Functional structure of European forest beetle communities is enhanced by rare species

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ARTICLE INFO

ABSTRACT

Biodiverse communities have been shown to sustain high levels of multifunctionality and thus a loss of species likely negatively impacts ecosystem functions. For most taxa, however, roles of individual species are poorly known. Rare species, often most likely to go extinct, may have unique traits and functional roles. Alternatively, rare species may be functionally redundant, such that their loss would not disrupt ecosystem functions. We quantified the functional role of rare species by using captures of wood-living (saproxylic) beetle species, combined with recent databases of morphological and ecological traits, from three regions in central and northern Europe. Using a rarity index based on species' local abundance, geographic range, and habitat breadth, we used local and regional species removal simulations to examine the contributions of both the rarest and the most common beetle species to three measures of community functional structure: functional richness, functional specialization, and functional originality. Both regionally and locally, all three measures declined more rapidly when rare species were removed than under common (or random) species removal scenarios. These consistent patterns across scales and among forest types give evidence that rare species provide unique functional contributions, and their loss may disproportionately impact ecosystem functions. This implies that conservation measures targeting rare and endangered species, such as preserving intact forests with dead wood and mature trees, can provide broader ecosystem-level benefits. Experimental research linking functional structure to ecosystem processes should be prioritized to increase understanding of the functional consequences of species loss and to develop more effective conservation strategies.

1. Introduction

Biodiversity loss is currently a major environmental challenge (Newbold et al., 2015; Brose and Hillebrand, 2016; Díaz et al., 2019). One can argue that species have intrinsic value that makes preservation for their own sake a worthwhile goal (Soulé, 1985; Ghilarov, 2000; Vucetich et al., 2015). More practically, species also have functional value, contributing to ecosystem multifunctionality (Soliveres et al., 2016b) and to services that provide humanity with tremendous benefits (Ehrlich and Ehrlich, 1997), on the order of $125 trillion USD annually

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(Costanza et al., 2014). A broader definition of biodiversity includes not just species but also their roles in ecosystems, i.e. their functional diversity (Petchey and Gaston, 2006; Cadotte et al., 2011). Many countries have adopted the Convention on Biological Diversity (CBD), which recognizes intrinsic and extrinsic values, and some have defined national targets to prevent local species extinctions (Rounsevell et al., 2020).

In ecological communities, only a minority of species are common whereas most species are rare (Violle et al., 2017). Rarity itself can take several forms – species can have narrow geographic ranges, be specialized to certain habitats, or have low site occupancy or low abundance when present (Rabinowitz, 1981; Jain et al., 2014; Violle et al., 2017; Kondratyeva et al., 2019). Rare species, by several definitions, are also those that are most often at risk of extinction (Davies et al., 2004; Harnik et al., 2012; Nordén et al., 2013). However, it is generally not known how important these rare species are for the ecosystem functions and services that their communities provide (Lyons et al., 2005), and the influence of rare species on ecosystem functionality has been explored in relatively few studies (Mouillot et al., 2013; Soliveres et al., 2016a; Zhang et al., 2022). One possibility is that rare species are often functionally redundant, filling roles that are also played by some common species or roles that are shared by a large group of other rare species. If this is the case, then it is possible that the loss of some rare species would have little effect on ecosystem functions. Alternatively, rare species may be functionally unique to varying degrees, contributing to ecosystem functions in ways that other species could not compensate for in their absence (Laureto et al., 2015; Brose and Hillebrand, 2016). Furthermore, important ecosystem services may depend not only on the presence of one or more species, but also on their indirect contributions via species interactions (Dee et al., 2019). In this case, extirpation of rare species could have disproportionate impacts on their ecosystems and on the services they provide (Soliveres et al., 2016a).

The ecological characteristics of many species are not well known, so morphological traits are often used as a proxy for ecological functions (Reiss et al., 2009). Morphological measurements are objective, readily obtainable from specimens, and in some cases correlate with ecological functions (Moretti et al., 2017). When available, however, ecological traits have the potential to provide a more direct link to species' ecosystem functions (Naeem and Wright, 2003). Ecological traits can include e.g. diet, feeding strategy, or micro-habitat preference. A challenge, though, is that such detailed ecological information is not yet available for many taxa, particularly for species in understudied regions or hyper-diverse groups, and ecological traits that are available are often

categorical and thus can be less informative. A mixture of morphological and ecological traits is therefore often necessary for understanding the roles of species within their communities.

The functional characteristics of communities, based on some combination of relevant traits, are often described using various measures of functional structure. Functional structure refers not only to the diversity of functional traits in a community, but also to how these traits are distributed among its species (Mouillot et al., 2011). More specifically, functional structure has recently been defined as a combination of three distinct but complementary measures: functional richness, functional specialization, and functional originality (Leitão et al., 2016) (Fig. 1). Functional richness refers to the total multi-dimensional volume of trait space occupied by the community. A community with higher functional richness will presumably be able to sustain a broader range of ecosystem functions (Wong et al., 2019). Functional specialization refers to the mean distance between each species and the centroid (mean location) of all species in multi-dimensional traits space (Leitão et al., 2016). Whereas functional richness is determined by those species setting the outer bounds of community traits space, functional specialization is affected by each species, describing whether most species are clustered near the center of total occupied trait space of the community or distributed more widely throughout that space. Finally, functional originality refers to the mean distance between each species and its nearest neighbor in multi-dimensional trait space. This essentially assesses the uniqueness of each species' combination of traits (Leitão et al., 2016).

The advantage of these measures of community functional structure, as opposed to measures of the functional distinctiveness of individual species (Mouillot et al., 2013), is that they make it possible to simulate species extinctions in order to understand the contribution of rare (or common) species to the community as a whole. Leitão et al. (2016) compared removal simulations of rare and common species in three taxonomic groups – rainforest tree, rainforest birds, and tropical stream fish – and found that in each of these groups all three measures of functional structure decrease much more rapidly when rare species are removed than when common species are lost.

