients across space in a variety of habitats and in regions with different climates (as is often assumed, e.g. Halvorsen et al., 2020), then species' responses are more likely to be similar through time as well. This would imply that niches are at least somewhat fixed, increasing confidence in future predictions based on current estimates of species' responses.

Alternatively, the strength (and even direction) of some species' responses to the environment may differ among bioclimatic regions (Delgado et al., 2020), implying that future changes in climate and forest management may modify how species respond, lowering the credibility of future predictions. Such apparent niche plasticity might also indicate that species have some capacity to adapt to changing future conditions (Morin & Thuiller, 2009; Van Heerwaarden & Sgrò, 2014).

Wood-living (saproxylic) beetles provide an excellent group to test these ideas. They are highly diverse, rely on resources (like dead wood) that are readily quantifiable and have much morphological and behavioural variation that can be linked to their ecology (Stokland et al., 2012). For example, body size in beetles has been linked to their extinction risk (Hagge et al., 2021), and relative wing size is likely linked to dispersal ability, which is important in fragmented landscapes (Bouget et al., 2015). Dead wood size and decay preferences (Seibold et al., 2015) should affect species' use of forests under different management regimes. We hypothesized that species traits would relate to niches in a consistent way among our study regions.

Here, we investigate the relationships between species traits, environmental gradients and species (co-) occurrences in saproxylic beetles, and examine the consistency of these relationships among several European bioclimatic regions. We model beetle capture

records as a function of climate and forest covariates and species traits and phylogeny using joint species distribution models (JSDMs).

Specifically, we ask:

1. To what extent do traits explain species' responses to environmental gradients (i.e. their niches)?
2. Are the relationships between traits and species' realized niches across entire communities consistent *among bioclimatic regions*?
3. Are species co-occurrence patterns correlated with trait similarity among species?
4. Are the relationships between traits and co-occurrences consistent *among bioclimatic regions*?
5. For each beetle species that occurs in multiple regions, are species' niches consistent *among bioclimatic regions*?

2 | MATERIALS AND METHODS

2.1 | Study sites and beetle sampling

We included saproxylic beetle capture data from flight intercept traps deployed in Norway, Finland and Germany (Figure 1) from several projects conducted between 1993 and 2019; see Supporting Information for sampling details for each bioclimatic region. The Norwegian and Finnish trap sites, in conifer-dominated hemiboreal and boreal forest, respectively, differed considerably in climate; the sites in Finland experience colder winters and lower annual precipitation. Norwegian and Finnish sites (n = 468 and 142 respectively) were at relatively low elevations (mean 250 and 140 m respectively). The German sites (n = 386), in deciduous and mixed temperate forests, ranged in elevation from 90 to 1420 m and so spanned a range of temperatures and precipitation levels overlapping with the Nordic sites, although Germany was warmer on average (Figure 2). Beside the broad climatic range, the sites in all three regions included forest stands that varied in several other environmental covariates (Figure 2), described below. Beetles were identified to species by expert taxonomists and designated as saproxylic based on the German reference list of saproxylic beetles (Köhler, 2000; Schmidl & Bußler, 2004). Species absent from the German list were designated as saproxylic using expert knowledge in the Nordic countries. Saproxylic beetle species detected in the three regions are presented in Table S1. Species names follow the GBIF backbone taxonomy (GBIF Secretariat, 2021). The beetle response variables were the presences/absences of each species at each site.

2.2 | Environmental covariates

We obtained information on several environmental covariates at the forest stand (~100 m radius) and landscape (1 km radius) scales around each trap location. We chose a 1-km radius for landscape covariates for comparability to other studies (Jacobsen et al., 2015, 2020; Jonsell et al., 1999), and because we found 1 km values to be highly correlated with values estimated at larger scales in our study. The environmental covariates were either measured on site or extracted from publicly available sources based on a range of local measurements, remote sensing data and modelling. See Supporting Information for source information for each covariate. Climate data were extracted from worldclim.org, which provides 30-year mean values at 1 km^2 resolution (Fick & Hijmans, 2017). All covariates have been shown to be important for saproxylic beetles (Jacobsen et al., 2020; Müller, Brustel, et al., 2015; Müller, Wende, et al., 2015; Müller et al., 2020; Sverdrup-Thygeson et al., 2014; Vindstad et al., 2020) and included:

