

Functional Ecology

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Title: Hierarchical trait filtering at different spatial scales determines beetle assemblages in deadwood

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Conflicts of interest

The authors declare no conflicts of interest.

Author's contributions

FN and MMG developed the ideas for the study, JH and RA helped to refine them and FN, MMG, JH and RA set up a first manuscript draft. FN analysed the data. All others provided data and contributed substantially to the revisions of the manuscript.

Data availability statement

This study is based on data originating from several projects conducted in the Biodiversity Exploratories programme (DFG Priority Program 1374). The data are archived in the Biodiversity Exploratories Information System (<https://doi.org/10.17616/R32P9Q>) and are publicly available or will become publicly available after an embargo period of 5 years after the end of data collection. Additional data, which are needed to reproduce the analyses, are archived in the Zenodo repository: <https://doi.org/10.5281/zenodo.7092201> (Neff et al., 2022). All R code relevant to reproduce the analyses is available from the repository located at https://github.com/nefffl/fcnt_blngdd.

SECOND ABSTRACT

1. Umweltfilter – einschliesslich solcher, die sich aus biotischen Wechselwirkungen ergeben – bestimmen massgeblich, wie sich lokale ökologischen Gemeinschaften aus einem Pool regional verfügbarer Arten zusammensetzen. Dabei spielen hierarchisch verschachtelte Filter auf verschiedenen räumlichen Ebenen eine Rolle. Diese wurden selten in Relation zueinander quantifiziert.
2. Totholzkäfer sind sehr gut geeignet, um solche hierarchisch verschachtelten Umweltfilter zu untersuchen. Hier schlagen wir drei räumliche Ebenen vor, auf denen

Umweltfilter die Zusammensetzung von Totholzkäfergemeinschaften beeinflussen.

Erstens müssen die Arten, ausgehend von einem regionalen Artenpool, geeignete Waldstandorten erreichen. Zweitens müssen die Arten innerhalb eines Standorts ein Habitat mit den bevorzugten mikroklimatischen Bedingungen finden. Drittens bestimmen die Charakteristika eines einzelnen Totholzobjekts (d.h. Baumart, Zersetzungsstadium) innerhalb des Habitats, welche Arten sich ansiedeln und etablieren.

3. Um die hierarchischen Filter zu untersuchen, nutzten wir einzigartige Langzeitdatensätze zu Totholzkäfergemeinschaften aus Fallenfängen an 29 Standorten und aus Emergenzfallen an 694 experimentell ausgebrachten Totholzstämmen an denselben Standorten in drei Regionen in Deutschland. Um die verschiedenen Umweltfilter mit den Käfergemeinschaften in Beziehung zu setzen, verwendeten wir 13 funktionelle Merkmale, von denen erwartet wird, dass sie mit verschiedenen Filtern auf verschiedenen Ebenen in Verbindung stehen.
4. Wir zeigen, dass Filter auf allen drei räumlichen Ebenen zu einer Verringerung der funktionellen Vielfalt und gleichzeitig zu Verschiebungen in der funktionellen Zusammensetzung von Käfergemeinschaften führten. Die funktionelle Zusammensetzung änderte sich am stärksten auf der letzten räumlichen Ebene, d.h. sie war stark abhängig von der Baumart und dem Zersetzungsstadium.
5. Indem wir in einem hierarchischen, mehrstufigen Prozess analysieren, wie sich Gemeinschaften zusammensetzen, zeigen wir, dass Umweltfilter auf verschiedenen räumlichen Ebenen die Totholzkäfergemeinschaften prägen. So können wir die Rolle, welche verschiedene Filter auf verschiedenen räumlichen Ebenen spielen, besser verstehen.

ABSTRACT

1. Environmental filters – including those resulting from biotic interactions – play a crucial role during the assembly of ecological communities. The importance of scale has thereby been acknowledged but filters at different scales have rarely been quantified in relation to each other, although these hierarchically nested filters eventually determine which communities assemble from a regional species pool.
2. Saproxylic beetles offer an ideal system to study such hierarchically nested environmental filters. Three steps of filtering during the community assembly of these deadwood-dependent beetles are proposed. First, starting from a regional species pool, species must disperse to forest sites. Second, within a site, individuals need to find a patch with preferred microclimatic conditions. Third, the conditions of a single deadwood object (i.e. tree species identity, decomposition stage) at this patch will determine, which species colonise and establish.
3. To study these hierarchical filters, we used unique long-term data sets of saproxylic beetle diversity from trap catches at 29 sites and from emergence traps on 694 experimentally installed deadwood logs at the same sites in three regions in Germany. To relate different environmental filters to beetle assemblages, we used a set of 13 functional traits that are hypothesised to relate to different filters at different scales.
4. We show that all three hierarchical filtering steps resulted in reductions of functional diversity and simultaneous shifts in the functional composition of beetle assemblages, reflecting the roles of different traits in response to different filters. Trait composition changed most strongly at the last filtering step, i.e. depended on tree species identity and decomposition stage.

5. We showed that if community assembly is analysed as a hierarchical multi-step process based on data from different spatial scales, environmental filters can be quantified at these scales. As such, a better understanding of the role that different filters play at different spatial scales can be reached.

KEYWORDS

community assembly, deadwood, functional traits, saproxylic beetles, scale-dependency,
trait-based ecology

INTRODUCTION

What determines the composition of communities is a question at the very core of community ecology, which manifests in the concept of community assembly (Diamond, 1975). During community assembly, species whose traits facilitate their colonisation, establishment and persistence under the prevailing environmental conditions and biotic interactions are filtered from a pool of regionally available species (Cadotte & Tucker, 2017; Keddy, 1992). Such filters can act at different spatial scales (Jiménez-Alfaro et al., 2018), ranging from small-scale microhabitat conditions and priority effects during microhabitat colonization (Song et al., 2017) up to landscape-scale or even continental and global scale factors (Harmon-Threatt & Ackerly, 2013; Mori et al., 2018). Thus, the assembly of local communities can be framed as a process of several hierarchical filtering events (Bauer et al., 2021). Studies addressing community assembly as a multi-scale process indicate the role of different mechanisms acting at different scales (e.g. Bae et al., 2021). Understanding how different filters select for different subsets of species at a progressively smaller spatial scale requires that sampling of communities occurs at these different scales simultaneously.