At the forefront of concerns about biodiversity loss, insects have been shown to be in decline in many ecosystems (Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019; Cardoso et al., 2020; van Klink et al., 2020; Wagner, 2020), but see also Didham et al. (2020) and Montgomery et al. (2020). Insects are a particularly important group for ecosystem services, providing pollination (Lebuhn et al., 2013), pest control (Kremen and Chaplin-Kramer, 2007) and decomposition
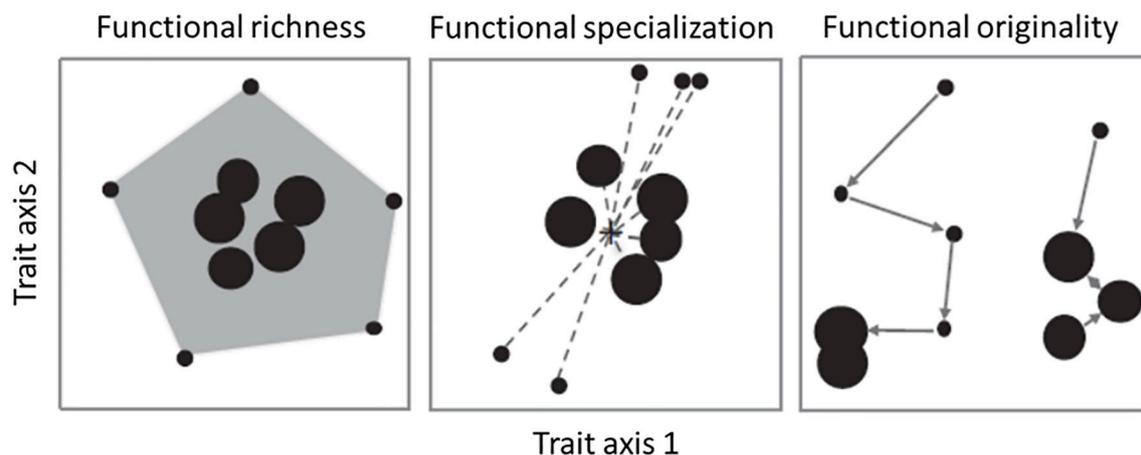

Fig. 1. Illustration of three complementary measures of community functional structure, based on a combination of morphological or ecological species traits. Functional richness represents the total volume of occupied multi-dimensional trait space, functional specialization represents the mean distance from each species to the center of that trait space, and functional originality measures the mean distance from each species to its nearest neighbor. Small and large points represent rare and common species, respectively; these examples show a hypothesized scenario where rare species contribute disproportionately to functional structure. Figure modified from Leitão et al. (2016).

services and nutrient cycling (Valentín et al., 2014; Ulyshen, 2016; Skelton et al., 2019; Seibold et al., 2021). Yet, little is known about the uniqueness and contributions of rare species in most insect assemblages.

Wood-living (saproxylic) beetles are an ecological group well suited for testing hypotheses about the functional structure of insect assemblages. This hyper-diverse group has large numbers of rare species, and beetles as a group contribute to important ecosystem services like wood decomposition, nutrient cycling, and predation (Ulyshen, 2018; Wetherbee et al., 2020). Beetles also serve a variety of ecological roles and differ in their ecology in ways that can be plausibly connected to morphological variation among species.

Across the European continent, forests differ in both their biogeographic and forest management histories and in their current management systems (Esseen et al., 1997; Brukas and Weber, 2009). This means that regional species pools of saproxylic beetles, and the relative abundances of these species, also vary. This provides an opportunity to compare the functional contributions of rare species in multiple regions to test for the generality of conclusions. Here, we use saproxylic beetle capture records, and databases of morphological and ecological traits, to examine the contribution of rare species to the functional structure of forest beetle assemblages across three bioclimatic regions in Europe.

Specifically, we ask:

1) If rare beetle species become regionally or locally extinct, what would be the impact on beetle communities as measured by functional richness, functional specialization, and functional originality?
2) How do these community impacts differ if species are instead lost at random, without regard to rarity, or if common species are lost first?

2. Material and methods

2.1. Beetle sampling

We compiled saproxylic beetle capture records from three bioclimatic regions in central and northern Europe, represented by forests in Norway, Finland, and Germany (Fig. 2). Beetles were sampled using window traps as part of several projects between 1993 and 2019. Between one and five window traps were placed per site, typically from May to August/September. Sites in Norway ($n = 468$) were in most cases sampled in multiple consecutive years ($n = 1111$ sampling events; mean 2.4 years per site) and so we merged these repeated sampling events to have more complete local community information for the local species loss scenarios. In Finland, eleven out of 142 sites were sampled twice but sampling events were separated by several years and so we treated these samples as separate communities ($n = 153$). In Germany, sites ($n = 386$) were each sampled in a single year.