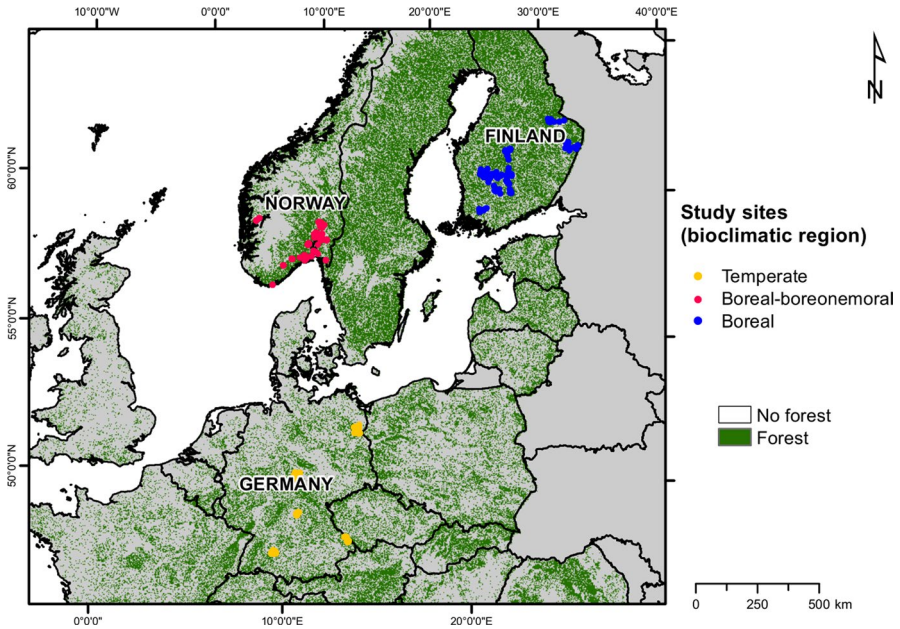

FIGURE 1 Saproxylic beetle capture sites across three bioclimatic regions in northern and central Europe. Forest area data originate from Copernicus HRL Forest products data (www.eea.europa.eu/data-and-maps/)

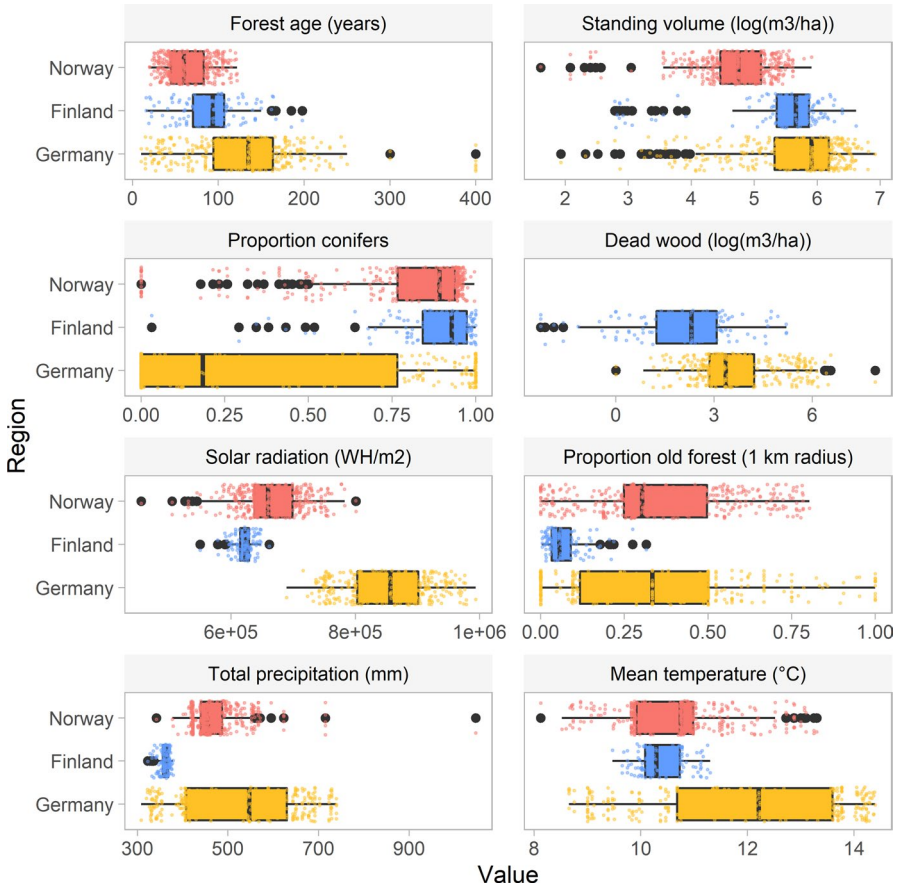

FIGURE 2 Environmental gradients in the three regions where beetle sampling occurred. Boxes show the 25th, 50th and 75th percentiles, and whiskers extend to a maximum of 1.5 × interquartile range. Points show sampling locations (n = 468, 142 and 386, for Norway, Finland and Germany respectively). Dead wood data were not available for sites in Norway. Forest age is mean age of the dominant trees. Climate values represent long-term averages during the vegetation season (April–September) from world clim.org

Stand-level covariates (~100 m radius):

1. forest age (mean age of the dominant trees)
2. standing wood volume (log-transformed)
3. proportion of conifers (by volume)
4. dead wood volume (log-transformed; not available for Norway)
5. total solar radiation in the vegetation period (April–September)

Landscape level covariates (1 km radius):

6. proportion of old forest ('old' defined appropriately for each forest type)
7. total precipitation in the vegetation period
8. mean temperature in the vegetation period

2.3 | Species traits

We tested for correlations between species responses to environmental covariates (i.e. their niches) and several ecological and morphological traits (see modelling details below). We used measurements of morphological traits of adult beetles from Hagge et al. (2021). Of these, we chose several traits that are relatively uncorrelated and that can be plausibly linked to species' ecology (Hagge et al., 2021). Ecological traits for larvae of each species were taken from Seibold et al. (2015) and from unpublished data. These ecological and morphological (with hypothesized ecological links) traits are shown in Table 1.