The community assembly of saproxylic, i.e. deadwood-dependent, beetles on single deadwood logs in forests presents an ideal model for studying filtering at different spatial scales (Seibold et al., 2015). Species colonising and establishing on a single deadwood object must first, starting from a regional species pool, overcome dispersal barriers and find suitable sites; second, locate patches with preferred microclimatic conditions at these sites; and third, colonise and establish on a deadwood object with matching characteristics (e.g. tree species identity, decomposition stage) at this patch (Fig. 1). Some characteristics of deadwood objects might already affect community assembly at larger spatial scales through visual and olfactory cues (Graf et al., 2022), but which characteristics are important at which scale is not known.

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In this study, we assessed saproxylic beetle assemblages at different spatial scales to infer how hierarchically nested filters jointly affect community assembly, with different filters playing a role at different scales. In the first filtering step (henceforth ‘region-to-site’), a subset of the species from the regional species pool forms the assemblage of a particular site, e.g. a forest stand. Filters are the surrounding landscape, as well as local forest stand properties. Important landscape properties might be forest cover, large-scale heterogeneity and the occurrence of old-growth forests providing large amount of deadwood and thus source populations (Müller et al., 2020; Sverdrup-Thygesen et al., 2014). Forest stand properties that affect colonisation and establishment of saproxylic beetles include deadwood amount and diversity, tree species composition, and forest structure (Burner et al., 2021; Gossner et al., 2016; Müller & Bütler, 2010). In the second filtering step (henceforth ‘site-to-patch’), not all species occurring at a site also occur at a particular patch. Microsite characteristics (temperature, humidity) and the deadwood available at the patch (size; orientation, i.e. standing/laying) can act as filters (Gossner et al., 2016; Müller et al., 2020; Seibold et al., 2015; Vogel et al., 2021). In the third filtering step (henceforth ‘patch-to-object’), deadwood species identity and decomposition stage influence which saproxylic beetle species colonise and establish on a particular deadwood object (Burner et al., 2021; Gossner et al., 2016; Müller et al., 2020; Vogel et al., 2021; Wende et al., 2017). Filters at this third step are particularly important determinants of saproxylic beetle community composition (Burner et al., 2021; Müller et al., 2020). Because wood characteristics of different tree species are expected to converge with ongoing decomposition and species-specific defence compounds become less important (Lachat et al., 2013; Stokland et al., 2012), beetle assemblages tend to be strongly bound to certain tree species at earlier decomposition stages, but these tree-identity effects diminish with ongoing decomposition (Seibold et al., 2022). Comparing community composition at the

different spatial scales and identifying which filters affect what species will improve our understanding of community assembly of saproxylic beetles.

Functional traits are important for understanding the link between organisms and their roles in the environment (McGill et al., 2006). Trait-based studies are thus recommended to predict patterns in biodiversity and ecosystem functions across space and time (Wong et al., 2019). Various traits might be involved in saproxylic beetle community assembly (Table 1). First, traits related to dispersal affect which species arrive at a site (region-to-site step). These include traits such as wing length or load, but also sensory traits, such as antenna length, that affect the ability to locate suitable habitats (Elgar et al., 2018). Second, traits related to habitat preference can determine whether a site or a patch are suitable for colonisation (region-to-site and site-to-patch steps). For example, a species' body colour might define its preferred ranges of solar radiation (Clusella-Trullas et al., 2008), which varies among differently open habitats. Third, traits related to small-scale locomotion determine how successful a species locates and moves to deadwood objects within a site (site-to-patch step). For instance, sensory traits, such as eye size, can affect if a deadwood object is found (Fountain-Jones et al., 2015). Fourth, traits related to microhabitat use influence whether a species will establish and propagate on a deadwood object (site-to-patch and patch-to-object steps), with microhabitat being defined both by the immediate surroundings, as well as by deadwood characteristics (orientation, size, species identity, decomposition stage). Traits such as body size and shape can determine which microhabitats a species uses (Hagge et al., 2021).

Here, we studied assemblages on deadwood logs of twelve different tree genera that were placed at different forest sites during a large-scale experiment across three regions in Ger-

many. We combined long-term community data collected from these logs at different decomposition stages with long-term data collected at the surrounding forest sites with multiple traps (Fig. 1). Based on a trait-based approach, we addressed the following hypotheses:

- H1 In the studied landscapes where forest types vary at small scales and old-growth forests are largely missing – a situation typical for Europe – the strongest filters act at the patch-to-object filtering step (related to tree genus identity and decomposition stage).
- H2 Different traits are filtered at different hierarchical filtering steps; dispersal traits at the region-to-site step, habitat preference traits at the region-to-site and site-to-patch steps, fine-scale locomotion traits at the site-to-patch step and microhabitat-use traits at the site-to-patch and patch-to-object steps.
- H3 Tree genus identity filters differ more strongly between tree genera at the beginning of decomposition, because wood characteristics and thus microhabitat are strongly determined by tree genus at this stage.