Sites in Norway and Finland were in conifer-dominated hemiboreal and boreal forest, respectively, and differed in climate. The sites in Norway are more oceanic and hence experience cooler summers, warmer winters, and higher annual precipitation. Norwegian and Finnish sites were at relatively low elevations (mean 250 m and 140 m, respectively). The German sites covered a spectrum of temperate forests (from deciduous to coniferous), and ranged in elevation from 100 m to 1500 m. The range of temperatures and precipitation levels in Germany thus overlapped with the Nordic sites (Supplementary Fig. S1). Sites in all three regions included forest stands that varied in mean forest age, living and dead wood volume, and landscape connectivity – spanning
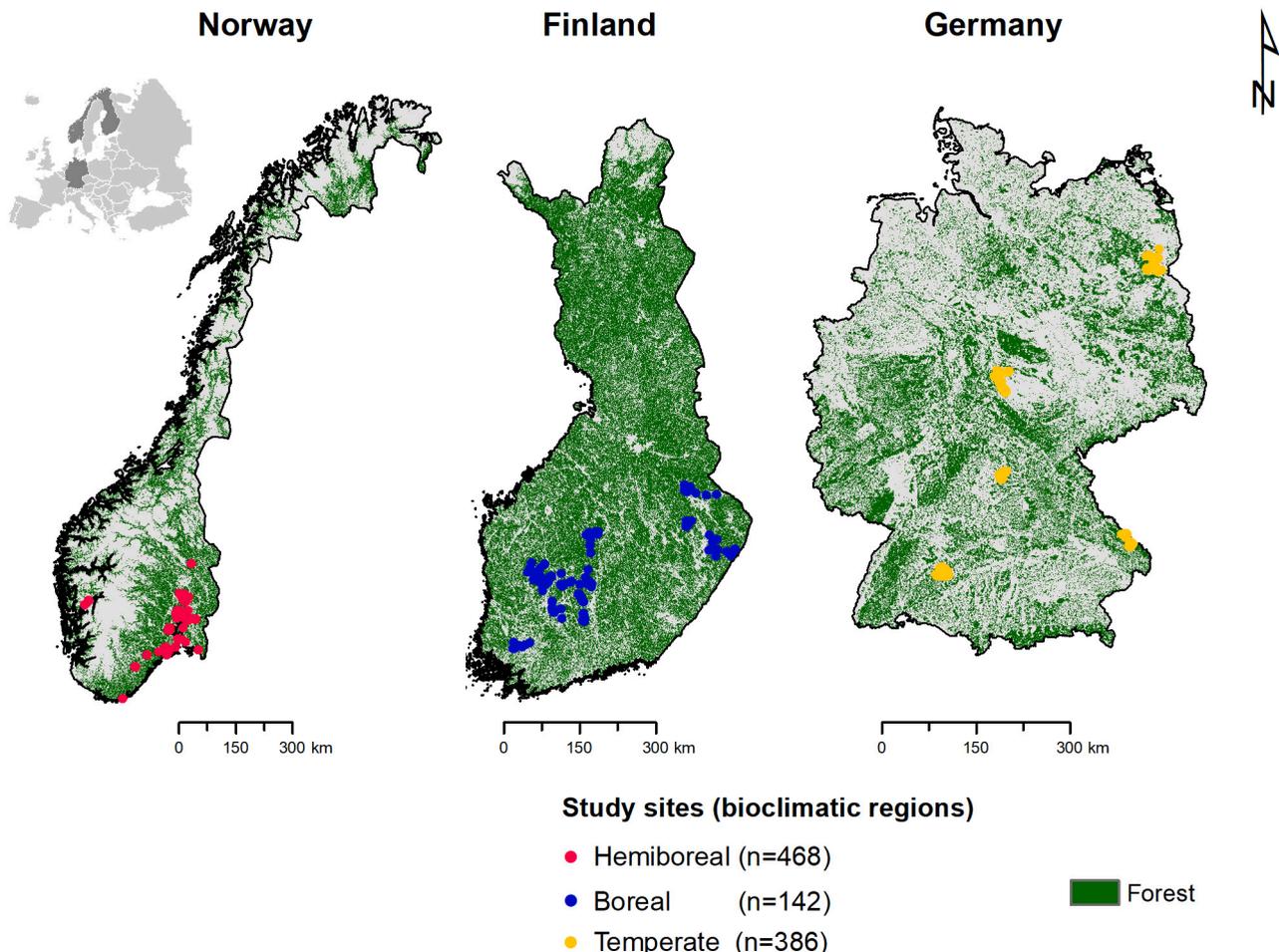

Fig. 2. Map of saproxylic beetle sampling sites in the three bioclimatic regions in central and northern Europe.

from commercially managed production forest to near-natural forest. Additional details about the sampling design are available in Burner et al. (2021c).

Beetles were identified to species level by expert taxonomists and designated as saproxylic using the German reference list of saproxylic beetles (Köhler, 2000; Schmidl and Bußler, 2004). Species names follow the GBIF backbone taxonomy (GBIF Secretariat, 2021). Our datasets consisted of 546, 392, and 515 saproxylic beetle species detected in Norway, Finland, and Germany, respectively (778 species in total; Table S1). These species were represented by 127,812 individuals in Norway, 82,018 in Finland, and 19,005 in Germany.

2.2. Beetle traits

We chose a diverse subset of twelve morphological and five ecological traits (Table 1) to represent community functional structure. The morphological traits, from Hagge et al. (2021), are related to aspects of species body size, dispersal (flight) capacity, feeding, and sensory perception. Our ecological traits, from Seibold et al. (2015) and related unpublished data, cover several components of wood-living beetles' life history, including the size, decay stage, and type of preferred microhabitat and the trophic feeding level of larvae.

Morphological measurements are generally highly correlated with body size, and so traits marked as 'relative' (Table 1) have been corrected for body length following Hagge et al. (2021). We did this by first fitting a linear regression between each log-transformed trait and the log-transformed body length and then extracting the residuals from this model as our trait values. These residuals represent the deviation from the expected trait value, given a species' body length. We did not use a phylogenetic correction, because our interest was in the distribution of trait values in a community, irrespective of any influence of phylogeny on these traits (de Bello et al., 2015). The model was fitted to the entire trait database for each trait, and residual values were extracted for each species as the relative value for that trait (such that e.g. a relative body width of zero indicated that a species had the mean body width predicted, given its body length). Other correlations among traits are not a problem for our metrics of functional structure because of our use of an ordination-based approach that reduces variation in all traits to several representative axes. However, our continuous traits were only minimally correlated (max variance inflation factor = 3.64), increasing our confidence that they represent a diverse range of characteristics.