Body length was log-transformed for modelling. Because many morphological measurements are highly correlated with body length, the traits designated as 'relative' (Table 1) were standardized for body length. This was done by fitting a phylogenetic generalized least squares regression in which the logged value of each trait was modelled as a function of body length. The model was fitted to the entire trait database (Hagge et al., 2021) for each trait, and the residual values from this model were used as the relative trait values for each species (i.e. the trait value for a given species reflects its deviation from the predicted trait value of that species, given its body length). Few species (n = 20) in the dataset were in the 'cavity' guild, so this guild was merged with the fungi guild. Similarly, few species were in the detritivorous guild (n = 8), so these species were included in the xylophagous feeding group to simplify models.

We filtered our datasets to include all saproxylic species for which sufficient trait information was available. First, we excluded all species that were missing a length measurement (2.5%, 7.7% and 3.8% of species in Norway, Finland and Germany respectively). Species missing only one or more of the relative morphological traits (2–4) were retained, and we replaced the missing values with zero (n = 37 of 468 total species, 7.9%). Finally, for species missing one or more ecological traits, the missing values were estimated using congeners and our own knowledge (n = 17 of 468 total species, 3.6%). Models included 384, 251 and 241 species in Norway, Finland and Germany respectively.

TABLE 1 Beetle traits used in examination of link between traits, species' niches (their responses to environmental gradients) and pairwise species associations. Morphological traits are based on measurements of adults. Ecological traits are based on habits of larvae

Trait type	Trait	Ecological link	Type of measure
Morphological	Body length	Sensitivity to disturbance	Continuous
	Relative wing length[a]	Locomotion	Continuous
	Relative eye length[a]	Sensory perception	Continuous
	Relative jaw length[a]	Foraging strategy	Continuous
Ecological	Wood decay stage niche	Niche position	Continuous
	Wood diameter niche	Niche position	Continuous
	Preferred tree species	Niche position	Categorical, three levels: *broadleaved*, *coniferous*, *both*
	Feeding guild	Foraging strategy	Categorical, two levels: *fungi*, *wood bark*
	Feeding type	Foraging strategy	Categorical, three levels: *mycetophagous*, *xylophagous*, *predatory*

[a]Morphological traits designated 'relative' were standardized for body length using a phylogenetic generalized least squares regression in which the logged value of each trait was modelled as a function of body length.

2.4 | Modelling

We used Bayesian hierarchical joint species distribution models (JSDMs) in the Hierarchical modelling of species communities 'Hmsc' R-package (Tikhonov et al., 2020) to estimate the responses of each beetle species to the environmental covariates (i.e. their niches), the influence of traits and phylogeny on these niches, and pairwise associations among species (Figure 3). JSDMs allow testing of hypotheses about the effects of traits on the community assembly process (Abrego et al., 2017), as well as quantifying species associations after controlling for species niches (Ovaskainen et al., 2016), and the 'Hmsc' R-package demonstrated higher predictive ability than most other methods in a large comparative study (Norberg et al., 2019). We fitted models to the full presence/absence dataset of species by trap sites in R (R Core Team, 2020). We used presence/absence models with a probit error distribution because the majority of our species counts at a given site were very low (<5), meaning that abundances contained relatively little information. Thus, the possible added value of modelling zero-inflated count data would be small compared to the need of making additional assumptions and fitting more complex models (Ovaskainen & Abrego, 2020). We fitted a similar model separately for each bioclimatic region and included all species that had trait data and were detected in at least five trap sites in a given bioclimatic region. We used separate models for each region, rather than combining all data, to test for consistency among regions without regional interaction terms that would have produced overly complex models.

Our primary model for each region included additive fixed effects of all the above environmental covariates (except for dead wood volume and mean temperature), and additive effects of all traits on species niches (Figure 3). We excluded temperature and dead wood from the primary models in each country for comparability—the former was highly correlated with precipitation in Germany, and the latter was missing from Norway. To evaluate the effects of temperature, we fitted an additional model for each country in which temperature was substituted for precipitation. To evaluate the effects of dead wood, we fitted models identical to the primary models for Finland and Germany, but with an additional dead wood covariate. Temperature and dead wood estimates that we present come from these models, whereas the rest of our results are from the primary models, which were consistent among countries. The maximum variance inflation factor of all covariates in any model was <4.7 (most were <2), indicating low multicollinearity (Naimi et al., 2014). The same was true for all traits.

