Facilitation: Isotopic evidence that wood-boring beetles drive the trophic diversity of secondary decomposers

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ABSTRACT

Deadwood heterogeneity is regarded as a primary causal driver of deadwood-associated soil biodiversity, but the underlying mechanisms remain elusive. This is partly due to the technical difficulties in disentangling and quantifying different components (e.g., deadwood is both habitat and food) of heterogeneity to which soil organisms may have context-dependent responses. Furthermore, non-trophic interactions, e.g., facilitation, also add complexity to deadwood heterogeneity-biodiversity relationships, yet their influences are unaccounted for in most deadwood biodiversity studies. To address these research gaps, we sampled isopod communities from 40 logs of two isotopically distinct tree species, which had been cut and incubated reciprocally for eight years in each of two environmentally contrasting sites (e.g., differences in background isotopic signatures and litter turnover rates). We then assessed the extent to which the variation in the biodiversity of isopod communities is explained by deadwood heterogeneity induced by wood-boring beetles. Stable isotope ratios (i.e., $\delta^{13}C$ and $\delta^{15}N$) were employed to examine the response of trophic diversity of isopod communities to the rarely tested food facet of deadwood heterogeneity. We hypothesized the deadwood heterogeneity is boosted by wood-boring beetles and thereby positively affects the abundance, taxonomic diversity and trophic diversity of isopod communities. Our results supported this hypothesis: the abundance and Shannon and Simpson diversity as well as trophic diversity of isopods were positively correlated to wood-boring beetle tunnel densities in both sites and across the two tree species. We observed significant tree species and reciprocal treatment effects on the δ15N values of isopods in one of the two sites. This result suggested that the use of deadwood as food sources versus habitats by isopods is environmentally dependent. This study demonstrates that there is substantial heterogeneity within deadwood that promotes the diversity and trophic diversity of macroinvertebrates. This relationship is mediated by saproxylic beetle facilitation, with implications for the roles of saproxylic beetles and within-deadwood heterogeneity in determining microbial wood decomposition in temperate forests.

1. Introduction

Soil biodiversity, comprising a substantial portion of global biodiversity, has been threatened by global changes such as ever-intensifying land use (Wall et al., 2015; Geisen et al., 2019). However, conservation policies have largely overlooked soil biodiversity due to the hidden nature of soil organisms (Bardgett and van der Putten, 2014; Guerra et al., 2020; Thakur et al., 2020). To address this research gap, we need to uncover blind spots in soil biodiversity research and better understand the processes that determine patterns of soil biodiversity. For example, there is rising awareness about the negative impact of deadwood removal on the maintenance and conservation of soil biodiversity

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in wood-land ecosystems, since deadwood increases forest habitat heterogeneity, which in turn contributes significantly to the enhancement of soil biodiversity (Lassauce et al., 2011; Stokland et al., 2012; Doerfler et al., 2018; Parajuli and Markwith, 2023). Although the connections between deadwood and soil-dwelling animals have been extensively documented, the majority of these studies have predominantly concentrated on factors such as host deadwood species and decomposition stage (Skubała and Marzec, 2013; Andringa et al., 2019; Kooch et al., 2023), environmental conditions (Raymond-Léonard et al., 2020), and anthropogenic activities (Siira-Pietikäinen and Haimi, 2009; Vanermen et al., 2021) that impact soil biodiversity at broader spatial scales (e.g., forest stand and above). There remains a gap in our understanding of the factors that maintain species-rich soil communities at finer scales (e.g., within deadwood object), such as interspecific interactions.

