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Research article

Forest patches as stepping stones: evidence from invertebrate taxonomic and functional diversity in experimentally created water-filled tree holes

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Tree-related microhabitats (TreMs), such as water-filled tree holes (WTHs), are important structures for forest biodiversity, providing habitats for many specialized species, which are however impaired by the intensive forest management of the past. Strategies to maintain and promote TreMs in managed forests, e.g. by establishing old-growth forest patches as stepping stones, have been implemented, but their success has rarely been tested. We experimentally created WTHs in old-growth patches that were established to connect forest nature reserves (FNRs) in a beech forest in Germany. Eight years after creation, we sampled, identified, and measured traits of the invertebrate community that colonized the WTHs. We then investigated how spatial and environmental variables affected taxonomic and functional attributes of communities and populations. A total of 2407 individuals of 13 species were sampled, the majority of which were insect larvae. Abundance, as well as taxonomic and functional diversity attributes and community composition, were influenced by environmental and spatial factors, generally supporting the patch-dynamics and species-sorting metacommunity archetype. At the population level, both spatial and environmental factors affected the abundance and functional diversity of body size distributions, suggesting that dispersal capacities, microhabitat requirements, and competitive abilities of individual species structure communities. The distance to the FNRs had a positive effect on total invertebrate abundance and the abundance of the specialized marsh beetle *Prionocyphon serricornis*, and a weak negative effect on the functional diversity of the community. Our study underpins the stepping-stone concept of connecting FNRs. The species colonized all newly created microhabitats from source populations, indicating that these patches increase connectivity between the FNRs and thus contribute to forest biodiversity conservation. The negative effects of distance to FNRs on functional

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diversity suggest that distances between habitat patches should be kept small for such a strategy to be successful and sustainable in the long term.

Keywords: competition, connectivity, dispersal, metacommunity, stepping stones, traits, tree-related microhabitat, water-filled tree holes

Introduction

Land-use change and intensity is one of the main drivers of biodiversity loss and changes in community composition (Sala et al. 2000, Newbold et al. 2015). In forests, insect communities lose species and become more similar in space and time in response to increased management intensity (Gossner et al. 2023). This is mainly because species with particular traits cannot cope with the environmental changes resulting from increased human impacts (Mori et al. 2018, Neff et al. 2022, Staab et al. 2023, Martinez-Nunez et al. 2024). As insect species are key players in many important ecosystem processes, a loss of biodiversity at various levels is also likely to affect the functioning and resilience of forest ecosystems (Mori et al. 2018).

The mechanisms underlying these changes in insect communities are still poorly understood (Wagner et al. 2021, Gossner et al. 2023). Insects in freshwater and terrestrial ecosystems are often organised in metacommunities linked by dispersal (Wilson 1992, Heino 2011). Therefore, habitat fragmentation limiting dispersal and changes in habitat quality acting as environmental filters may explain these shifts. Island biogeography predicts that the difference in the number of species present in a habitat patch is solely the result of isolation and thus reflects dispersal limitations in species. It states that species richness is controlled by extinction and colonisation processes, with the former being constant and the latter a function of the distance to source populations (MacArthur and Wilson 1967). Metacommunity archetypes provide a different prediction regarding the role of isolation and microhabitat properties for metacommunity dynamics (Leibold et al. 2004). The neutral archetype is related to the processes of island biogeography as dynamics of species diversity are solely based on probabilities of species loss (extinction, immigration) and gain (immigration, speciation). It assumes that species are similar in species traits, such as competitive ability, dispersal and fitness (Hubbell 2001). In contrast, the species-sorting archetype predicts that communities in habitat patches are solely controlled by microhabitat properties and only those species for which the microhabitat provides a suitable niche will enter a community. However, in closely connected habitat patches, mass effects by highly dispersive species might homogenize communities irrespective of their abiotic microhabitat properties and obscure species sorting. The patch-dynamics archetype assumes that habitat patches are identical and capable of containing populations. Both isolation and microhabitat properties become important, and a competition-dispersal trade-off will determine which species will enter and persist in the community. However, the mechanisms and processes underlying the structure of metacommunities are likely more complex, e.g. dependent on site and species. Current metacommunity theory therefore emphasizes the need to better integrate the basic processes of community assembly, i.e. drift, selection, and dispersal, which are influenced by species interactions, food web structure, biogeography, phylogeny, and micro-evolution, across gradients and scales (Leibold and Chase 2018, Leibold et al. 2022). This would allow more direct assessments of how these basic processes affect metacommunities and the importance of inferred processes, i.e. unstructured, biotic, environmental, and spatial effects. However, testing very discrete, even dichotomic hypotheses based on the four metacommunity archetypes can still be valuable for application in conservation planning. In particular, they provide a heuristic tool that facilitates comparisons across systems, highlights dominant processes in different contexts, and helps translate ecological theory into conservation planning at specific spatial and temporal scales. They may also serve to illustrate and communicate otherwise complex models in a more categorical way, thereby facilitating decision-making.

A better understanding of the role of spatial and environmental factors in shaping communities in habitat patches is of great importance for applied forest management and conservation, as habitat fragmentation and habitat loss are harmful consequences of intensive management and important drivers of biodiversity loss (Haddad et al. 2015, Fahrig 2017). Therefore, many efforts have been made to increase habitat availability in forests, e.g. by increasing the amount of deadwood, an important structure for a plethora of forest species (Doerfler et al. 2017), and positive effects of such strategies on biodiversity have already been observed ten years after implementation (Doerfler et al. 2018, Roth et al. 2019). Tree-related microhabitats (TreMs) have also become increasingly important in nature conservation-oriented management (Asbeck et al. 2021, Martin et al. 2022). Habitat trees that form TreMs are protected and used as stepping stones between forest nature reserves and smaller old-growth patches (Bütler et al. 2013, Saura et al. 2014). TreMs are also increasingly being promoted in forest management through artificial creation in order to increase the connectivity and diversity of habitats in managed forest landscapes (Großmann et al. 2024). However, direct positive effects of TreMs biodiversity are still difficult to prove (Asbeck et al. 2021).

Water-filled tree holes (WTHs) are one of 47 types of TreMs according to the typology of Larrieu et al. (2018). They can be easily mimicked and manipulated using artificial containers (Yanoviak and Fincke 2005, Petermann et al.