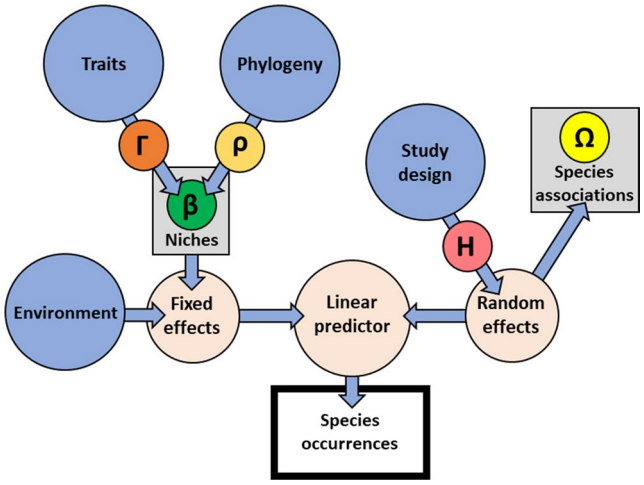

FIGURE 3 Simplified representation of model structure of Bayesian hierarchical modelling of species communities (Hmsc) models. Blue circles represent explanatory input data and Greek letters show model parameters. Species' niche parameters (β) in these joint species distribution models (JSDMs) are modelled as a function of species' shared traits and phylogeny with associated parameters (Γ, ρ) estimating these relationships. Residual species associations (Ω), those not explained by species niches, are estimated using a latent variable structure. Random effects that reflect study design (H, etc.) are also included. Figure based on diagrams in Ovaskainen and Abrego (2020)

Models also included a covariate log(effort), with effort reflecting the total trap surface area at a trap site, to account for differences in number and size of traps per site (Ovaskainen & Abrego, 2020). A phylogeny was also included to test for phylogenetic correlation in species niches. The phylogeny was based on the species-level insect tree from Chesters (2017). We used branch lengths in this tree to estimate an ultrametric tree, which allowed us to add missing beetle species randomly to the appropriate genus ($n = 69$) or family ($n = 11$). Each model also included random effects of site for use in estimation of species associations (Ovaskainen et al., 2016) and (for Norway and Finland) to account for the non-independence of samples from sites that were sampled in multiple years. Finally, we included random effects of sampling cluster in all models. Sampling in each region occurred during multiple years and in multiple spatial clusters of points. Each spatial cluster of sampling points in each year was given a unique cluster ID, resulting in random effects with 26 (Norway), 12 (Finland) and 15 (Germany) levels (see Supporting Information for additional details).

We fitted the HMSC models assuming the default prior distributions (Ovaskainen & Abrego, 2020). We sampled the posterior distribution with six Markov Chain Monte Carlo (MCMC) chains, each of which was run for at least 6500 iterations, of which the first 5000 were discarded as burn-in. The chains were thinned by 10 or more to yield 150 posterior samples per chain (900 in total; see Supporting Information for MCMC settings for each region). We evaluated effective sample size to assure adequate independence of samples, and potential scale reduction factors (Brooks & Gelman, 1998) to assure model convergence. Model fitting was conducted with high-performance computational resources provided by Louisiana State University (http://www.hpc.lsu.edu) and Uppsala University (https://www.uppmax.uu.se). Model fit was assessed using Tjur R^2, and the relative importance of covariates was assessed using variance partitioning (Ovaskainen & Abrego, 2020).

2.5 | Evaluating model results

To determine whether species' traits predict their responses to environmental gradients across the communities, we examined the gamma (Γ) parameters from each model. These gamma parameters are the hierarchical level of HMSC models that estimate the relationship between traits and betas (β; the parameters associated with environmental variables, see Figure 3). To test for consistency of these trait–environment relationships among regions, we compared the signs (positive, negative or no response; 90% credible intervals) of corresponding gamma parameters. We hypothesized that inconsistency among regions will be rare, and to subject this prediction to a more challenging test we used 90% CIs, rather than more restrictive 95% CIs, to increase the number of informative non-zero estimates for comparison. To test for phylogenetic signal in species niches, we examined the rho (ρ) parameter.

To test whether residual pairwise species association scores can be predicted by differences in trait values between species, we fitted a series of regressions for each region (Abrego et al., 2017). Each model had a single predictor variable, the difference in trait values (one trait per model) between the species in each pair. Dependencies in residual species association matrices can result not only from biology but also from the dependency in the data generated by the same species being present in several pairs of species, as well as from the latent variable structure (Ovaskainen et al., 2016) that is used by HMSC to estimate pairwise associations. To determine if our regression parameters were detecting true correlations with trait values, rather than artefactual correlations resulting from model structure, we conducted permutation tests. As a null model, we fitted regression models to these same species association matrices but using trait differences calculated from 1000 random permutations of the species trait matrix. We compared regression coefficients for each trait against this null model expectation. We then evaluated the consistency in these trait—association relationships among regions.

To test if species associations were phylogenetically structured, we quantified the correlation between the lower triangles of a log-transformed phylogenetic distance matrix and the posterior mean of species association scores. This analysis was completed separately for each region. As with the analyses related to traits, we compared the correlation value with 1000 null simulations in which we randomly reordered the rows (and corresponding columns) of the phylogenetic distance matrix.