Of 546, 392, and 515 saproxylic beetle species detected in Norway, Finland, and Germany, respectively, we were able to compile trait data for 89%, 85%, and 91% of these species, respectively. These included 83% (n = 643 of 778) of all species. A subset of these species with trait data were missing one (or, rarely, two or more) of the 'relative' morphological measurements; in those cases, we retained the species to have more complete beetle assemblages but filled the missing values with zeros. A zero in this case is the mean expectation (residual value; see above) and thus represents a conservative choice that should not bias the functional structure measures. This was the case for 9%, 7%, and 11% of beetle species for which we had trait data in Norway, Finland, and Germany, respectively. The remaining species, which lacked body length or ecological trait data, were excluded from our analyses. For the relative rarity values of species with and without traits, see below.

A total of 226 (35%) of those species with traits were detected in all three of our study regions, whereas 196 (30%) were detected in two of the regions, and 221 (34%) were unique to a single region. Norway and Germany shared the most species (n = 336), followed by Norway and Finland (n = 295), and Finland and Germany (n = 243). The three regions thus represented unique regional and local beetle assemblages, but had considerable overlap in species as well.

To compare our rarity index with species' red list status, we obtained red list status for species in Norway (Henriksen and Hilmo, 2015), Finland (Hyvärinen et al., 2019), and Germany (Schmidl and Büche unpublished data). In addition to the standard red list categories of Least Concern (LC), Near-threatened (NT), Vulnerable (VU), Endangered (EN), Critical (CR), and Data Deficient (DD), the German Red List included several legacy categories, including Indeterminate (I) and Rare (R). For the purposes of analyses, we lumped these final two categories in with DD species. Red list status was less informative for Finland, because all but three species were classified as LC. Red list status for each region is listed in Table S1.

2.3. Quantifying rarity

Species can be rare in several respects; they can be geographically restricted, have low site occupancy within their range (due to e.g. high habitat specificity), or occur in low numbers when present (Rabinowitz, 1981; Violle et al., 2017). We used a single rarity index, combining local abundance, geographic range size, and habitat breadth components (Leitão et al., 2016). We estimated local abundance separately for each study region because species' abundances vary among regions (although they are correlated; Fig. S2). We did this by calculating both the proportion of sites occupied and mean abundance when present for each species, then logging each of these values to decrease the magnitude of the values and scaling each to range from zero to one. These occupancy and mean abundance values were then averaged for each species to make a local abundance score. For geographic range size, we extracted a list of countries occupied by each beetle species from Löbl and Smetana (2013) and summed the area of these countries (large countries, e.g. Russia and China, are further subdivided into biogeographic zones in this database). For missing species (n = 8), we extracted lists of occupied countries from gbif.org. The summed area of countries occupied by each species was log transformed and values scaled to range from zero to one. For habitat breadth, we calculated a co-occurrence-based habitat specialist-generalist score following the methods of Fridley et al. (2007) and Manthey and Fridley (2009). We chose this method because detailed niche information is not available for many beetle species. Briefly, this method is based on the empirical observation that habitat specialists will cooccur with a smaller subset of species than will habitat generalists (Fridley et al., 2007). We calculated a habitat specialist-generalist score for each species based on the multiple Simpson similarity index (Baselga et al., 2007) using the entire merged dataset from our three study

Table 1
Morphological and ecological traits used for calculation of functional structure of European beetle assemblages.

Trait	Mean ± SD (continuous) or Levels (categorical)
Morphological[*]	
Hairiness (log-transformed)	2.7 ± 1.5
Body length (log-tr.)	1.5 ± 0.7
Body roundness (log-tr.)	−0.3 ± 0.2
Wing aspect (log-tr.)	1.0 ± 0.1
Wing load	0.2 ± 0.6
Relative body width[**]	0.0 ± 0.3
Rel. head length	0.0 ± 0.3
Rel. wing length	0.0 ± 0.2
Rel. leg length (front femur)	0.0 ± 0.2
Rel. antenna length	0.0 ± 0.5
Rel. eye length	−0.1 ± 0.3
Rel. jaw length	0.0 ± 0.3
Ecological[†]	
Preferred wood diameter	2.4 ± 0.7
Pref. wood decay stage	2.9 ± 0.8
Larval microhabitat	Fungi, wood bark
Preferred host tree type	Broadleaf, conifers, both
Larval feeding type	Xylophagous, mycetophagous, predatory

[*] Morphological trait measurements are from Hagge et al. (2021).

[**] Relative (Rel.) morphological traits are corrected for body length using residuals of linear models relating each log-transformed trait to log-transformed body length based on all species in Hagge et al. (2021).

[†] Ecological trait information comes from Seibold et al. (2015), and from unpublished data.

regions. These values were also scaled to range from specialist (zero) to generalist (one). These specialist-generalist scores could only be calculated for species detected at five or more sites in the combined dataset; for species detected at fewer trap sites (30%), we instead used the mean of the standardized local abundance and geographic range scores.

We combined these local abundance, geographic range, and habitat breadth components into a single rarity index for each study region ranging from the rarest (0) to the most common (1). We did this by taking a weighted average, in which the score for each component was down-weighted by its correlation with the other two using the formulas of Leitão et al. (2016). Local abundance varied by region for each species, but range size and habitat breadth scores were the same among regions. Mean local abundance for species (averaged across regions) was weakly correlated with geographic range ($R^2 = 0.20$; $p < 0.001$) and habitat breadth ($R^2 = 0.40$; $p < 0.001$), but range and habitat breadth were not correlated with each other (Fig. S3).