2016), but can also be artificially created by cutting holes in tree trunks. Ecological communities inhabiting WTHs typically exhibit metacommunity dynamics (Srivastava and Lawton 1998, Srivastava et al. 2004) and are thus ideal model systems for testing the importance of isolation and microhabitat properties on community assembly. WTHs within terrestrial ecosystems provide small aquatic microcosms that are connected by dispersal and have more or less clear boundaries (Kitching 2000, Petermann and Gossner 2022). In addition, they contain communities that are small enough to be sampled completely but comprise different functional groups and trophic levels. Insect communities of WTHs are composed of many species for which larval development occurs in the water, while adults use terrestrial resources (e.g. adult female mosquitoes consume vertebrate blood and adult hoverflies consume nectar). These communities are characterised by a wide variety of life history traits (Petermann et al. 2020). It has been shown that adult wing length impacts dispersal of freshwater insects (Malmqvist 2000), and thus dispersal distance may be limiting to some tree-hole inhabiting insect species. In addition, in temperate systems, the overwintering stage might be crucial for early colonization of new microhabitats in spring, with species overwintering as pupae likely to emerge first and have an advantage as early colonizers (Miall and Hammond 1900, Rozkošný et al. 1997). Insects in WTHs are also strongly affected by microhabitat properties, such as tree-hole size and detritus amount, and physical and chemical properties (Gossner et al. 2016, Petermann et al. 2020, Petermann and Gossner 2022). Because of their complexity, results from these microcosms can likely be transferred to larger ecosystems (Srivastava et al. 2004).

In this study, we experimentally created WTHs in beech trees *Fagus sylvatica* in small old-growth patches connecting two forest nature reserves (FNRs) in the Steigerwald, Germany. Due to different creation methods and independent development, the tree holes encompassed a variation in microhabitat properties. With this design we addressed the question whether microhabitat properties or space is more important in structuring the communities in WTHs, sampled eight years after their creation. At this relatively small landscape scale, dispersal limitation is likely to be less important than environmental variables, as communities should be able to track fluctuations in environmental conditions (species sorting) or be influenced by mass effects (Heino 2011). Nevertheless, spatial factors, such as distance to the nearest FNR as source pool for colonization due to the higher abundance of WTHs in unmanaged forests (Gossner et al. 2016), and species interactions, could still be relevant. Specifically, we tested the hypotheses that: 1) abundance, as well as taxonomic and functional diversity of insect communities in WTHs, is affected by microhabitat properties (size, detritus amount, water chemistry) as well as spatial factors (distance to FNRs as potential source habitats), following the patch-dynamics (differences in patch properties limited) and species-sorting (slight differences in patch quality cause spatial niche separation) archetype. This is expected, as it has been shown in previous studies that, besides microhabitat properties, the abundance of tree holes at a forest site is also important for insect communities in WTHs (Gossner et al. 2016, Petermann et al. 2020); 2) taxonomic and functional (life history traits, larval size distributions) community composition is determined by differences in microhabitat properties as well as spatial distance, following the same rationale as in H1; 3) abundance and functional diversity at the population level, measured as larval length diversity, is also determined by spatial and environmental factors reflecting their dispersal capacities, microhabitat requirements, and competitive abilities; 4) functional diversity at the population level, measured as larval length diversity, is determined by distance to nature reserves, which provide source habitats and allow for multiple colonisations. By analysing different diversity metrics (species richness, evenness, diversity) across taxonomic and functional diversity attributes, we aimed to gain a better understanding of the potential mechanisms structuring communities in TreMs. For detailed expectations of responses of different biodiversity attributes to microhabitat properties and spatial factors, see the Supporting information. Our study provides insights into whether the implementation of the stepping-stone concept, aiming at connecting FNRs by old-growth habitat islands, was successful.

Material and methods

Study sites and tree-hole creation

The study was conducted in the Steigerwald forest in northern Bavaria, Germany. There, a conservation strategy had been implemented that created stepping stones to connect two forest nature reserves (FNRs), with the aim of facilitating species exchange between them and thus improving biodiversity (Doerfler et al. 2017, 2018, Mergner and Kraus 2020).

To connect the two FNRs, Brunnstube and Waldhaus, six small old-growth forest patches were protected (Fig. 1). These patches exhibit structural characteristics more closely aligned with forest nature reserves (FNRs) than with the managed forest matrix, particularly in terms of mean forest height and canopy cover (Supporting information) and may be considered as intermediate in structure between the two categories. In 2009, in each of these patches artificial tree holes (WTHs) were created in eight beech trees at a height of 1.3 m. We applied four different treatments, which varied in the direction of cutting and the type of filling used (Supporting information). These differences, and the ability of the different trees to overcome the injury, resulted in a variation in opening area and other microhabitat properties, making them an interesting study object for testing the role of space and environment for the colonization of these WTHs by invertebrates (for details, see Weigelmeier and Schmidl 2024).

Measuring spatial variables and microhabitat properties

In each old-growth patch, we randomly sampled four WTHs in June 2017 (Supporting information). As spatial variables, we used the distance to the border of the closest FNR as a