MATERIALS AND METHODS

Study system

The study was conducted within the framework of the Biodiversity Exploratories (Fischer et al., 2010), comprising field sites in three regions of Germany: The UNESCO Biosphere Reserve Schorfheide-Chorin ('SCH') in the North-East (52°47'25"–53°13'26"N, 13°23'27"–14°08'53"E; 10–140 m a.s.l.), the Hainich-Dün region ('HAI') with the National Park Hainich and its surroundings in the centre (50°56'14"–51°22'43"N, 10°10'24"–10°46'45"E; 285–550 m a.s.l.) and the UNESCO Biosphere Reserve Schwäbische Alb ('ALB') in the South-West (48°20'28"–48°32'02"N, 9°10'49"–09°35'54"E; 462–858 m a.s.l.). Field work permits were issued by the responsible state environmental offices of Brandenburg, Thüringen, and Baden-Württemberg (according to §72 BbgNatSchG). The study was conducted on 29 plots (9 in SCH, 11 in HAI, 9 in ALB; see Fig. S1 in Supporting Information for a detailed map) of 100 m × 100 m, which covered the main forest management types in each region (Fischer et al., 2010 for details). The plots included unmanaged beech forests (3 in ALB/SCH, 2 in HAI), where European beech (*Fagus sylvatica*), the climax species of forests in all three regions, was the dominating tree species (Leuschner & Ellenberg, 2017); differently managed beech forests, i.e. even-aged stands of different developmental stages in all three regions (3 per region), and uneven-aged forests in HAI (3); and forest stands consisting largely of non-naturally occurring coniferous trees (*Picea abies* in ALB/HAI, *Pinus sylvestris* in SCH) (3 per region).

The Biodiversity Exploratory Long-term Deadwood experiment ('BELongDead') was set up in 2009. In each study plot, logs of 13 tree genera were exposed (Table S1), replicated at three subplots. We only used logs of 12 genera (*Prunus* had incomplete replication) and one

subplot (beetle sampling was only conducted on this subplot across all years). In total, 347 logs were analysed (one replicate of *Larix* was missing). The logs were approx. 4 m in length and 31 ± 5.9 cm (mean \pm SD) in diameter. All logs originated from trees that were cut in winter 2008/2009 in the state of Thuringia (Germany). The 13 logs per subplot covering all tree genera were randomly placed next to each other (approx. 1 m apart; see Fig. S2). Prior to log placement, a protocol to minimize the potential bias by colonization of logs prior to translocation was followed (Gossner et al., 2016 for details).

Environmental filters

Different potential environmental filters for community assembly of saproxylic beetles were assessed at site scale (100 m \times 100 m study plot) and at patch scale (subplot where the logs were placed) (see Table S2 for inclusion rationale). At site scale, these included the forest cover in the plot surroundings (2000 m radius), total deadwood volume, tree species composition, and stand structural complexity. Canopy closure was quantified at site scale across the whole plot as well as at patch scale directly above the subplots where the logs were placed. Tree species composition was quantified with nonmetric multidimensional scaling (NMDS) based on recorded basal areas of tree species on the plots. NMDS axis 1 represented a gradient from coniferous to broadleaf (beech) forest (henceforth ‘broadleaf share’), whereas NMDS axis 2 represented a regional gradient from ALB and HAI plot to SCH plots defined by the different stand-forming conifer types present in the region (*Picea* in ALB and HAI; *Pinus* in SCH) (henceforth ‘conifer type’) (see Fig. S3). For details on environmental filters, see Appendix S1.

Saproxyllic beetle assemblages and traits

We used a wide array of sampling techniques to ensure a high coverage of the saproxyllic species assemblages at a plot (site scale) (Fig. 1a). Flight-interception traps in the understory (2008–2016) and in the canopy (2008–2010) as well as pitfall traps (2008–2010) were used to sample flying and ground-dwelling beetles. To assess community assembly at the dead-wood logs, beetles colonizing and developing in the logs were monitored during eight years (2010–2017) using closed emergence traps. Adult beetles were identified to the species level by taxonomic experts (cf. Acknowledgements) and only saproxyllic species (Schmidl & Bussler, 2004) were used for analyses. Further details on sampling procedures are given in Appendix S1.

To describe the beetle assemblages functionally, we used 13 morphological traits (Table 1; Hagge et al., 2021). Details on trait measurements and sources are given in Appendix S1.

Statistical analyses

All analyses were performed in R v. 4.0.0 (R Core Team, 2020).

Species pools and null models

In the multi-step framework investigated here, the assemblage at one spatial scale will not only be determined by filtering, but also by the composition of the higher-scale species pool. Thus, observed assemblages need to be compared to random assemblages from the relevant species pool (i.e. next higher scale) to detect environmental filtering (Chalmandrier et al., 2013). Therefore, assemblages / species pools were formed at four different scales to analyse the three filtering steps (Fig. 1): Object, patch, site, and region. The object-scale assemblage was defined as the pooled abundance of all emergence traps records on each log made across

years of two different time periods. This was done to account for differences in decomposition stage: the 1st period representing earlier decomposition stages (2010–2013) and the 2nd period representing later decomposition stages (2014–2017). The patch-scale assemblage / species pool was determined by pooling all observations from emergence traps across all eight sampling years and across all twelve logs per plot. To determine the site-scale assemblage / species pool, species abundance data recorded by the four different sampling methods were combined (flight-interception traps at two heights, pitfall traps and emergence traps). To this end, each sampling data set was pooled per plot and across all years and then standardised by setting the total abundance per plot and sampling to 1. Then, the different sampling data sets per plot were summed, representing the site-scale assemblage / species pool. Finally, the regional species pool was composed of the sum of all site-scale species pools in a region (SCH, HAI, ALB).