To determine if species' niches (responses to environmental gradients) were similar among the three bioclimatic regions, we compared the signs of each species' regression slope parameter (beta) associated with each environmental covariate in each region in which that species occurred. We tested for consistency of negative, neutral or positive relationships (90% CI). We first categorized betas according to posterior support, rather than using all MCMC samples to compute the probability that betas from two regions had the same sign, because we were interested not only in the consistency of the signs among regions but also in the strength of the evidence that each beta being compared differed from zero. We compared betas for 282 species that were detected in five or more trap sites in at least two of the three bioclimatic regions. Norway–Finland, Norway–Germany and Finland–Germany had 215, 186 and 133 species in common respectively (Table S1). For clarity, and to categorize responses according to their level of posterior support, we focus on a comparison of the signs of the beta estimates rather than the precise values of those estimates. However, we also present a series of regressions comparing the median parameter estimates (regardless of support levels) in Supporting Information.

3 | RESULTS

We fitted a JSDM for each of the three bioclimatic regions, including 384, 251 and 241 species for Norway, Finland and Germany respectively. Mean explanatory Tjur R^2 values for all species in our primary models for the three regions were 18.3%, 17.9% and 14.8% respectively. The relative importance of the environmental covariates

differed among countries (Table S2); precipitation and temperature were important in Germany (where each accounted for about one-third of the variation explained by their respective models), as was proportion of conifers. Temperature was also important in Norway and Finland; however in Finland, forest age and standing volume were the most important, accounting for a combined one-third of explained variation. Random effects played a larger role in models in Norway, due partly to more repeated sampling at trap sites among years.

3.1 | Traits and response to environment

Of 32 relationships between morphological traits and niche dimensions (4 traits × 8 environmental covariates) that we estimated (i.e. gamma parameters), 14 (44%) differed from zero (90% CI) in at least one study region (Figure S1). Of these 14, three had non-zero estimates in two regions. In two of these three cases, the sign of the estimates differed among the two regions. Of the 92 total morphological trait–niche–region relationships that we examined (4 traits × 8 covariates × 3 regions, minus 4 for lack of dead wood data in Norway), 17 (18%) differed from zero (90% CI).

For ecological traits, of 64 ecological trait–niche relationships (gamma parameters) that we examined, 21 (33%) had estimates that differed from zero (90% CI) in at least one region (Figure S2). Of these 21, two had estimates that differed from zero in two regions. In both cases, the signs of the estimates for the two non-zero regions were similar—species that preferred coniferous host trees responded positively to higher proportions of conifers and responded negatively to warmer temperatures. Of the total 184 ecological trait–environment region relationships that we examined (8 trait levels × 8 covariates × 3 regions, minus 8 for lack of deadwood data in Norway), 23 (12.5%) differed from zero (90% CI). When we considered reduced models with only either morphological or ecological traits, more of the traits had highly supported values but there was still little consistency among regions (Figure S3). Phylogenetic correlation in species responses to environmental covariates was high across all bioclimatic regions (rho parameter; 95% CIs: Norway: 0.82–0.90; Finland: 0.68–0.84; Germany: 0.96–0.99). These correlations were on a scale of 0–1, where 0 indicates a random distribution on the phylogeny and 1 indicates that responses are fully phylogenetically structured.

3.2 | Traits and species associations

Our models showed many more positive than negative associations among species, and both types of associations were spread across the phylogeny (Figures S4–S6). HMSC models provide estimates of residual rather than raw associations among species, meaning that these are associations that remain after controlling for species' niches. Of all species pairs, 2.0% and 0.2% had negative associations (95% posterior support) in Norway and Germany respectively. Each negatively associated species pair in Germany included *Tetratoma ancora*, a species detected in 3% of sites (median occupancy of all species was 3.4%). Our model for Finland detected only positive associations. The proportion of all species pairs with positive associations differed among bioclimatic regions, from 6.4% in Finland and 10.9% in Germany to 17.3% in Norway.

Difference in trait values between pairs of species was not a consistent predictor of species associations (Figure 4). Of 27 estimated regression coefficients (nine traits by three bioclimatic regions) in models to predict pairwise association scores, 15 fell outside of the 50% CI from the null simulation. Of these, eight coefficients were negative, meaning that a larger difference in traits between species lowered their species association score. The remaining seven were positive, meaning a larger difference in traits increased association scores. However, only 4 of these 15 estimates fell outside of the 95% CI of the simulations. The sign (positive vs. negative) of coefficients often differed among the three regions.

We found strong evidence for a phylogenetic correlation in species associations in Norway, where phylogenetically distant species were less likely to co-occur ($p = 0.001$; Figure S7). The correlation between phylogenetic distance and association scores was also negative in Finland ($p = 0.17$), but positive in Germany ($p = 0.14$), and the values fell within the simulated null distribution for these two regions.

3.3 | Consistency in species' environmental responses among regions

The probability of occurrence for species detected in at least two of our three study regions increased the most on average with increasing temperature, dead wood and solar radiation and with decreasing precipitation (Figure S8). The mean effect of the other covariates on the community as a whole was relatively neutral. For all species that were included in models from a given pair of regions, we compared the direction of each species' response (90% CI) to each covariate among regions (i.e. signs of the beta parameters: positive, negative or neutral; Figure 5). The bioclimatic regions shared 215, 186 and 133 species for Norway–Finland, Norway–Germany and Finland–Germany, respectively, for a total of 282 species occurring in two or more regions.