Abundant ecologically similar soil animals (e.g., isopods) can be found living sympatrically in deadwood. Strong intra- and inter-specific interactions are therefore expected to be important for community assembly in such a restricted space. While facilitation between species has been proposed as a key driver of soil animal co-existence in deadwood (Zuo et al., 2016b), there is scarce evidence to substantiate the causal mechanisms. The challenge may stem from disentangling the dual functionality (i.e., food and habitat) of deadwood for soil animals (Fujii et al., 2020, 2023), complicating the separation of facilitated habitat and food aspects of deadwood resources. For example, studies have shown wood and bark boring beetles facilitate other invertebrate groups by helping them unlock deadwood resources (Sydenham et al., 2016; Zuo et al., 2016b; Priest et al., 2021). However, their involvement in the process may entail two mutually non-exclusive interactions (i.e., habitat creation and food quality improvement) with the beneficiaries (Brin and Bouget, 2018). Specifically, in terms of facilitating living-space, beetles, particularly longhorn beetles (Cerambycidae), excavate tunnels through deadwood during the larval stage (Ulyshen, 2016; Seibold et al., 2022). These tunnels reduce the structural integrity and rigidity of deadwood and create cavities, which have strong positive effects on the invertebrates that cannot excavate tunnels themselves. Food resources-wise, beetle larvae likely increase resource heterogeneity in deadwood by converting lignified woody materials into more nutrient-rich and palatable frass for secondary invertebrate decomposers (Ulyshen, 2016). In addition, beetles can bring in microbial organisms that may further improve food availability for microbe-feeding invertebrates (Birkemoe et al., 2018; Peris et al., 2021). In a sense, wood-boring beetles facilitate other soil organisms by modifying both the food and habitat facets of deadwood heterogeneity, which implies that deadwood with a higher degree of beetle-infestation should have higher food and habitat availability and associated biodiversity than deadwood with a low degree of beetle infestation. However, to our knowledge, there have been no studies that simultaneously considered the facilitation of both facets influencing the deadwood community assembly. In the present study, we focused on isopods because they are among the most abundant and functionally important soil macro-invertebrates in terrestrial ecosystems, while their relatively strong sensitivity to microclimatic variation makes them an ideal model for testing responses to fine-scale environmental heterogeneity (David and Handa, 2010). Furthermore, living in a restricted environment and having comparable diets may intensify pressure from predators (e.g., chilopods), and foster competition within the isopod group, as well as with other saprophagous fauna for limited resources. Consequently, isopod species are likely to gain benefits from the activities of xylophylic beetles.

Besides quantifying habitat creation (as often indicated by beetle holes) by wood-boring beetles, stable isotope analysis (SIA) is useful to evaluate how wood-boring beetles regulate the provision of deadwood as a food source for isopods. Such a tool has been proven effective to quantify food resource heterogeneity at small spatial scales (Lehmitz and Maraun, 2016; Potapov et al., 2018). Wood-boring beetles

transform woody materials by facilitating microbial colonization of deadwood, which boosts microbial activity (e.g., carbon consumption and nitrogen fixation) and consequently enhances isotopic enrichment in deadwood tissues (Makipaa et al., 2017). Additionally, frass produced by wood-boring beetle carries different isotopic signatures from wood tissues, since it is the product of processing by the digestive system of beetle larvae and spurs microbial nitrogen-fixation activity (Ulyshen, 2016; Ceja-Navarro et al., 2019). These factors may also contribute to isotopic variability in deadwood owing to varying decomposition rates. To be exhaustive, moss attached to deadwood as a potential food source should be considered, given it is favored by many deadwood inhabitants. SIA should enable the inference of the food axis of deadwood by examining the isotopic variability in deadwood (Potapov et al., 2018), and further to connect the food axis of deadwood heterogeneity (food availability) to beetle facilitative effects.