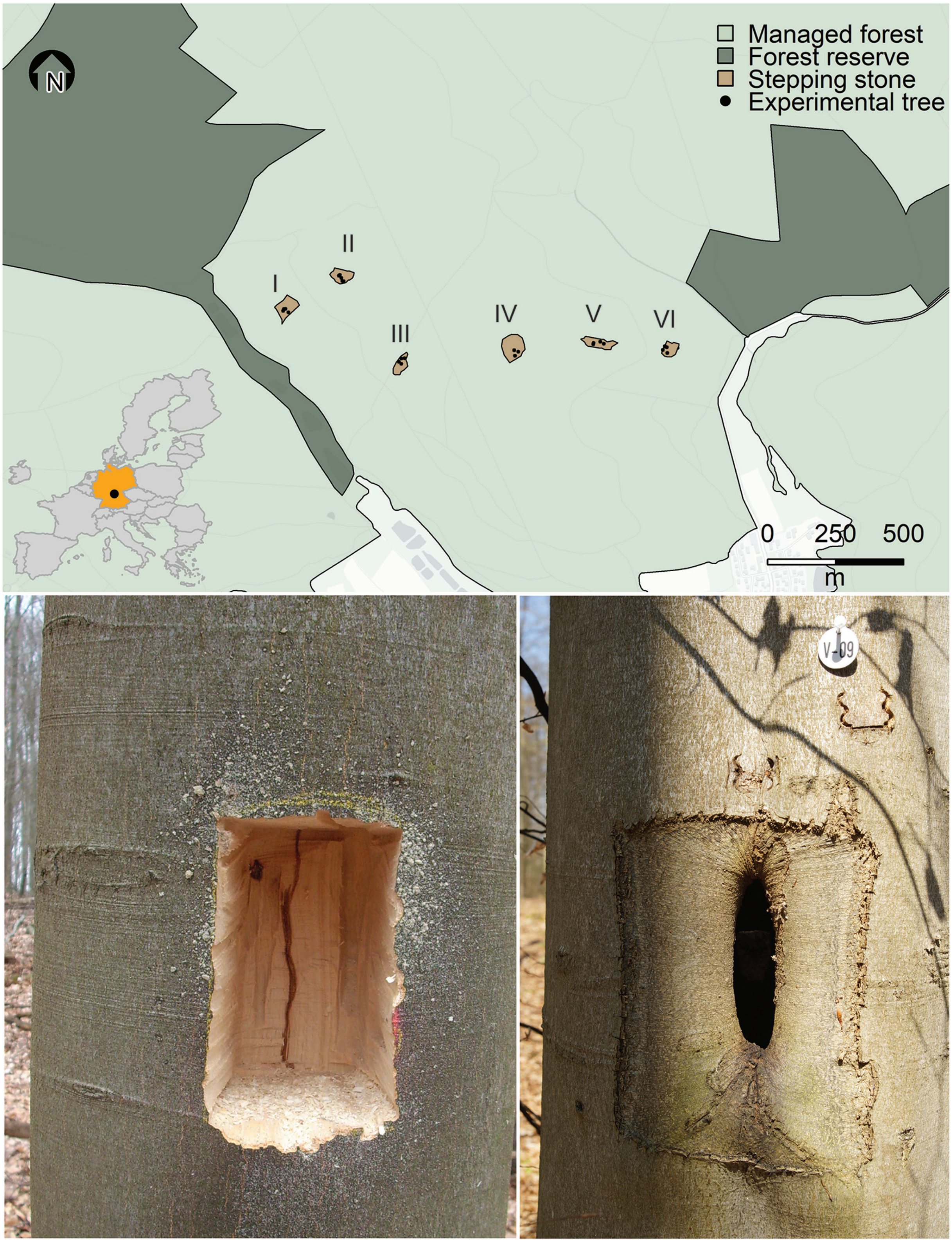

Figure 1. Top: To connect the two forest nature reserves (dark green) Waldhaus (left) and Brunnstube (right) six old-growth patches in which management was abandoned (brown) were established as stepping stones in a managed beech-dominated forest (light green). Ten beech trees were used for creating artificial tree holes in each of them, four of these (black dots) that naturally filled up with water were randomly selected for the study (for details, see the Supporting information). The inset shows the geographical location in Europe. Bottom: Example of an artificial tree hole in 2009 (creation; left) and 2017 (sampling; right).

design variable, as we hypothesize that colonisation is limited by distance from FNRs, the main source habitat. Additionally, we assessed coordinates (longitude, latitude) to account for additional spatial autocorrelation. The following microhabitat properties (water parameters, physical characteristics) of each hole were measured on site: oxygen (percentage and absolute), pH, and conductivity in $\mu S\ cm^{-2}$ using a multiprobe device (Oxi 330, pH 330, WTW GmbH), maximum and actual volume, opening width and length (from which we calculated opening area in cm^2), depth, orientation (accuracy 15°), and temperature. We took 20 ml water samples to measure nitrate (NO_3^-), ammonium (NH_4^+), phosphate (PO_4^{3-}) (all in $mg\ l^{-1}$) and Redox potential in mV. Due to technical issues from lab measurements only the phosphate content and the Redox potential could be used for further analyses.

Sampling, identification, and trait assignment of invertebrate communities

We used a tube to suck out all water and material from each tree hole (Supporting information), which was transferred to the laboratory for further processing. There, all material was rinsed through several sieves of different mesh sizes, ending with a rinse through filter paper. All fractions were sorted for insect larvae and other living invertebrates. The detritus fractions were finally divided into coarse detritus (≥ 0.5 mm mesh size, CD) and fine detritus (< 0.05 mm, FD). The two fractions were dried in a drying oven at 60°C for at least 48 h. When no further change in weight was observed, the weight for CD and FD was measured in mg at an accuracy of 1 mg. After sampling, the tree holes were filled with rainwater to accelerate recovery of the microhabitats (Supporting information).

All invertebrates were identified to the lowest taxonomic level possible using common identification keys for freshwater invertebrates (Supporting information). A few individuals per morphospecies were barcoded to verify the morphological identification.

Life history traits and larval length distribution

We selected the following life history traits for each species based on literature trait data: 1) maximum larval length, 2) trophic level, 3) feeding mode, 4) air breathing (yes/no), 5) type of breathing tube, 6) pupal location, 7) female food source, 8) male food source, 9) number of generations per year, 10) location of oviposition, 11) egg formation, 12) body length adults, 13) tree-hole specialist (yes/no), 14) overwintering stage, 15) relative adult wing length, and 16) stratum within hole (for details, see the Supporting information).

To determine the larval length distribution at the community and population level, all individuals per morphospecies were photographed, and the length of each specimen was measured using a LEICA DVM6 digital microscope.

Invertebrate diversity and community composition of tree holes

To better understand the dynamics related to colonization of the communities in the newly created tree holes from surrounding source habitats and test our predictions in relation to different processes (Supporting information), we focused on a range of comparable taxonomic and functional community attributes.

As **taxonomic community attributes** we used abundance, species richness, Pielou's index of evenness, and exponential Shannon index (Hill number of order 1), which reflects the effective number of common species in a community (Jost 2006), as well as community composition.

As **functional community** and **population** attributes we calculated functional richness (FRic), functional evenness (FEve), functional diversity (functional divergence, FDiv), and functional community composition. Functional metrics were either based on life history traits (community level) or larval length distributions (community and population level).

We calculated taxonomic diversity metrics with the function *diversity* in the 'vegan' R package (Oksanen et al. 2022), and distance-based functional diversity indices using the *dbFD* function implemented in the R package 'FD' (Laliberté and Legendre 2010, Laliberté et al. 2014).

We calculated taxonomic and functional (based on community weighted means) community composition based on Bray–Curtis distances and performed a non-metric multidimensional scaling NMDS using the 'vegan' package (Oksanen et al. 2022). The first two or three axes (depending on the stress value) were used for statistical analyses. To show the factors explaining the distribution in the ordination plot the environmental variables were plotted using the *envfit* function.

Intra- and inter-specific distributions of larval length

We estimated intra- and inter-specific distributions of larval length using trait probability density (TPD) functions based on measurements of individual larvae, employing the TPD framework outlined by Carmona et al. (2016) and using the 'TPD' package in R (Carmona 2019). For details, see the Supporting information.

Statistical analyses

All analyses were conducted in R ver. 4.1.2 (www.r-project.org). For additional statistical details, see the Supporting information.