A null-model approach (Gotelli & Graves, 1996) was used to analyse filtering at each spatial scale. Besides accounting for previous filtering by explicitly comparing observed assemblages to random assemblages from higher-level species pools, null models also correct for differences in functional measures, such as functional diversity, that are driven solely by species richness and abundance distribution (e.g. Botta-Dukát & Czucz, 2016). We used a null-model approach where assemblages were randomly compiled from the one higher-scale species pool while leaving species richness and abundance distribution constant (Fig. 1b), an approach suitable to detect environmental filtering (Götzenberger et al., 2016). For each of the three filtering steps, these null-model draws represented expected community composition in the absence of any filtering. To better account for the abundance distribution in the species pools, which might largely shape the abundance distribution in an observed assemblage, drawing probability for the null models was chosen to be proportional to species abundances.

As such, ecologically unrealistic scenarios, such as rare species becoming dominant (Mori et al., 2015), were less likely to be included in the null models. Technically, species names were drawn randomly from the next higher species pool with probabilities being proportional to species abundances within this higher pool and assigned sequentially to the observed abundances of the focal-scale pool, starting from the highest reported abundance. Thus, species richness and abundance distribution were the same in the observed pool and in the null-model representations. For each observation, 1999 null models were generated.

Community weighted means and functional diversity

To assess whether environmental filtering was taking place at the different scales and which traits were related to the different environmental filters, we assessed community weighted means (CWMs) and functional diversity (FD). Changes in CWMs of observed assemblages that differed from null-model based expectations showed shifts in the functional composition of communities. In combination with a reduction of FD (compared to null-model expectations), such changes indicated environmental filtering. CWMs of all 13 traits were determined from observed and null-model assemblages at different scales (site, patch, object) and from species-level functional traits for each observation unit (study plot for site and patch scale; single logs for object scale) as

$$\text{CWM} = \sum_{i=1}^N p_i x_i \quad (1)$$

where N is the number of species, p_i is the relative abundance of species i in the observation unit, and x_i is the trait value of species i . FD was determined based on twelve of these traits (wing aspect was excluded because of missing values for apterous species) using Rao's Q (Botta-Dukát, 2005) calculated as

$$\text{FD} = \sum_{i=1}^{N-1} \sum_{j=i+1}^N p_i p_j d_{ij} \quad (2)$$

where N is the number of species, p_i is the relative abundance of species i , p_j is the relative abundance of species j , and d_{ij} is the Euclidean distance between species i and j based on all twelve traits (centred and scaled to unit variance). Rao's Q is a suitable measure for FD that allows to detect environmental filtering during community assembly (Botta-Dukát & Czúcz, 2016). Both CWMs and FD were calculated with the package 'FD' (Laliberté et al., 2014).

Linear models

Each filtering step (Fig. 1b) was analysed using a separate linear model with different predictor variables. Response variables were the differences between observed and null-model averaged values for all CWMs and for FD. For example, at the region-to-site step, there was one observed FD value and one null-model FD average for each plot, resulting in 29 differences that were analysed at this step. Replicate numbers for the other steps were 29 (site-to-patch) and 694 (patch-to-object). In the model of the region-to-site filtering step, predictor variables included forest cover in the plot surroundings, deadwood volume, broadleaf share (NMDS axis 1), conifer type (NMDS axis 2), stand structural complexity and site-scale canopy closure (Table S2 for rationales). In the model for the site-to-patch filtering step, deadwood volume, stand structural complexity and patch-scale canopy closure were included as predictors (Table S2 for rationales). In the model for the patch-to-object filtering step, decomposition stage (1st or 2nd period), tree genus identity and their interaction were included (Table S2 for rationales). The model for this last filtering step included additional random intercepts for plot and log identity. These linear mixed effect models were fitted using the package 'glmmTMB' (Magnusson et al., 2020). To compare effect sizes for continuous and factor variables, all continuous predictors were scaled to SD 0.5 at the level of recording prior to analyses (Gelman & Hill, 2007). For different scenarios (1 SD increase for continuous var-

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iables while leaving all other variables constant for the first two filtering steps; different combinations of decomposition stage and tree identity for the third filtering step), differences between CWM/FD values and null model means were predicted based on the models. These differences were transformed back to the original CWM/FD scale by combining it with the null-model averages for the respective CWM/FD. In this way, the effects of the different predictor variables across the three different filtering steps could be represented in the same space of absolute CWM/FD values. Prior to running the models, it was necessary to scale all predictor variables to mean 0 and to use sum-to-zero contrasts for factor variables, such that model intercepts represented means of response variables for all models.

RESULTS

The analyses were based on 123,552 individuals (4260 ± 1277 per plot; mean \pm SD) of 621 saproxylic beetle species (219 ± 44 per plot). The subset of log-based assemblages (patch and object scale) included 78,449 individuals (2705 ± 938 per plot; 226 ± 236 per log) of 485 species (156 ± 34 per plot; 44 ± 15 per log) (Table S3).

All three filtering steps affected community assembly of saproxylic beetles. Functional diversity (FD) decreased with each filtering step, with strongest decreases at the first two steps (region-to-site and site-to-patch) (Fig. 2, Fig. S4). At the region-to-site step, there was a clear reduction of FD in coniferous forests. Other potential filters, such as landscape properties, had no significant effect. At the site-to-patch step, the logs were strong filters per se, indicated by the strong reduction in FD observed for patch-based assemblages compared to what would have been expected based on the site-scale assemblages (Fig. 2). Furthermore, patch-scale FD was particularly low if patch-scale canopy closure was high. At the patch-to-object step, there was only a weak reduction in FD (Fig. 2). Tree genus identity was related to FD, which was driven by particularly high FD on *Fraxinus* logs. Neither decomposition stage nor the interaction of tree genus and decomposition stage were related to FD.

Community-weighted means (CWMs) were affected by the first two filtering steps, but the strongest effects were observed at the patch-to-object step (Fig. 3, Figs S5–S17). At the region-to-site step, CWMs of several traits related to dispersal and habitat preference (Table 1) were associated to corresponding filters (Fig. 3, Table 2). Particularly, CWMs were strongly related to broadleaf share. Compared to broadleaf forests, assemblages in coniferous forests had longer wings, higher wing loading, shorter bodies and longer antenna (traits related to dispersal), but also less round bodies and shorter heads (traits related to microhabitat use).