Species that were excluded for lack of trait data were rarer on average in each region than were species that had trait information (Fig. S4; $p < 0.01$). Rarity index values were unimodally distributed in each of the three regions (Fig. S5). Rarity differed with red list status of species in Norway and Germany (Fig. S6; $p < 0.05$) but not in Finland where few species were red listed. For species shared among pairs of regions, rarity among regions was highly correlated (Fig. S2; $R^2 = 0.77–0.86$). Any rarity index based partially on occurrence records is influenced to some extent by probability of capture as well as rarity. Detection probabilities of most beetle species cannot be quantified using currently available data, but we have no indication that trapability of individuals is not randomly distributed among rare and common species.

2.4. Functional indices

We calculated three complementary measures of functional structure, including functional richness, functional specialization, and functional originality, using the methods of Leitão et al. (2016), and the traits presented in Table 1. For each region, we first calculated the Gower distance (Pavoine et al., 2009) between all species using the 'cluster' (Maechler et al., 2019) package in R (R Core Team, 2021). Gower distance allows computation of distance using a combination of continuous and categorical (both ordered and unordered) traits (Gower, 1971). We then ran a principle component analysis (PCoA) with Cailliez correction on this functional distance matrix (Paradis and Schliep, 2019). To determine the number of PCoA dimensions necessary to represent the functional distances among species, we used the R function presented by Maire et al. (2015) and found that five PCoA dimensions were sufficient in each of our bioclimatic regions. Functional richness, specialization, and originality have each been shown to be robust to differences in the number and identity of traits included, as well as the number of PCoA dimensions that are used (Leitão et al., 2016).

Functional richness of an assemblage of species is the total volume of the minimal convex polygon that contains all those species in multidimensional trait space. We calculated this volume based on the first five PCoA dimensions of functional diversity, using the 'geometry' package (Habel et al., 2019). In the scenarios of species loss, functional richness at each species removal simulation step was standardized as a proportion of the total volume filled by the entire species pool in a given dataset. Functional specialization was calculated as the mean distance (in multi-dimensional functional space) between each species and the average position of all species present. Functional originality was calculated as the mean distance between each species and its nearest neighbor. Both functional specialization and functional originality were standardized to be between zero and one, by dividing them by their respective maximum values observed over all species in a dataset (Leitão et al., 2016). These three functional structure metrics were based solely on traits of all species present and thus were not influenced by species' rarity.

2.5. Simulating scenarios of species loss

Rare species are often those that are most at risk of extinction (Davies et al., 2004; Harnik et al., 2012). Losses of species due to regional extinction will reduce the species pool available to occupy sites in that region, so it is useful to know how the loss of rare (or common) species would impact the functional structure of the regional species pool as a whole. However, at the scale of local assemblages, rare species could on average be either less or more important for functional structure relative to the regional scale. Extirpation of large numbers of common species is unlikely, but comparing the effects of rare vs. common extirpations is useful to contrast these species' contributions to functional structure. Therefore, we simulated two scenarios of species loss at both the regional and the local level: rare species lost first, and common species lost first. At both scales, we additionally removed species randomly as a null model comparison. Both the regional and local species loss simulations were conducted separately for each of our bioclimatic regions (Norway, Finland, and Germany). In totally, we completed 27 simulations at the regional scale (3 bioclimatic regions * 3 functional indices * 3 species loss scenarios), and the same 27 simulations were conducted at local scale as well. In each case, a 'local' site is a single beetle sampling location consisting of one or more traps placed within 25 m of each other. We used the same rarity index for local and regional species loss in a given region because our rarity index included both local and global measures of rarity.

For the regional simulations, we started with the full species pool in each region, then removed species one at a time according to each of the three scenarios and calculated each of the FS indices at each step. For the random species loss scenario, we ran 500 simulations with species removed in a different random order each time. This random scenario provided a baseline against which to compare the rare-first and common-first scenarios.

In local communities, species removal simulations are complicated because most local samples contain few of the rarest species. This is in part because comprehensive sampling of diverse communities is difficult (Martikainen and Kouki, 2003; Burner et al., 2021a), but is also because rare species by definition occur in fewer locations than do more common species. To account for variable sampling effort, we excluded sites with <80% estimated sampling completeness based on the *iNext* R-package from Hsieh et al. (2016). We chose to present results from this cutoff value because it selected sites ($n = 309$, 136, and 89 in Norway, Finland, and Germany, respectively) with relatively high sampling coverage without eliminating too many sites. To check the robustness of our results to this cutoff value, we also report results from a stricter 90% threshold, repeating the same analyses for this subset of 151, 67 and 20 sites, respectively (Fig. S8). In the sites that met the 80% cutoff, we detected an average of 52.8, 63.2, and 22.5, species per site in the three regions (Fig. S7a). In these local samples (each from a unique trap site), an average of 6.0% of detected species came from the rarest 25% of species in the region for Norway and Finland, which was lower ($p < 0.01$) than the mean 10.2% rare species found per site in Germany (Fig. S7b). This means that removing even the rarest 15% of species from a local sample would result in the removal of many species that are not especially rare. For this reason, our local species loss scenarios estimated the change in each measure of functional structure when all species belonging to the rarest 25% of species (based on each regions' rarity index) were removed from each local community. We then compared this change to the effects when we removed an equal number of the most common species at a site. Finally, we conducted 100 simulations per site in which we removed this same number of species, but with species chosen at random, to determine where our rare and common species removal scenarios fell in this distribution of expected values under a null model. Calculating the percentile of this null distribution into which the rare and common removal scenarios fell for each site allowed us to test if the rare- or common-species removal scenarios had a disproportionately high (or low) effect on functional structure relative to random species

removals.