To test for the relationship between spatial and environmental factors and community attributes we used generalized linear mixed-effects models with the *glmmTMB* function in the 'glmmTMB' package (Brooks et al. 2017). Among community attributes (response variables) we used abundance, taxonomic diversity, and functional diversity based on life history traits as well as on body size distributions, as well as taxonomic and functional composition using the scores of the first two axes of the respective NMDS. At population level we used the abundance and functional diversity based on body size distributions of the four most abundant species (the models of the fifth and sixth most abundant species did not converge) as response variables. As predictors we used spatial as well as microhabitat properties. In case of species richness, we added log abundance as an additional predictor. The old-growth patch was included as random term in all models. To test for possible nonlinear effects of distance to the next FNR on our response variables, we additionally included a quadratic term of this predictor and compared the model performance based on the AIC using the *anova* function in the base R package. The addition of the quadratic term did not improve the model in any case, so we only used the linear predictor. All quantitative predictors were scales to zero mean and unit variance using the *decostand* function in the 'vegan' package (Oksanen et al. 2022).

We additionally tested for positive and negative associations between species by conducting a species association analysis based on Pearson correlation coefficients using the *sp. pair* function in the 'spaa' package (Zhang 2016).

Results

The physical and chemical microhabitat properties of all tree holes changed considerably in the eight years up to the time of sampling, but the development of the cavities varied greatly from tree to tree. This resulted in a large variation in the environmental conditions of the individual tree hole in each of the six old-growth patches connecting the two FNRs (Supporting information).

A total of 2407 individuals of 13 invertebrate species were sampled, including one Lumbricidae (*Eisenia eiseni*) and twelve insect species (Supporting information). The chironomid *Metriocnemus cavicola* was the most abundant species while the Psychodidae *Pericoma* sp. and the Scirtidae *Prionocyphon serricornis* showed the highest frequency of occurrence.

General importance of space and microhabitat properties for community attributes

The predictors explained about 50% or more of the variation in our models for most community attributes (Fig. 2). Both space and microhabitat properties determined the community taxonomic and functional attributes, supporting our hypothesis 1. Overall, microhabitat properties were more important than space. However, spatial factors were particularly important for overall abundance and explained more functional than taxonomic community attributes (Fig. 2).

Effect of space and microhabitat properties on community-level diversity

Overall abundance of communities was strongly affected by the minimum distance to a forest nature reserve (Fig. 2, 3), and this relationship was positive (Supporting information). In addition, oxygen content, detritus amount, and maximum water volume affected abundance positively, while temperature and pH had a negative effect.

Species richness was positively related to abundance but not affected by spatial factors (Supporting information). The depth affected the species richness positively while detritus amount had a negative effect. Evenness and diversity showed very weak responses. With higher detritus amount, evenness tended to be higher ($p < 0.10$), while diversity tended to be lower ($p < 0.10$).

Functional diversity (FD) showed the strongest response among the analysed functional community attributes. With increasing distance to the next FNR the functional diversity (life history traits, body size distributions) decreased significantly (Fig. 3; Supporting information). Regarding life history traits, opening size affected FD negatively, while oxygen content and actual water volume showed a positive effect. Depth (positive; GLMM, $p < 0.06$) and phosphorus (negative; GLMM, $p < 0.09$) showed either a marginally significant effect on FD or at least a trend. No effect of environmental factors on the functional diversity of body-size distributions were observed. Functional richness did not respond significantly to any of our predictors, neither when using life history traits nor when using size distribution densities. Functional evenness of life history traits showed a spatial response, i.e. it was positively associated with latitude.

Effect of space and microhabitat properties on community composition

The composition of the communities in terms of species or traits was mainly affected by environmental factors (Fig. 4; Supporting information). The minimum distance to the next FNR showed no effect, only latitude (longitude was excluded from the model due to multicollinearity of variables in most cases) had a significant effect on species (NMDS, axis2) and life history trait (NMDS, axis1) composition.

The species composition (Fig. 4A) was mainly (GLMM, $p < 0.05$) affected by pH (NMDS, axis1 and axis3), maximum water volume (NMDS, axis1), i.e. the size, and the depth (NMDS2) of the tree hole. The actual water volume (NMDS, axis2; GLMM, $p < 0.06$) and the opening area (NMDS, axis3; GLMM, $p < 0.07$) showed a marginally significant effect and the temperature (NMDS, axis2) showed a trend (GLMM, $p < 0.10$).

The life history trait composition (Fig. 4B) responded significantly to the oxygen content, the temperature, and the actual water volume (NMDS, axis1). Depth and the pH showed a trend (GLMM, $p < 0.09$). The trait probability distribution of body size (Fig. 4C, D) was significantly affected by temperature (NMDS, axis1), oxygen content, and pH (NMDS, axis2).

General importance of space and microhabitat properties for population attributes

Population-level analyses were conducted for all species that occurred in more than 80% of all tree holes, i.e. *Prionocyphon serricornis*, *Pericoma* sp. (both 95.83%), *Metriocnemus cavicola* (87.5%), and *Phaonia exoleta* (83.3%). For species with lower frequencies, models did not converge.

The predictors explained about 50% or more of the variation in our models for most population attributes (Fig. 2). Both space and microhabitat properties determined the abundance and functional characteristics of populations (Fig. 2), supporting our hypothesis 3. Overall, microhabitat properties were more important than spatial factors, but spatial factors were also relatively important for the abundance