High canopy closure (site) changed CWMs of traits related to dispersal and habitat preference (longer and lighter bodies, shorter antennae), but also microhabitat use (rounder bodies and more robust mandibles). The other potential filters (forest cover in the surroundings, dead-wood volume, conifer type, stand structural complexity) showed no consistent relationships with CWMs (Table 2).

At the site-to-patch step, logs per se were strong filters for CWMs (Fig. 3, Table 2). Species that colonised a patch differed from the site-scale pool in terms of fine-scale locomotion and microhabitat-use traits (shorter bodies, shorter legs, smaller eyes, thinner bodies, shorter heads and less robust mandibles) and also had higher wing loading. Among filters analysed in this step, higher patch-scale canopy closure had most associations with CWMs and resulted in species with higher wing loading, less round bodies and less robust mandibles.

At the patch-to-object step, CWMs of all traits were strongly affected by tree genus identity, decomposition stage and their interaction. These filters were apparent for traits related to microhabitat use (e.g. mandibular aspect), but also for traits related to dispersal, habitat preference or fine-scale locomotion (e.g. wing aspect, antenna length, lightness) (Fig. 3, Table 2). For several traits, object-scale assemblages were functionally more dissimilar in the first period (2010–2013) than in the second period (2014–2017), as was evident by CWMs spanning a smaller range of values in the second period (Fig. 3).

Across filtering steps, the observed patterns mostly persisted when analyses were based on presence-absence data (Fig. S18). Relatively, effect sizes at the patch-to-object step were even larger compared to the analyses accounting for species abundances.

DISCUSSION

While all three hierarchical filtering steps from region to object scale were related to changes in functional diversity (FD) and community-weighted means (CWMs) of functional traits, CWMs were most strongly affected at patch-to-object scale, supporting H1 that strongest filters act at this last filtering step. At this filtering step, assemblages strongly diverged functionally between the different tree genera and decomposition stages, which also resulted in a slight reduction in FD compared to the patch-scale species pool. This corroborates findings from other studies that show a strong relation of the diversity and composition of beetle assemblages to tree identity (Gossner et al., 2016; Vogel et al., 2021) and decomposition stage (Müller et al., 2020). Additionally, CWMs of several traits were related to filters at the first two filtering steps and FD was most strongly reduced by these filters. This indicates that only species representing a subset of the available trait space arrived and established on the investigated logs.

At the region-to-site step, forest stand properties in general and tree species composition in particular showed to be the strongest filter. Assemblages in coniferous forests represented a smaller proportion of the functional space, a finding that is supported by results from saproxylic beetle assemblages in subtropical forests (Staab et al., 2021). Given that most saproxylic beetle species are specialised to colonise either gymnosperms or angiosperms and with more species found exclusively on angiosperms (Stokland et al., 2012), the smaller FD in coniferous forests might reflect a smaller species pool, particularly given the short history of coniferous forests in the study regions (see below). Other forest stand properties did not have clear relations to FD or CWMs. For deadwood amount, which is generally a strong driver of saproxylic beetle diversity (Müller & Bütler, 2010), the absence of clear effects might reflect the generally low deadwood amounts even in the study plots (5.8 m³/ha to 74.5 m³/ha with

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diameter > 7cm). These amounts diverge significantly from what is observed in unmanaged old-growth forests (Christensen et al., 2005). Thus, our gradient in the amount of deadwood may have simply not been wide enough to fully account for the importance of this factor. Landscape properties did not show any relation to FD or CWMs, supporting the view that saproxylic beetles are generally not strongly dispersal-limited (Komonen & Müller, 2018), at least at the investigated scale (2000 m). Additionally, old-growth forest specialists, which tend to be dispersal limited (Hagge et al., 2021), were largely missing from the studied assemblages (less than 0.1% of records from species categorised as primeval forest relict species; only 10 of 168 relict species recorded (Eckelt et al., 2018)) due to the lack of large-scale old-growth forests in the study regions (Nieto & Alexander, 2010). Thus, dispersal related trait-filtering might be more important in landscapes where these species are still present.

The reduction in FD and shifts in several CWMs between site-scale and patch-scale assemblages indicate that the investigated deadwood logs with their uniform orientation (laying) and size were a strong filter on their own. When deadwood stocks comprise different constitutions (size, orientation), species richness of saproxylic beetle assemblages (Seibold et al., 2015, 2016) and likely also FD are higher. Thus, our experimental setting probably underestimated the relevance of the patch-to-object filtering step under natural conditions. Particularly low FD was observed if logs were under a highly closed canopy. Canopy closure determines microclimatic conditions (Thom et al., 2020) with higher microclimate-induced habitat heterogeneity in sun-exposed deadwood (Lettenmaier et al., 2022). Our results indicate that under a closed canopy, lower habitat heterogeneity filters for a subset of the available pool characterised by certain traits.

Our hypothesis that different traits are filtered at different spatial scales (H2) was supported by the fact that CWMs of different traits changed during the different filtering steps, and relations mostly matched our detailed hypotheses (Table 1). Traits related to dispersal and habitat preference were expected to be affected by the first filtering step (region-to-site). We found strong relations to site-scale environmental filters for all these traits (except wing aspect). Most strikingly, species with traits related to lower dispersal capabilities (short wings, low wing loading, short antennae) were less abundant in forests with low broadleaf share. Because coniferous forests were only spreading in Central Europe during the last centuries due to targeted management and with a clear timber production focus (Leuschner & Ellenberg, 2017), many conifer specialists with low dispersal abilities might not yet have established in these forests (cf. Buse, 2012). Traits related to fine-scale locomotion were expected to be mostly affected by environmental conditions during the site-to-patch step, which could not be confirmed with our analyses. Instead, we found strong relationships of several traits (e.g. body length) to general patch-scale characteristics, most of which are related to microhabitat use and might reflect adaptation to the microhabitat conditions that generally apply for all logs (e.g. size, orientation). The patch-to-object step based on tree genus identity and decomposition stage was strongly associated with several traits. This shows that species' preferences for certain tree genera (Gossner et al., 2016; Vogel et al., 2021) or decomposition stages (Lee et al., 2014) are associated with certain trait characteristics. That this not only included traits related to microhabitat use likely reflects trade-offs or phylogenetic linkage among traits with different functions, i.e. that certain trait combinations are more common at the species level.