3. Results

3.1. Regional species loss

At the regional level, functional richness declined more rapidly when rare species were removed first than it did when common species were lost first in each region (Fig. 3). This effect was most pronounced in Finland, where functional richness was below the 95% CI of the random simulations when fewer than 5% of the rarest species were removed. Functional specialization was similar among removal scenarios when only 5% of species were removed, but was lowest in the rare species loss scenario when 25–75% of species were removed in each region. The same was true for functional originality. Although both rare and common species removal scenarios were often within the outer bounds of the null simulation, there was a consistent tendency for functional structure measures to be lower when rare species were removed first.

3.2. Local species loss

At the local level we also found clear evidence that the rarest species contribute more to functional structure than do the most common species. Functional richness, specialization, and originality were lower when the rarest species were removed than when an equivalent number of most common species were removed in all three regions (Fig. 4). The only exceptions were that functional originality was slightly higher in Norway when rare species were removed, and that functional

specialization in Finland did not differ among the two scenarios. However, mean values of most metrics of functional structure in all regions fell within the middle third of expected distributions from the null model, indicating that on average both the rarest and the most common species differ subtly rather than drastically from the overall mean. Results were similar for Norway and Finland when only sites meeting a stricter 90% sampling completeness threshold were included (Fig. S8). In Germany, however, removal scenarios did not differ significantly from each other or from the null model for any metric when using this 90% cutoff, likely because of the small number of sites that remained (n = 20; Fig. S8).

4. Discussion

Effects on functional structure from simulated removal of either the rarest or the most common wood-living (saproxylic) beetle species were most pronounced at the scale of regional species pools in our three study regions in forests of central and northern Europe (Fig. 3). Each metric of functional structure declined rapidly when rare species were removed, relative both to the removal of common species and to random removals. At the local scale, these measures were also lower when rare species were removed first, although both rare- and common-species removal scenarios fell within the range of values that are possible due to chance (null expected distributions; Fig. 4). Nonetheless, consistent results across multiple regions and at multiple scales highlight that the contributions of rare species to the functional structure of communities are unique relative to their common counterparts.

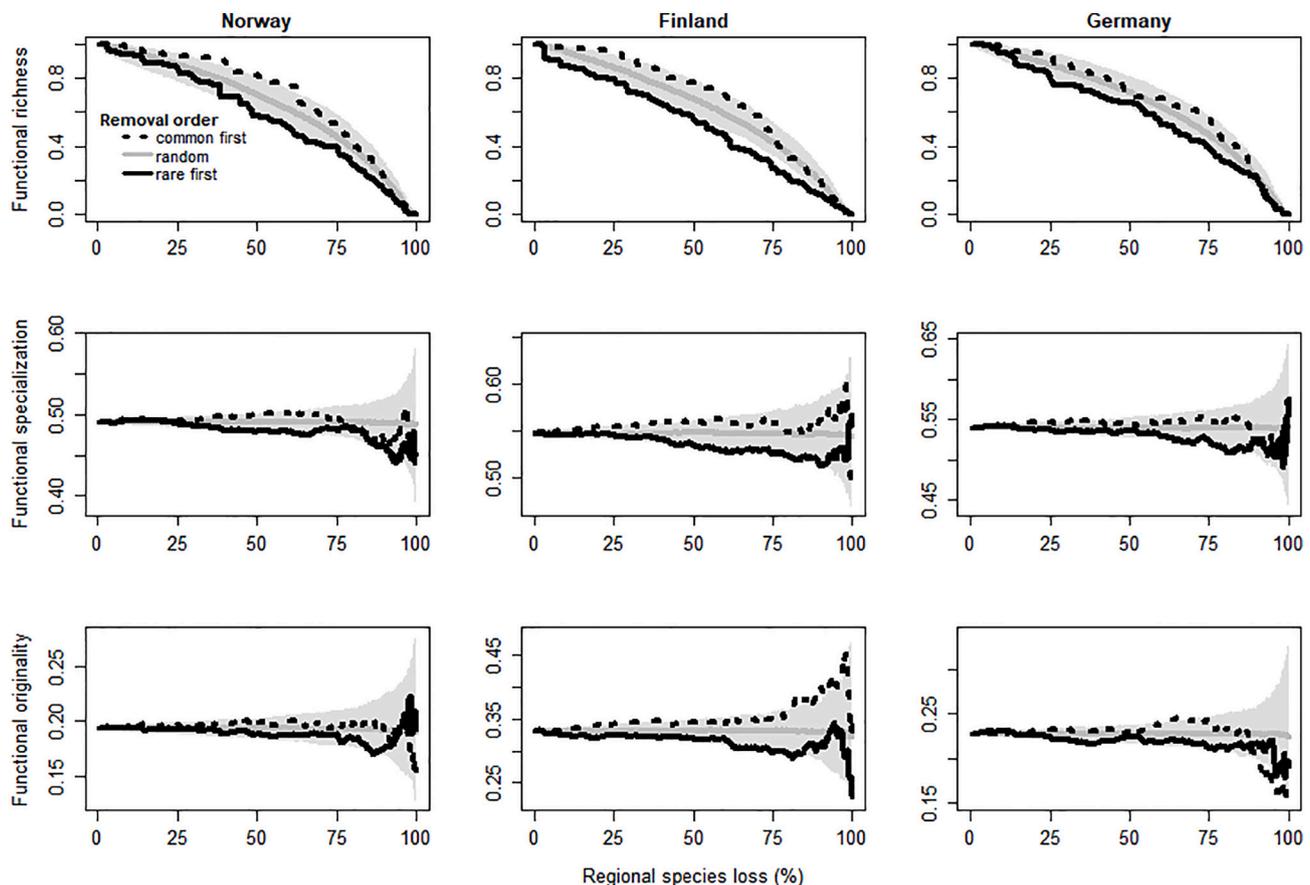Local rarity among our three bioclimatic regions was strongly