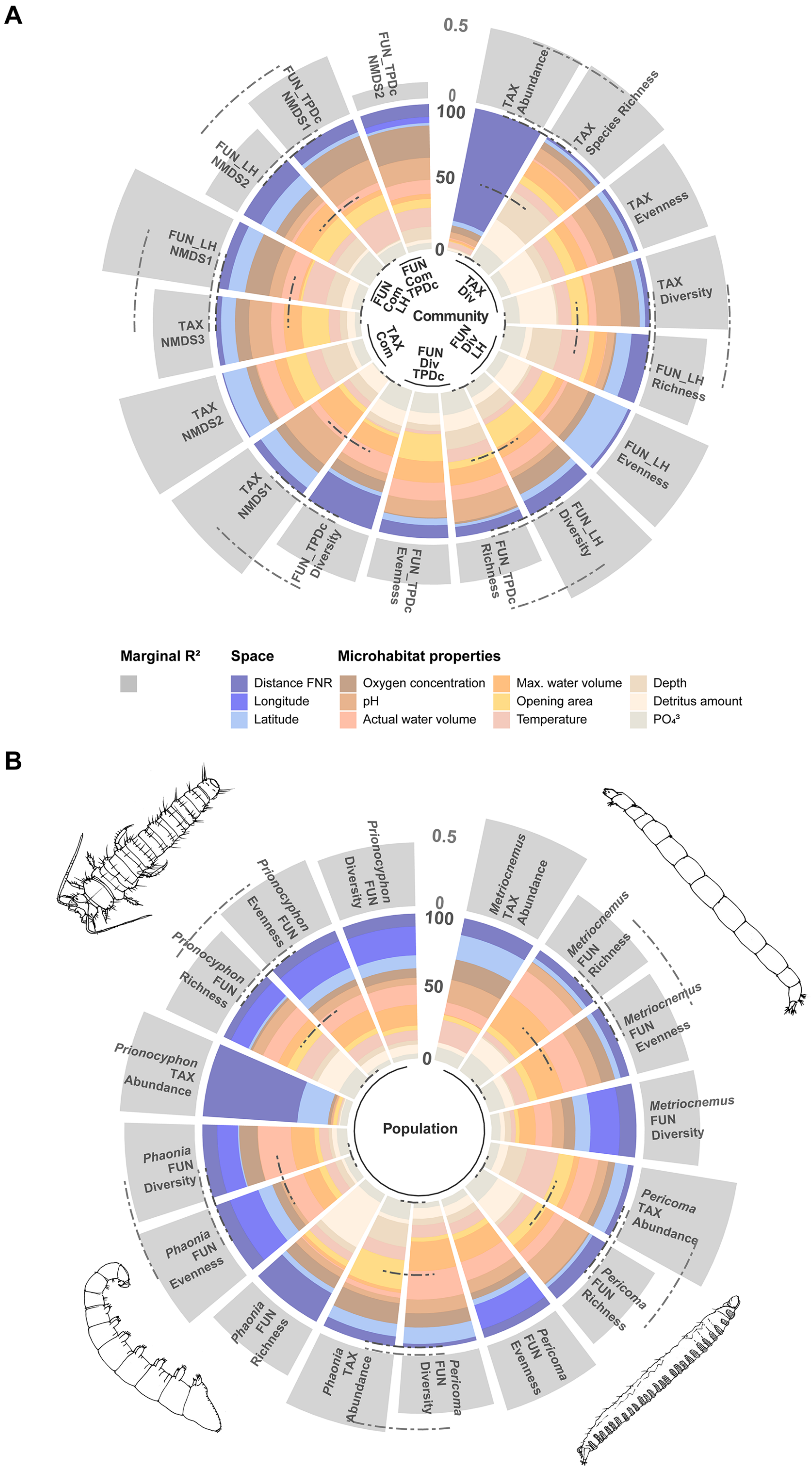

Figure 2. The relative importance of environmental and spatial factors for taxonomic (TAX) and functional (FUN) community (Com) attributes (A) and for individual species abundance (Abu) and functional population attributes (B) related to body size (trait probability density), based on standardized estimates from the GLMM models (inner circle). The outer grey circle shows the marginal R^2 values of the models (see the Supporting information for significance). The dash-dot lines in the inner and outer circle of each graph refer to the proportions and R^2 values at the top of the figure. LH: life history traits; TPDc: trait probability density of communities (body size). The four larval illustrations correspond to the four different genera.

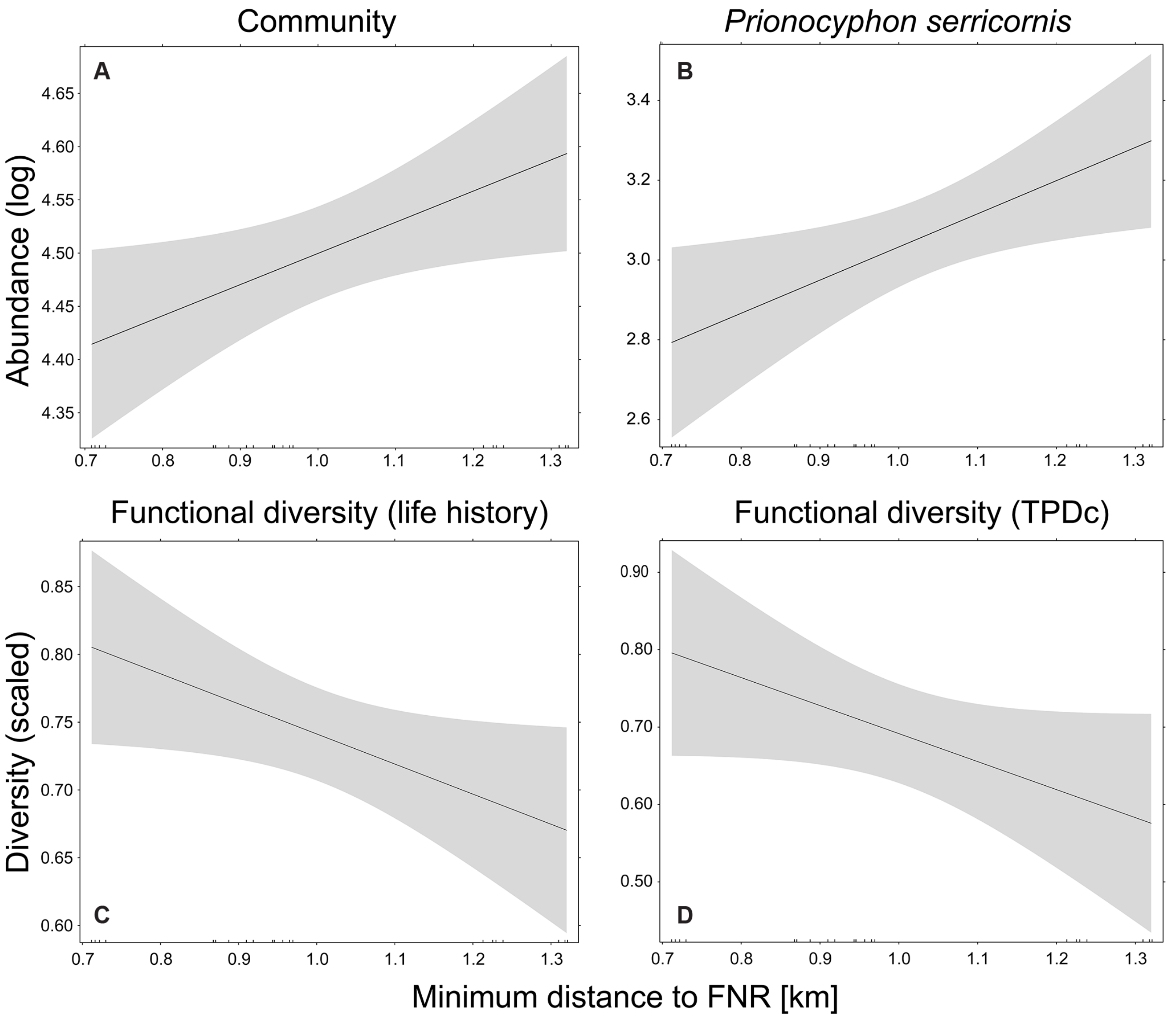

Figure 3. Effects of minimum distance to the next forest nature reserve (FNR) on overall abundance (A), abundance of *Prionocyphon serricornis* (B), and functional diversity in terms of life history traits (C) and body size distributions (D). Other community and population attributes did not show a significant relationship with the minimum distance to a forest nature reserve. Model-based predicted means and 95% confidence bands are shown. Please note that the y-axis in the case of abundance is log-transformed.