Of a total of 3871 pairwise comparisons of beta parameters for a given species among regions (Figure 5; Figure S9), 51.4% of the parameter estimates shared the same sign (positive, negative or zero; 90% CI) in both regions. For 43.6% of comparisons, one estimate was non-zero in one region but did not differ from zero in the other. In only 5.0% of cases did the sign of the coefficient for the same species and environmental covariate flip between two regions. These reversals are most common between Finland and Germany (7.4%) and least common between Norway and Finland (4.0%). The proportion of reversals did not differ strongly among covariates ($p = 0.063$). Rather than being concentrated in a few plastic or 'inconsistent' species, these relatively few reversals were spread among 109 (39%) of the 282 shared species, with only 14 species having more than two

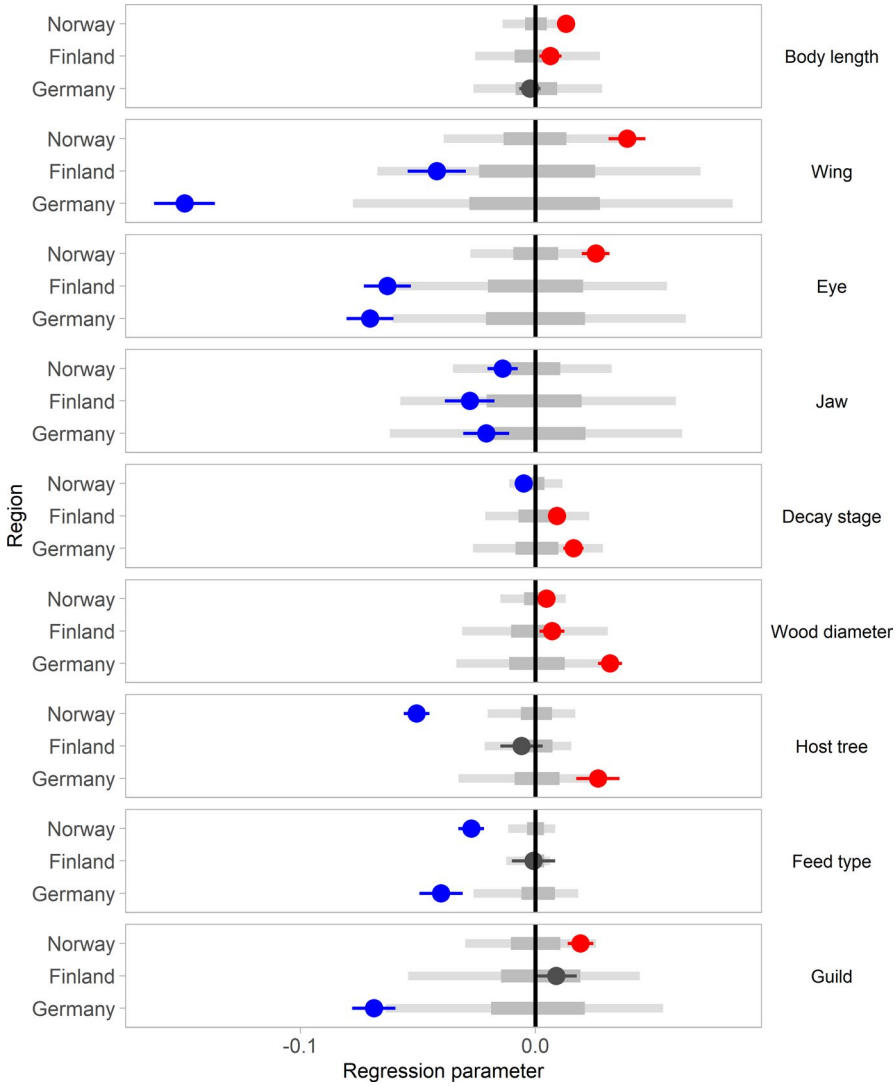

FIGURE 4 Relationships between species traits and pairwise association scores among European forest beetles. Association scores range from never co-occurring (−1) to always co-occurring (1) and reflect only those associations not explained by species niches, i.e. 'residual' associations. Negative regression parameter estimates indicate that a larger difference in traits between pairs of species lowered their association scores (positive values indicate the opposite). Points show regression parameters from linear models in which species association scores are a function of the difference in trait values between each pair of species. A separate regression was fitted for associations for each combination of region (Norway, Germany and Finland; *y*-axis) and trait (plot facets; labeled on the right). Colour of points shows estimates that are positive (red; 95% CI) or negative (blue). Dark and light grey bars show null expected values (50% and 95% respectively) from 1000 random permutations of the species trait matrices. For trait information, see Table 1

reversals. When we compared the values of the median parameter estimates for the 282 shared species, rather than the sign of estimates (>90% support), values were correlated in one-third of the 21 region-covariate comparisons (95% CI); only for proportion of conifers were species responses correlated in all three regions (Figures S10 and S11).

4 | DISCUSSION

We compiled wood-living beetle capture records from three European bioclimatic regions to estimate species niches (i.e. their responses to environmental gradients) and species associations, and to relate both of these to species' traits and phylogenetic relationships. We also compared species niches, and the effects of traits, among the regions. Morphological and ecological traits helped predict species niches, but not in ways that were consistent among bioclimatic regions. Phylogenetic signal in niches, however, was consistently high, indicating that phylogenetically correlated but unmeasured traits likely play a role in determining niches. Species associations were predominately positive but could not be consistently predicted by traits. Nevertheless, species niches showed relative consistency in the direction of their responses to most environmental covariates among regions.