Fig. 3. Changes in three measures of functional structure (rows) of saproxylic beetle assemblages as species are lost from the regional species pool in three bioclimatic regions of Europe (columns). Losses were simulated according to three scenarios: rare species lost first (solid black line), common species lost first (dotted black line), and species lost in a random order (solid gray line; gray ribbon shows 95% CI from 500 simulations). Species rarity was assessed using a three-part index that combined of local abundance, geographic range, and habitat breadth.
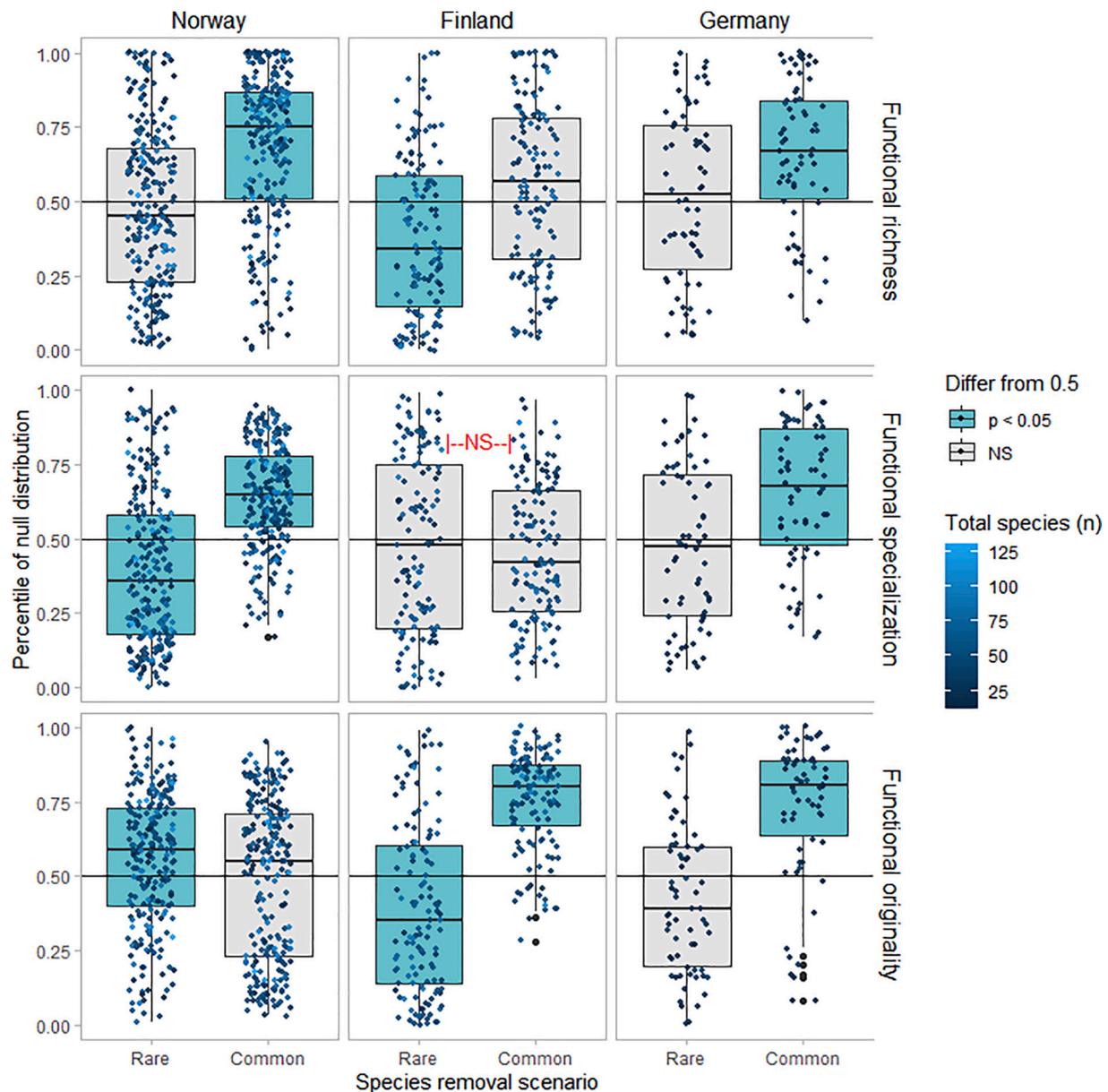
Fig. 4. Changes in functional structure after simulating removal of the rarest beetle species, or an equal number of the most common species, from local communities. Only sites where sampling completeness exceeded 80%, based on estimates from the *iNext* R-package (Hsieh et al., 2016), were included. For results when a stricter 90% cutoff was chosen, see Fig. S8. These rare- and common-species removal scenarios (X-axis) were compared to 100 null model simulations at each site in which an equivalent number of random species were removed. Values (Y-axis) represent the percentile of this null distribution into which each scenario fell, indicating how rare and common species compare to the community as a whole. For the rare-species removal scenario, all species falling in the lowest quartile of rarity scores in a given region (column) were removed. The number of these species detected at a given site determined how many of the most common (and random) species were removed for the common-species and null scenarios, respectively. In each simulation, we calculated three metrics of functional structure (rows; see Fig. 1 for details). Sites were also excluded that had no species from the rarest quantile, or that would have had fewer than ten species remaining after removals. Means differ among rare and common scenarios in all plots ($p < 0.05$) except the center plot (marked 'NS'). Boxplots with mean values that differ ($p < 0.05$) from the median of the null simulation (0.5) are colored blue green. Each point represents a single sampling site, and point color indicates total species richness. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

correlated for those species detected in two or more of the regions. This is noteworthy, because some rare beetles in Europe appear to be common in central Asia, and vice versa (Müller et al., 2013), probably because of differences in timber harvest and forest fire regimes. Rarity is thus to some extent a function of land use and the resulting environmental conditions, rather than being intrinsic to species themselves. Some of the rarest forest beetles in Europe are those relying strongly on dead wood (Nieto and Alexander, 2010), likely because forest management practices across Europe aim to maximize yields and reduce natural disturbances, thereby reducing the amount and diversity of

coarse woody debris. Red list status was only weakly linked to rarity of our species, probably because the IUCN criteria focus more on declining populations than on rarity itself (Gärdenfors et al., 2008).