and body size distributions of certain species and facets of functional diversity (Fig. 2).

Effect of space and microhabitat properties on population-level diversity

The abundance of individual species was only influenced by spatial factors in the case of *Prionocyphon serricornis*. As with overall abundance, the minimum distance to an FNR had a positive effect on abundance (Fig. 3B; Supporting information). In addition, microhabitat properties were associated with the abundance of individual species, but often in opposite ways. For example, oxygen content had a positive effect on the abundance of *P. serricornis* and *Metriocnemus cavicola*, but a negative effect on that of *Phaonia exoleta*. *Prionocyphon serricornis* was additionally positively influenced by opening area and phosphate. *Pericoma* sp. responded negatively to the size of the tree hole (actual water volume, opening area, depth) and to the temperature. *Metriocnemus cavicola* showed a positive response to the actual water volume, but was negatively influenced by opening area, pH, temperature, and phosphate. In contrast, *P. exoleta* was positively influenced by opening area and phosphate, but negatively by the depth of the tree hole. The different responses of the species to space and microhabitat properties resulted in either positive or negative associations of species (Fig. 5).

Functional richness of body size was not influenced by space or microhabitat properties in all four species (Supporting information). Functional evenness and diversity were not

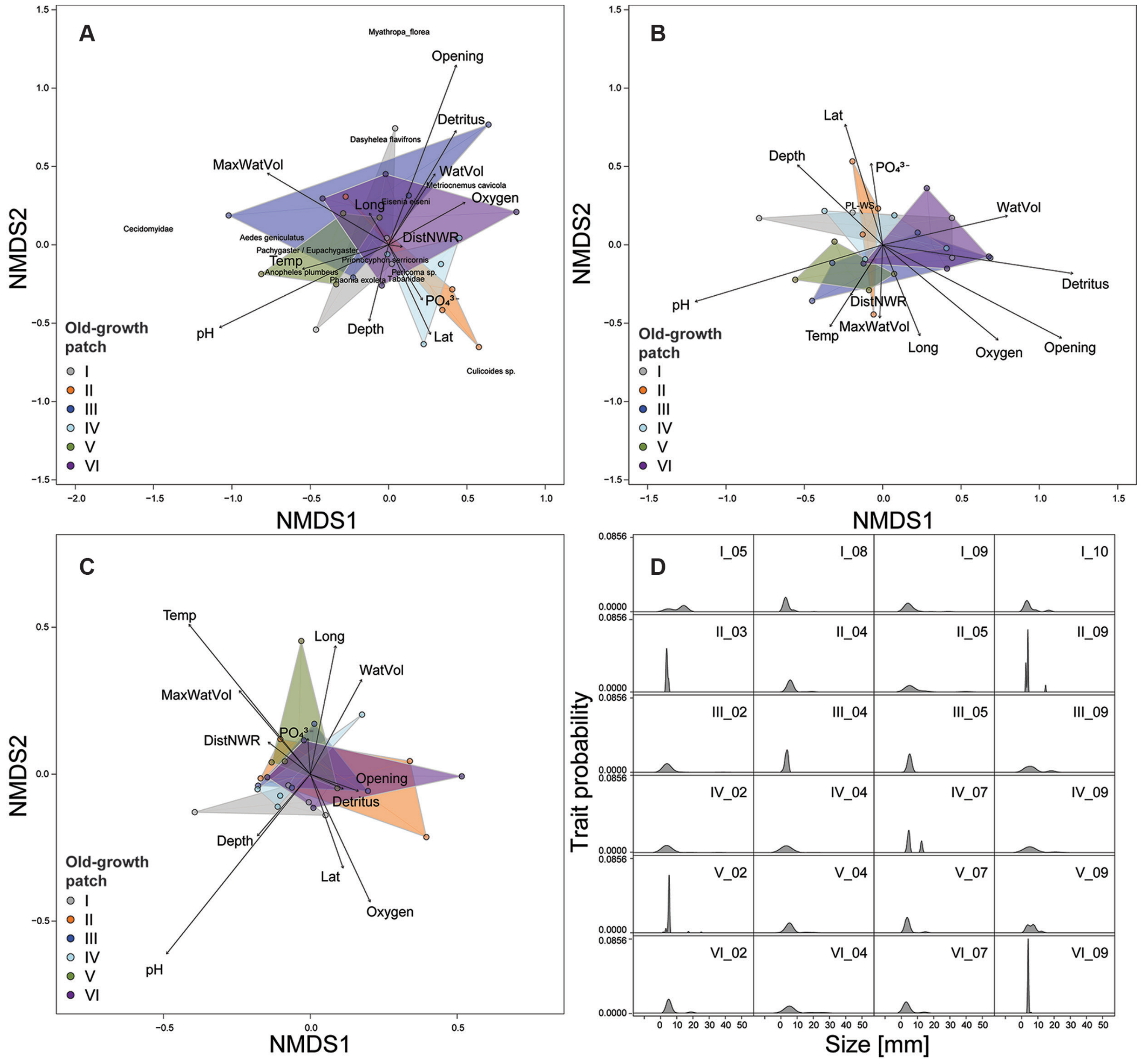

Figure 4. Ordination plots showing the community composition of the studied tree holes based on: (A) species composition (the position of the species are shown), k = 3, stress: 0.127, (B) life history trait composition, k = 2, stress: 0.130, and (C) trait probability densities calculated based on body sizes of each sampled individual, k = 2, stress: 0.059. Coloured hulls illustrate the six old-growth patches connecting the two forest nature reserves. Spatial and environmental variables were plotted using the *envfit* function in in the R package 'vegan'. The position of the traits in (B) are shown in the Supporting information. (D) shows the trait probability densities of body sizes used in (C) for each sampled tree hole. The number indicates the creation type of the tree holes (see the Supporting information).

influenced by space in all four species, so that our hypothesis 4 is not supported. However, microhabitat properties had a significant effect on both functional evenness and diversity of each species. Actual water volume mainly had a negative effect, whereas maximum water volume had a positive effect for all species. In addition, detritus amount, tree-hole depth (both on functional evenness), and pH (functional evenness and diversity) had a negative effect on *P. serricornis* and *Pericoma* sp., while oxygen content and temperature had a positive effect on at least one of the functional measures (with the exception of *M. cavicola*), and phosphate had a positive effect on functional evenness of *Pericoma* sp.