Species' traits by necessity determine their niches (Winemiller et al., 2015). Morphological trait measurements are often easier to obtain than are behavioural or ecological traits, but the extent to which morphological traits can be used to predict niches appears to differ among taxonomic groups (Raine et al., 2018; Ricklefs & Miles, 1994; Yates et al., 2014). In our models, traits explained species niches slightly better than would be expected by chance—13% of all environment–trait relationships we examined had high posterior support. However, most of these relationships were not consistent among bioclimatic regions, implying that the relationships between our morphological and ecological traits and species niches are either weak or idiosyncratic. In the two cases where we did see consistency of trait effects among two countries, the results are intuitive and demonstrate that our methods can detect these relationships—beetles that rely on coniferous hosts are more common in forests that contain more conifers, and in cooler forests (Figure S2), perhaps

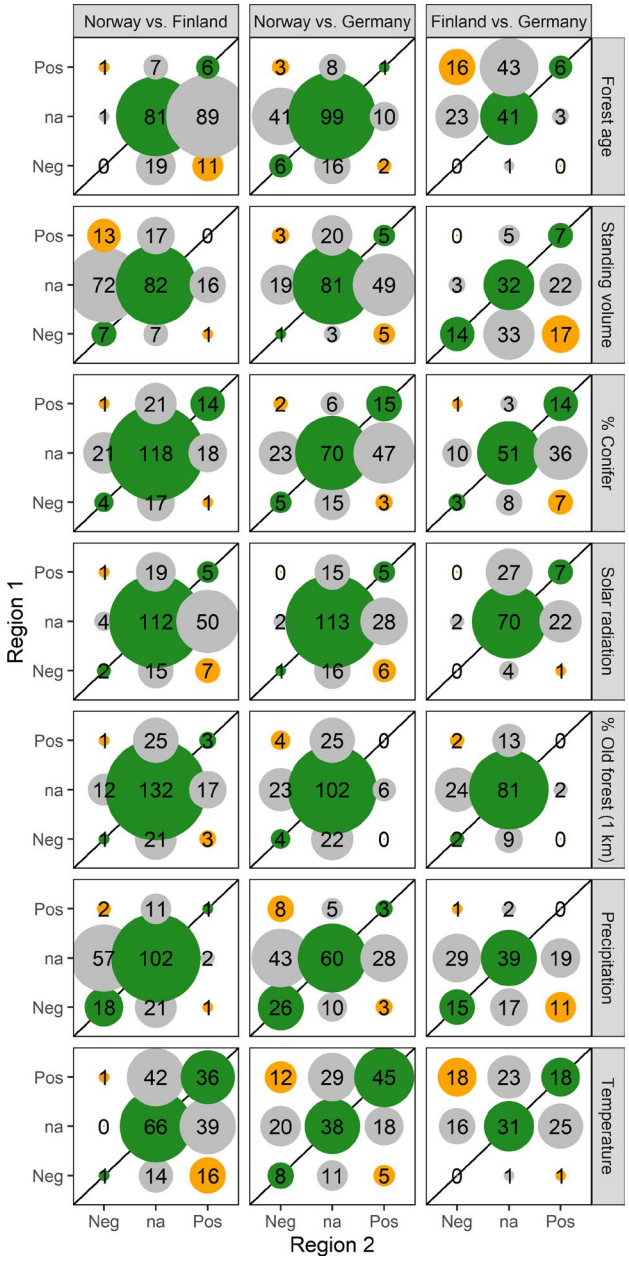

FIGURE 5 Comparison of beetle species niches among pairs of sampling regions. Species' responses to each environmental covariate (Beta parameters) were classified as positive ('Pos'; 90% CI), negative ('Neg') or neutral ('na'), and tallied to produce species totals (numeric values) for each pair of regions. Green circles (along the diagonal line) represent species that respond similarly in both regions, orange circles indicate opposite responses and grey circles represent species that show a response in only one of the two regions. Area of the circles is proportional to counts of species (number labels) in each category. Each grid cell represents one pair of regions (heading labels; first listed region on the *y*-axis) and one environmental covariate (labels on right vertical axis). Norway shared 215 and 186 species, respectively, with Finland and Germany, which shared 133 species with each other. Using 90% CIs (rather than 95%) subjects our prediction, that opposite responses among regions will be rare, to a more challenging test. Dead wood volume information was not available for Norway; for comparison of the other two regions, see Figure S9. For regression comparisons of median parameter estimates, see Figures S10 and S11

because conifers are less common in southern Norway and at low elevations in Germany. Past work with saproxylic beetle traits has shown that morphological traits can help predict extinction risk (Hagge et al., 2021; Seibold et al., 2015), and that functional diversity of communities (a combination of morphological and ecological traits) can vary with tree age and forest disturbance (Kozák et al., 2021; Wetherbee et al., 2020). However, examples of strong links between beetle traits and distributions are relatively few.