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Lastly, we hypothesised that tree genus identity filters differ more strongly among each other in the earlier decomposition stage (H3). In line with a study with a more taxonomic perspective (Seibold et al., 2022), CWMs for several traits showed a larger spread at the early compared to the later decomposition stage. With decomposition advancing, assemblages tend to get functionally more similar (converging CWMs), resulting in functional homogenisation among logs. Simultaneous changes in CWMs of some traits (e.g. mandibular aspect) across tree genera indicate the accompanying directed shifts in community composition, e.g. in terms of feeding guilds, following succession with ongoing decomposition (Stokland et al., 2012).

While this study was designed and envisioned to quantify environmental filters at different spatial scales, some limitations exist on how to interpret the results. Firstly, the framing of community assembly as a hierarchical process alone does not prove its validity. As expected, and shown by the results, characteristics of deadwood objects are crucially linked to the establishing saproxylic beetle assemblages such that beetles might directly navigate to suitable objects irrespective of the site or patch conditions (Graf et al., 2022), thus simply overcoming potential previous filters. Site and patch conditions might then rather affect establishment (i.e. survival rates), and not the colonisation. However, even though beetles might largely be guided by object-level cues, the probability of colonisation might still be highly dependent on the pool of species that are locally available and abundant. By not only sampling assemblages after successful colonisation (i.e. emergence traps) but also assemblages available for colonisation (i.e. flight-interception and pitfall traps), we were able to quantify a site's species pool largely irrespective of available deadwood objects. Thus, we could evaluate filters acting at larger than object scale, such as the filter imposed by tree species composition of stands, and

show that although saproxylic beetles might be largely guided by the availability of deadwood objects, site-specific conditions still play a role in defining the pool of available species. Secondly, we need to acknowledge that other mechanisms besides environmental filters also affect community assembly (Cadotte & Tucker, 2017), which were not specifically addressed here. Namely, biotic interactions might contribute greatly to the assembly of ecological communities (Bauer et al., 2021), particularly through species sorting at small spatial scales resulting in trait divergence, i.e. an increase in FD (Weiher & Keddy, 1995). Thus, we would expect the greatest contribution of biotic interactions to the patch-to-object step. That we found a slight reduction of FD at the object compared to the patch scale indicates that environmental filtering is the determining mechanism for saproxylic beetles. We cannot rule out that species sorting due to biotic interactions partly blurred filtering effects, which would, however, only strengthen our conclusions. Furthermore, we did not specifically address neutral mechanisms, such as ecological drift (Weiher et al., 2011). However, the strong relationship of the different filters to functional traits – generally following our initial hypotheses – in combination with the null-model approach clearly support the crucial role of environmental filtering in our study system (Cadotte & Tucker, 2017).

In the unique setting of a deadwood experiment embedded in forests differing in environmental conditions, we were able to simultaneously study several hierarchically nested steps of filtering during community assembly. Framing community assembly as a multi-step process, which has been proposed frequently (e.g. Cadotte & Tucker, 2017; Jiménez-Alfaro et al., 2018; Seibold et al., 2015), allowed us to evaluate the relative importance of processes at different scales, which has rarely been done in community ecology and ecological application. As such, we were able to disentangle the contribution of different environmental filters, which affect different functions and thus are related to different traits. This is important for

the planning of management and conservation strategies, as measures at different scales need to consider different filters. More specifically, our results show that to support functionally distinct saproxylic beetle assemblages and to prevent functional homogenisation, it is most important to promote deadwood diverse in constitution, tree identity and decomposition stage. Furthermore, a tree species composition of stands closely resembling the composition of unmanaged forests (which would, in similar regions, mean few coniferous trees) might support higher functional diversity of beetles, as can suitable microclimatic conditions (i.e. low canopy cover). Thus, to conserve and promote functionally diverse saproxylic beetle assemblages, management ideally integrates several spatial scales, ranging from single deadwood objects up to forest stand properties.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.

Table S1 Investigated tree genera

Table S2 Environmental variables

Table S3 Sampling numbers

Table S4 Species used for missing trait estimation

Fig. S1 Map

Fig. S2 Photo of experiment

Fig. S3 Biplot of NMDS on tree species composition

Fig. S4–S18 Detailed results

Appendix S1 Supplementary Methods

TABLE LEGENDS

Table 1 Overview and definition of the 13 functional traits that were used to describe the functional composition and diversity of the saproxylic beetle assemblages. Additional columns indicate whether a trait was corrected for body length and/or log-transformed to meet distributional assumptions. The functions to which a trait is hypothesised to contribute to are indicated as well as the filtering step, at which these functions should be affected (dispersal: region-to-site; habitat preference: region-to-site and site-to-patch; fine-scale locomotion: site-to-patch; microhabitat use: site-to-patch and patch-to-object). Some traits such as body length are expected to be linked to several different functions

Table 2 Summary of significant relationships between environmental filters at different steps and community weighted means of traits from three separate models analysing the difference between observed values and mean null-model values for each step. Positive relationships are indicated by blue upward-facing triangles, negative relationships by red downward-facing triangles. Significant relations to factor variables are indicated by the overlay of both triangles. Significant model intercepts represent significant differences between observed values and null-model based expectations. Detailed results including effect sizes are given in Fig. 3.