Discussion

Our experimental study provides strong empirical evidence for the success of creating old-growth forest patches as

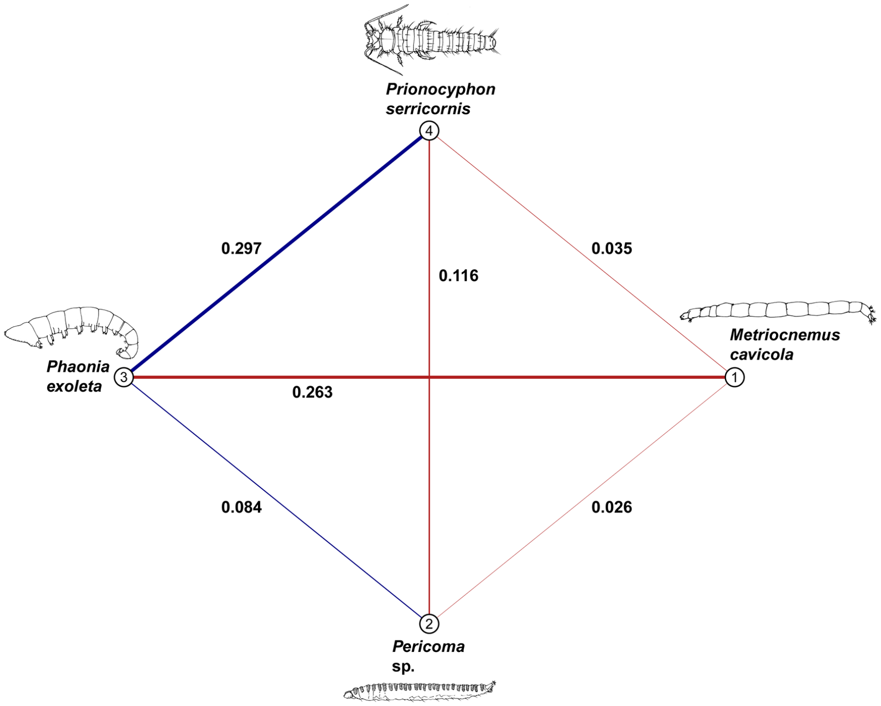

Figure 5. Pearson correlation network illustrating the associations between each pair of the four most frequent species. Red lines indicate negative and blue lines positive relationships. Line width is scaled to the correlation strength (Pearson r).

stepping stones in managed forests to connect FNR for biotic communities associated with TreMs. Abundance as well as taxonomic and functional diversity and community composition in experimentally created artificial water-filled tree holes (WTHs) were influenced by space and microhabitat properties, generally supporting the patch-dynamics and species-sorting metacommunity archetype (Leibold et al. 2004). This supports our hypothesis 1 and partly supports hypothesis 2. In line with hypothesis 3, both space and microhabitat properties affected abundance and functional diversity of body size distributions, at the population level suggesting that dispersal capacities, microhabitat requirements, and competitive abilities of individual species structure tree-hole invertebrate communities. The distance to the FNRs had a positive effect on the total abundance and the abundance of the specialized marsh beetle *Prionocyphon serricornis* and a slightly negative effect on the functional diversity of the community, in contrast to our hypothesis 4. This underlines the success of the stepping stone concept, as communities far from the reserves were still functionally diverse.

General effects of space and microhabitat properties on communities

The high explanatory value of our models and the high importance of both space and microhabitat properties for structuring communities and populations in WTHs in our study (Fig. 2) generally supports the patch-dynamics and species-sorting archetype (Leibold et al. 2004). We limited the variation in patch quality by simultaneously creating rot holes in tree trunks artificially, providing the basis for the patch-dynamic scenario that assumes that habitat patches are identical. According to this archetype, a competition–colonization trade-off structures communities, as some species are superior colonists and others are superior competitors. The slightly different environmental conditions of our artificially created WTHs, which explained much of the variation in our data, may have additionally shaped the competitive ability of individual species and thus the local and colonization–extinction dynamics due to known microhabitat preferences of individual species (Schmidl et al. 2008, Gossner and Petermann 2022). However, our results also give some support to the species-sorting archetype as the differences in microhabitat properties between WTHs might have caused differences in quality among habitat patches that are sufficiently strong to affect the demography of individual species and the outcome of species interactions. This is supported by the negative and positive associations of individual species observed in our study (Fig. 5). Thus, spatial niche separation might be important in our system beyond spatial dynamics. The results of previous studies on natural tree-hole metacommunities are inconclusive regarding the role of spatial and environmental factors in community structuring. While there is some evidence for the importance of spatial factors in actively dispersing invertebrates (Gossner et al. 2016, Petermann et al. 2020) and passively dispersing bacteria (Bell 2010), other studies found no influence of space on passively and actively dispersing organisms (Schulz et al. 2012). The enormous variation in microhabitat properties of natural tree holes may have obscured the importance of spatial factors in some studies. The dispersal abilities of active dispersers such as insects are generally high, and relatively large dispersal distances can also be achieved by the rather erratic dispersal of passive dispersers. However, there are probably differences in the dispersal abilities between species of both groups (Bock et al. 2020, Sarremejane et al. 2020, Barbour et al. 2023). Further studies are needed that explicitly address metacommunity theory in tree holes, which are classic examples of metacommunities (Srivastava et al. 2004, Ellis et al. 2006). One possibility would be to experimentally manipulate the spatial arrangement and microhabitat properties and specifically study dispersal, e.g. by isotope labelling or population genetics (Petermann and Gossner 2022).