This lack of consistency in trait–niche relationships means that the role of traits in beetle community assembly remains unclear. It also means that we currently cannot infer much about the ecology and habitat requirements of poorly known species by examining their traits, an important goal both for basic ecology and for the conservation of highly diverse taxa (Mouillot et al., 2013). However, phylogenetic signal in species' responses to the environment was very high in all three regions. This implies that some phylogenetically structured but unmeasured traits do play a strong role in setting species niches (Ovaskainen & Abrego, 2020), and so indicates that a continued search for important traits in these taxa is well justified. Analyses that relate larval traits to larval (rather than adult) distributions could be a fruitful next step, as could accounting for the range of intraspecific variability in trait values. Given the continued difficulty in identifying these relevant traits, and the strong phylogenic signal in niches, we recommend continuing analyses that combine phylogeny and traits when considering ecological distance among species (Cadotte et al., 2013; Thorn et al., 2016) and when trying to understand community assembly in beetles.

Just as traits must ultimately determine species niches, they also must determine how species interact with each other (Minden & Olde Venterink, 2019). We cannot assess interactions directly through distribution modelling (Blanchet et al., 2020), but we can quantify 'residual' associations among species that are not explained by our environmental covariates (Ovaskainen et al., 2016). Many associations that we detected may imply some form of interaction, but perhaps more plausibly could also reflect differing responses to unmeasured environmental covariates (Barner et al., 2018). In either case, knowing whether these associations are predicted by trait similarity can provide clues to the mechanisms behind them. As in the case of species niches, we found some effects of traits on species co-occurrences, but not in ways that were consistent among bioclimatic regions. Perhaps the relationship between traits and species associations is idiosyncratic, or depends on complex interactions among traits, but species association patterns can also covary along environmental gradients (Tikhonov et al., 2017; Tylianakis et al., 2008). As in the case of species niches, species associations decreased with increasing phylogenetic distance in at least one of our bioclimatic regions, which provides additional support for the idea that unmeasured but phylogenetically correlated traits play a role in community assembly.

Consistency in species niches among regions was relatively high despite inconsistency in the effects of species traits. For 282 species that occurred in two or more of the regions, the direction of responses to eight environmental covariates was consistent among

pairs of regions in half of all cases (Figure 5), although in the majority of these cases species showed no response in either country. For most of the remaining cases, the comparison was ambiguous (positive or negative in one region, but no response in the other), leaving <5% of cases in which the direction of species responses differed among regions. These few apparent reversals were distributed over many species, rather than being concentrated in a few. It therefore seems likely that many of these apparent reversals simply represent statistical noise rather than pointing to a distinct subset of ecologically plastic species. Sampling hyperdiverse communities is always challenging (Burner et al., 2021; Martikainen & Kouki, 2003), and our ability to precisely define the niches of many rare species was limited by their low prevalence or detectability. These species are important because of their disproportionately large contribution to community functional structure (Burner et al., in revision). Our results confirm that dead wood is an important predictor of beetle occurrences, and forestry practices that allow the build-up of dead wood will likely benefit many species. High deadwood volume may be partly responsible for the associations of many beetle species to near-natural forests (Burner et al., 2020; Jacobsen et al., 2020).

Consistency in species niches among regions is consistent with the hypothesis that niches would remain relatively stable in coming decades with changing landscape and climate, because of the relatively slow speed of adaptation (Jezkova & Wiens, 2016). This information is important for predictive ecology, because predicting the impacts of climate and land-use change is a first step in adaptation and mitigation. However, the relative importance of the environmental covariates differed among the regions. To some extent, this may be a function of the range of variation in each covariate in the various regions—precipitation, temperature and proportion of conifers all span a wide gradient in Germany, and all are important. But it also likely reflects something about the underlying importance of each as a dimension of niche space by region—forest age and volume vary relatively little in Finland, yet both are important covariates there. Differences in covariate importance among regions thus makes it likely that some niche dimensions will increase or decrease in importance as climate changes. These potential interactive effects have been demonstrated in a European study on saproxylic beetles. Müller, Brustel, et al. (2015) showed a consistently positive relationship between species richness and abundance and dead wood volume, a limited resource in managed forests, but dead wood was less important at warmer temperatures. However, not all interactions among niche dimensions are likely to facilitate adaptation, and environmental stressors are more likely to multiply rather than mitigate each another (Forister et al., 2010). These interactions, combined with the probability that the magnitude (rather than direction; see Figures S10 and S11) of species responses to the environment does vary across space, remain a challenge for predictive ecology.

Much work remains to understand the link between beetles' traits and their distributions and interactions, which would allow us to understand community assembly and predict future distributions. Nevertheless, we demonstrated the presence of phylogenetic signal in species niches, showing that the search for these links is likely to be a productive area of future research. Consistency in species niches among regions is good news for predictive ecology but, less cheerfully, could mean that niches may be less plastic in the short term than future climate and land use will demand. Interactions among niche dimensions need to be better understood to develop effective habitat protection strategies, which will become increasingly important to mitigate effects of environmental change.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data are available on Dryad: https://doi.org/10.5061/dryad.tmpg4f50b.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of the article at the publisher's website.

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