FIGURE LEGENDS

Fig. 1 (a) Illustration of the sampling schemes employed to represent the assemblages at different scales. Beetle assemblages of an object (defined by a single deadwood log) were sampled with emergence traps; the merged assemblages across all logs of a site built the patch-scale pool; to represent site-scale assemblages, additional samples from flight-interception traps at two heights and from pitfall traps were included; the merged site-scale assemblages per region built the regional pool. **(b)** Conceptual representation of the three hierarchical filtering steps that determine community assembly of saproxylic beetles on deadwood objects. Beetle assemblages are described in terms of different functional traits, here represented by two exemplary traits (body length, wing length). Points represent species, point size represents relative abundance in the respective pool. In the first step (green), species from a regional species pool are filtered by environmental variables at landscape scale (e.g. forest cover) and at site scale (e.g. tree species composition of a stand) to form the site-scale assemblage. In the second step (orange), assemblages that locate a preferred patch with suitable deadwood available for colonisation might represent a subset of the site-scale species pool due to filters related to general log characteristics but also microhabitat of the patch, on which the logs are laid out. In the third step (blue), the assemblage of a deadwood object (single log) is filtered from the patch-scale community by filters related to tree genus identity and decomposition stage. In each step, the observed assemblages are compared to random draws from the originating species pool (null models, illustrated by the replicated assemblages at the bottom).

Fig. 2 Predictions from models analysing the relation of different environmental filters with functional diversity (Rao's Q) of saproxylic beetle assemblages at three different filtering steps. Points show parameter estimates and vertical lines show 95% confidence intervals. For

each filtering step, separate models analyse the difference of observed values from null-model means (based on replication units) with null models representing random assemblages from the species pool of the next higher hierarchical scale. The distribution of the null-model based values is indicated by the grey shading. Based on null-model means, the difference from null models is transformed back to absolute values. The position of the mean difference (i.e. model intercept) in absolute terms is indicated by the horizontal lines, from which parameter estimates for the different environmental filters deviate. For continuous variables (all region-to-site and site-to-patch variables), predicted changes in functional diversity for an increase of the respective variable of 1 SD are shown (variables were scaled to SD 0.5). For the factor variables tree genus identity, decomposition stage (1st four years, 2nd four years) and their interaction, predictions for the different combinations of the levels of the two factors are shown. Each pair of points, connected by a line, shows predictions for one of the 12 investigated tree genera at the earlier decomposition stage (1st period) and the later decomposition stage (2nd period). The significance of the main effects of tree genus (T), decomposition stage (D) and their interaction (×) is shown in the upper-right corner, with bold font indicating significant effects at $\alpha = 0.05$. Significance of continuous variables is indicated by bold confidence intervals. Detailed results including confidence intervals for the effects of the different tree genera are shown in Fig. S4.

Fig. 3 Predictions from models analysing the relation of different environmental filters with the community weighted means (CWM) of the 13 analysed functional traits of saproxylic beetle assemblages at three different filtering steps. A detailed explanation of the figure composition is given in Fig. 2. Here, null-model shadings were excluded to improve clarity. Detailed results including null-model shadings and confidence intervals for the effects of the dif-

ferent tree genera are shown in Figs S5–S17. The coloured shapes next to the trait names indicate the hypotheses for the main filtering steps of the respective trait (green circle: region-to-site; orange square: site-to-patch; blue triangle: patch-to-object) (Table 1). A summary of significant relationships is given in Table 2.

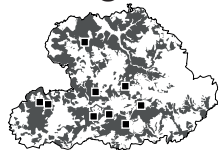
TABLE 1

Trait	Definition	Transformation		Hypothesised function					Hypothesised filtering step		
		Body length	Logarithm	Dispersal	Habitat preference	Fine-scale locomotion	Microhabitat use		Region to site	Site to patch	Patch to object
Wing length	Hind wing length	x		x					●		
Wing loading	Wing area / body mass		x	x					●		
Wing aspect	Wing length / wing width			x		x			●	■	
Body length	Mean length from literature		x	x	x		x		●	■	▲
Leg length	Mean of all legs (femur, tibia)	x		x		x	x		●	■	▲
Lightness	Colour lightness				x				●	■	
Antenna length	Total antenna length	x		x		x			●	■	
Eye length	Maximum eye length	x				x				■	
Hairiness	Pronotum hair count per mm		x			x	x			■	▲
Body width	Maximum body width	x					x			■	▲
Body roundness	Body height / body width						x			■	▲
Head length	Total head length	x					x			■	▲
Mandibular aspect	proximal mandible width / mandible length						x			■	▲

TABLE 2

Trait	Region-to-site							Site-to-patch				Patch-to-object			
	Intercept	Forest sur- roundings	Deadwood vol- ume	Broadleaf share	Conifer type	Structural com- plexity	Canopy closure site	Intercept	Deadwood vol- ume	Structural com- plexity	Canopy closure patch	Intercept	Tree genus	Decomposition stage	Tree genus x decomp. stage
Wing length				▼				▲				▼	▲		▲
Wing loading	▼			▼				▲			▲		▲	▲	▲
Wing aspect	▲											▼	▲	▲	▲
Body length			▼	▲			▲	▼					▲	▲	▲
Leg length	▲				▼			▼					▲	▲	▲
Lightness	▲				▼	▼	▲					▼	▲	▲	▲
Antenna length	▼			▼			▼	▼				▲	▲	▲	▲
Eye length	▲											▼	▲	▲	▲
Hairiness	▼							▼		▼		▲	▲	▲	▲
Body width	▲							▼				▼	▲	▲	▲
Body round- ness	▲			▲			▲				▼	▼	▲	▲	▲
Head length	▲			▲				▼					▲	▲	▲
Mandibular aspect							▲	▼			▼		▲	▲	▲