Assuming that FNRs serve as the main source of populations colonizing our artificially created tree holes, our observed pattern could have also been shaped by mass effects (Leibold et al. 2004). Since species differ in their dispersal and competitive abilities, a potential mass colonization by good dispersers might have outweighed the competitive advantage of good competitors, in particular in patches close to the source populations (FNRs). The strong increase in overall abundance with increasing distance to the FNRs especially in *P. serricornis* (Fig. 3; Supporting information) could be an indication for this. *Prionocyphon serricornis* develops exclusively in water-filled tree holes and has a relatively high dispersal capacity, but probably also a high competitive ability under favourable microhabitat conditions (large tree holes with permanent water availability; Klausnitzer 2020), conditions that are fulfilled in our study design. In addition, mass effects may have negated the advantages of species that are better adapted to certain microhabitat conditions according to the species-sorting archetype. This could have shaped the communities of a particular tree-hole quality with distance from the FNR and reduced the effect size of microhabitat characteristics for individual species.

The role of species traits

Trait-based analyses can provide mechanistic insights into community assembly and metacommunity processes (Leibold et al. 2004, Wong et al. 2019, Petermann and Gossner 2022). In our study, functional metrics were better explained by spatial factors than taxonomic metrics (Fig. 2), highlighting the importance of species traits for the metacommunity processes across the old-growth forest patches. The minimum distance to the FNRs negatively affected the functional diversity of life history traits and body-size distributions (Fig. 3; Supporting information). We had predicted a hump-shaped relationship with highest diversity at intermediate distance, through two partly compensating processes (Supporting information); first, a negative effect of distance on functional richness due to a loss of species with certain traits (e.g. low dispersal capacities) and decreasing colonization events decreasing the richness in size distributions; second, a hump-shaped relationship of evenness, reflecting highest evenness at intermediate distance due to a trade-off between dispersal limitations and competition. However, neither functional richness nor evenness were affected by the distance from FNRs. This indicates that all the traits we considered were still present at a large distance, but their abundance distribution changed. This suggests that large and highly competitive species become more abundant relative to small and high dispersive species that are poor competitors. The above-mentioned positive response of *P. serricornis* to the distance to FNRs (Fig. 4; Supporting information) points in the same direction. Overall, our trait-based analyses revealed strong functional responses of communities, providing evidence for the role of traits related to dispersal and competition in explaining spatial pattern in our study. However, due to the limited knowledge of the traits of insect species developing in WTHs (Petermann and Gossner 2022), a direct link between individual traits and observed patterns is difficult. In addition, the relationships with distance are likely scale-dependent, and the scale studied may be too small to detect a hump-shaped relationship. Unmeasured factors as well as other processes such as mass (Leibold et al. 2004) or priority (Zou and Rudolf 2023) effects could also have modulated these dynamics.

Microhabitat properties shaping communities and populations

The overall community abundance was positively affected by the size (maximum volume) and the basic resource availability (detritus amount) in the system (Supporting information). This confirms general relationships observed in WTHs worldwide (Petermann and Gossner 2022). This also translated into a higher number of species, but not species richness if the differences in abundance are accounted for. Depth of the tree hole, another measure of tree-hole size, however, was also positively associated with species richness and may indicate vertical niche segregation in WTHs (Supporting information). Of the physical and chemical water properties, oxygen content was positively associated with overall abundance and diversity in life history traits, and pH and temperature were negatively associated with abundance (Supporting information). These tree-hole properties were also relevant for the taxonomic and functional composition of the communities (Supporting information). This supports the results of other studies that have shown how important these properties are for the abundance of individual species and for community diversity and composition (Schmidl et al. 2008, Gossner et al. 2016, Gossner and Petermann 2022).

The populations of the four most abundant species showed contrasting responses to microhabitat properties regarding tree-hole size as well as physical and chemical properties (Supporting information). These differences reflect differences in microhabitat requirements of the studied species and support findings of previous studies (Schmidl et al. 2008, Gossner and Petermann 2022). The abundance of individual species is likely additionally shaped by interactions between species. These interactions can be positive through facilitation in the processing chain of detritus, i.e. processing chain commensalism (Heard 1994, Paradise and Dunson 1997, Paradise 1999, Paradise and Kuhn 1999), or negative through competition (Fincke 1992) and predation (Paradise et al. 2008). Among the four most abundant and frequent species was one predator, *Phaonia exoleta*. This species likely predates on *Metriocnemus cavicola* (negative association; Fig. 5) but has similar habitat requirements as *P. serricornis* and *Pericoma* sp. (positive association). The negative associations between *P. serricornis*, *Pericoma* sp., and *M. cavicola* provides some indication for the role of competition. We did not find any hint for the importance of facilitation in our study, a result that is also supported by a previous study of Schmidl et al. (2008).

Future directions

Overall, our study demonstrates that even at small spatial scales, it is difficult to categorize metacommunity dynamics into discrete categories, i.e. metacommunity archetypes. Our study provides evidence that processes likely act differently on individual species and that, in addition to spatial and environmental factors, biotic interactions also influence community assembly. Therefore, our study supports the recent conceptual developments in metacommunity theory, which call for a better integration of between-species and between-site variation, as well as biotic interactions, to better account for the complex mechanisms and processes of metacommunity dynamics.

Implications for forest management and conservation

The ecological concept of TreMs is rapidly gaining importance, but the concrete relationships with biodiversity remain difficult to assess, especially at the landscape scale (Asbeck et al. 2021). Our study thus represents an important milestone in demonstrating the ecological role of TreMs, i.e. WTHs. Despite limited spatial replication, our study underpins the stepping stone concept of connecting FNRs by establishing old-growth forest patches. Although we observed distance effects on communities in the artificially created WTHs, these were mainly due to competition-dispersal trade-offs and probable mass effects of highly dispersive species into tree holes near the FNRs. These processes likely increase the community heterogeneity in these habitats and thus beta- and gamma-diversity at the landscape scale. The overall negative effects of the distance to FNRs on functional diversity were significant but weak, suggesting that distances between old-growth forest patches should be kept small to allow sufficient dispersal for less dispersive species. By increasing the variability of environmental conditions in TreMs of individual old-growth patches, species diversity could be further increased. Despite the overall success of this nature conservation strategy, continued availability of diversity of TreMs must be sought for such a strategy to be successful and sustainable in the long term.

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Martin M. Gossner: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Project administration (supporting); Supervision (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Nicolas Roth**: Formal analysis (supporting); Investigation (equal); Visualization (supporting); Writing – review and editing (equal). **Julia Rothacher**: Investigation (equal); Writing – review and editing (equal). **Mark Wong**: Formal analysis (supporting); Writing – review and editing (equal). **Jürgen Schmidl**: Conceptualization (equal); Investigation (equal); Methodology (supporting); Project administration (equal); Writing – review and editing (supporting).

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Data are available from the Envidat Digital Repository: https://www.doi.org/10.16904/envidat.708 (Gossner et al. 2025).

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