Globally, a substantial number of invertebrates are thought to be threatened or endangered, and thus considerable losses of species in many ecosystems are likely (Dirzo et al., 2014; Sánchez-Bayo and Wyckhuys, 2019; Wagner, 2020). We show that losses of relatively few species can have substantial impacts on the total functional space occupied by a community, as well as on the amount of functional redundancy among species. This is particularly troubling because rare

species are typically those that are most prone to extinction (Davies et al., 2004; Régnier et al., 2015). Our simulations can provide important insight into the functional structure of assemblages, revealing that rare species are more unique, less functionally redundant, and more broadly distributed in multidimensional trait space than are their more common cousins. Therefore, non-random species loss can have a disproportionate effect on ecosystem function (Soliveres et al., 2016a; Engel et al., 2017).

One limitation of our study, and any such study, is that it is challenging to sample rare species (Martikainen and Kouki, 2003), and we have no doubt failed to detect many species that were locally present (Burner et al., 2021a), and some from the regional species pools as well. We also had to remove species for which trait information was not available, and these species were somewhat rarer on average than were the species that were retained (although we did have traits for the majority of even the rarest species). However, we compiled beetle sampling records from nearly 1000 sites in three bioclimatic regions of northern Europe, and used the most comprehensive database of beetle morphological traits available (Hagge et al., 2021), allowing us to characterize the beetle assemblages that we studied. Our results should thus be representative of the rarest subset of saproxylic beetles in these regions. When combined with similar results from other taxa (Leitão et al., 2016; Zhang et al., 2022), this builds a strong case for the ecological value of preservation of rare species.

Coincident with an increased appreciation for the value humans receive from ecosystem services (Farley, 2012; Polasky et al., 2015), attention in biodiversity research in the last two decades has similarly broadened (IPBES, 2019). Conservation biologists now look beyond species richness and turnover to consider functional diversity as well (Kondratyeva et al., 2019). There is empirical evidence (Larsen et al., 2005; Aanderud et al., 2015), as well as theoretical support (Säterberg et al., 2019), for the importance of rare species to ecosystem functions and for the disproportionate impacts that could result from their loss. The extent of these impacts, though, may depend on the functional and trophic structure of the community as a whole (Heilpern et al., 2018), and on the measures of rarity used (Jain et al., 2014). Common species also appear to provide unique contributions to functional structure in some cases (Chapman et al., 2018). The present study has demonstrated the unique contribution that rare beetle species make to functional structure. Although the connection between the functional structure of communities and the function of ecosystems is less well studied (Dee et al., 2019), these examples suggest that the importance of common and rare species to functional structure, and therefore to ecosystem functionality, is context dependent. However, our study provides evidence that rare species play an exceptionally important functional role in saproxylic beetles. To safeguard the rare, specialist species, forest structures that are prevalent in old growth forest but largely absent from modern industrial forests must be preserved (Brumelis et al., 2011; Jonsson et al., 2016; Schowalter, 2017; Watson et al., 2018; Jacobsen et al., 2020; Burner et al., 2021b). These include abundant decayed coarse woody debris, burned dead wood, and hollow trees. Measures and instruments to identify and protect forests with high conservation value must also be strengthened.

Today, however, the trend is rather the opposite. Intact forests worldwide (defined as >500 km^2 with no human pressure) declined by 7% from 2000 to 2013 (Potapov et al., 2017). A study of recent global forest loss trends demonstrated accelerating rates of forest loss even within protected areas, and the trend was more pronounced in the highest protection IUCN categories (Leberger et al., 2020). In the Nordic countries, represented by two of the three countries studied here, protection of sufficient proportions of forest of high conservation value, which likely hosts a disproportionate share of rare species, is hotly debated.

In order to safeguard intact forests and counteract these negative trends, the recent UN Global Forest Goals Report 2021 (United Nations Forum on Forests Secretariat, 2021) emphasizes the need to focus on the socio-economic benefits that forests provide to critical development issues such as poverty eradication, income generation, employment, health, and food security. The post-2020 biodiversity framework must target this connection between functionally intact forests, biodiversity conservation, nature-based solutions to climate change, and human well-being (Maxwell et al., 2020; Seddon et al., 2021).

We found that rare species contribute disproportionately to the functional structure of beetle communities, as in a variety of other taxa (Leitão et al., 2016; Zhang et al., 2022). This pattern is consistent, although not universal. It is a reasonable inference that community functional structure is linked to ecosystem function, but experimental research describing this connection should be a priority when possible (Dee et al., 2019), such as recent work with plant communities (Cadotte, 2017; Fanin et al., 2019), to move beyond the limited inferences available from observational studies. Arguments from the perspective of functional structure and diversity make important contributions to the broader conservation rationale and agenda; more direct evidence for the link between functional structure and ecosystem functions could help better prioritize conservation effort.

Data availability

Data are available on Zenodo: https://doi.org/10.5281/zenodo.5950610

CRediT authorship contribution statement

Declaration of competing interest

The authors have no conflict of interest to declare.

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.biocon.2022.109491.

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