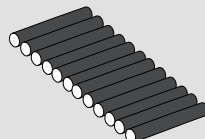
Region



Site



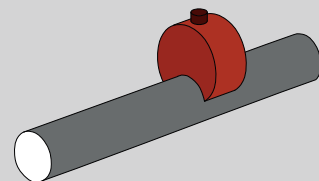
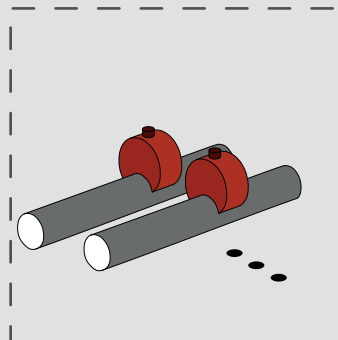
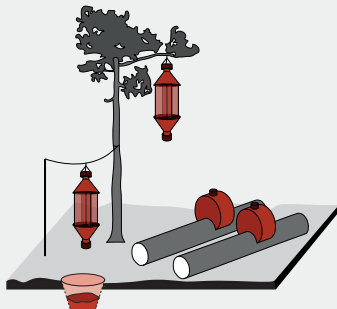
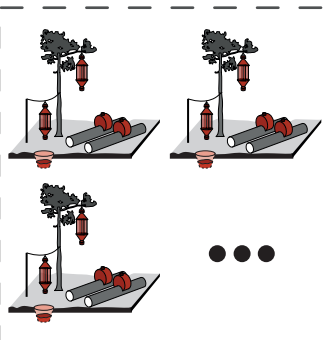
Patch



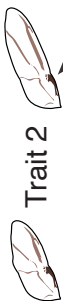
Object



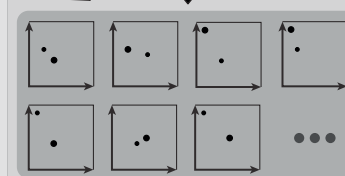
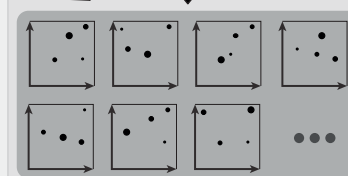
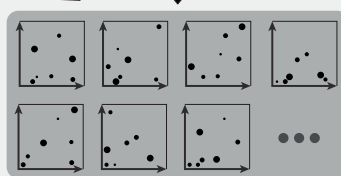
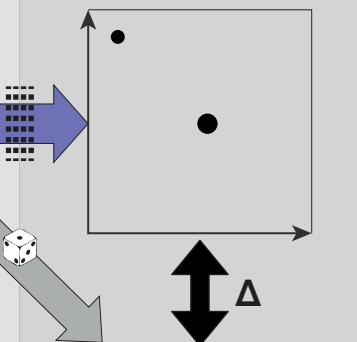
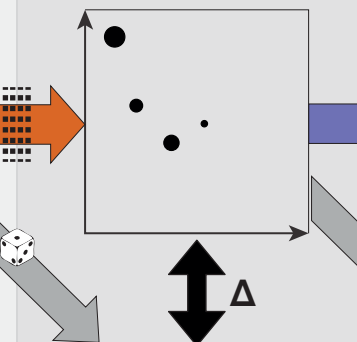
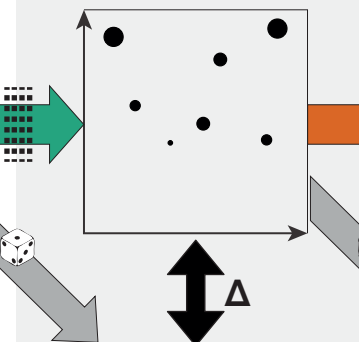
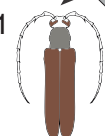
(a) Sampling

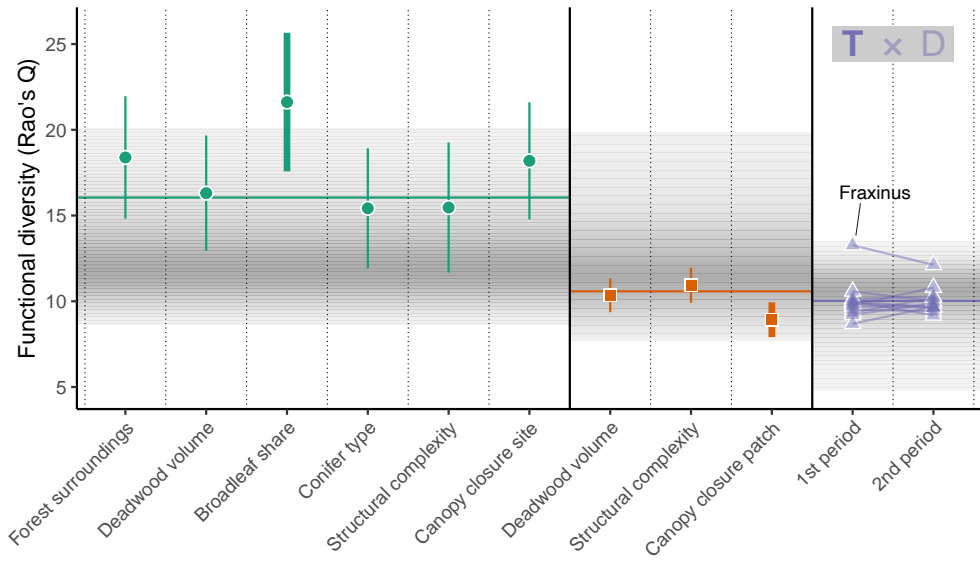


(b) Hierarchical filtering



Trait 1







Predicted CWM