We determined the variations in $\delta^{13}C$ and $\delta^{15}N$ signatures of the different isopod species occurring in deadwood to calculate isotopic metrics of the deadwood community. We expected the variability of $\delta^{13}C$ to reflect diet breadth of deadwood dwelling species, and the variability of $\delta^{15}N$ to reflect their trophic positions (Maraun et al., 2023). The space occupancy demarcated by all species in $\delta^{13}C–\delta^{15}N$ bi-plot space should represent the isotopic trophic niche, which is a proxy for the real trophic niche (Layman et al., 2012; Potapov et al., 2018). We then examined how isotopic metrics of isopod communities change with the food axis of deadwood heterogeneity (as indicated by isotope signatures) under different beetle infestation scenarios. To test the responses of isopod communities to potential effects of beetle facilitation, we made use of a long-term deadwood decomposition experiment conducted in two environmentally contrasting forest sites, where one site has a low litter turnover rate and hence a thick layer of leaf litter and humus, whereas in the other site the leaf litter layer is virtually non-existent due to fast leaf decomposition. We extracted isopods from logs of two phylogenetically distinct tree species namely, pedunculate oak and Norway spruce; these logs had been incubated in two sites simultaneously and reciprocally, and had various levels of wood-boring beetle infestation. Given that logs collected from two sites bear clearly distinct ^{15}N signatures due to the unique geologies of these sites, the reciprocal treatment would allow us to determine whether isopods use deadwood as important habitats or primary food sources. We used beetle hole density in dead logs as an indicator of beetle influence. We hypothesize that wood-boring beetles facilitate isopod diversity by enhancing the heterogeneity of deadwood microhabitats. Specifically, we expect that deadwood logs with more beetle holes 1) exhibit larger internal isotopic variability of basal resources and 2) accommodate more isopods with higher species diversity, 3) which should be linked with larger community-wide isotopic spacing within $\delta^{13}C–\delta^{15}N$ bi-plot space.

2. Materials and methods

2.1. Study area

Our study made use of the long-term common garden project known as "Loglife" (Cornelissen et al., 2012), which features two environmentally contrasting sites that represent predominant forest and soil types in NW Europe: (1) the Hollandse Hout forest plantation in Flevoland (site F) (52.46°N, 5.42° E) and (2) the forest estate of Schovenhorst in the Veluwe region (site S) (52.25° N, 5.63° E). Both sites lie in the central part of the Netherlands. The young soils in site F are clayey and are calcareous, moist, fertile (with total N at 520 mg/m² and total P at 207 mg/m² for the top 10 cm of the soil), and exhibit an average pH-KCl of 7.7. The soils are also ^{15}N and ^{13}C-rich relative to the air, since the region was once submerged under the North Sea and later reclaimed in the 1960s. Due to the fast turnover rate in incubation site F, the soil organic layer was shallow, measuring less than 5 mm, and there was an absence of a litter layer. Site F was largely covered with monospecific

stands for commercial forestry; the incubation plots at this site were in a rather light-open *Populus x canadensis* Moench stand. Site S harbors postglacial sandy deposits characterized by well-drained, acidic podzolic soils with an average pH-KCl of 3.7. These soils, characterized by low fertility (with total N at 109 mg/m^2 and total P at 33 mg/m^2 for the top 10 cm of soil), exhibit depletion in ^{15}N and ^{13}C compared to atmospheric air. The soil organic layer in site S could be up to 90 mm thick and was covered by a >10 mm thick leaf litter layer all year around. Site S also hosted mostly monospecific stands; here the light-open incubation plot had a lower and more open ground layer of predominantly the acidophilic grass *Deschampsia flexuosa* (L.) Trin. intermingled with mosses and patches of the dwarf shrub *Vaccinium myrtillus* L.

2.2. Reciprocal exchange of logs

Two tree species of distant phylogeny were selected from each of the two contrasting sites to test our hypotheses: the gymnosperm *Picea abies* (D. Don) Lindl. (Norway spruce) and the angiosperm *Quercus robur* L. (pedunculate oak). From each site ten individuals per tree species were extracted in 2011, five of which had been interchanged with the same number of individuals from the other site in order to examine the effects of site-specific growing conditions on the decomposition process. For our research goals, this reciprocal exchange of both species worked to our advantage, since the isotopic signatures of plants were markedly distinct in these two sites, owing to the difference in underlying geology, which made it easier to discern where organisms sourced their food. The age of selected trees ranged between 40 and 50 years for *P.abies* and between 40 and 120 years for *Q. robur*. Every tree individual was sawn into five roughly equal-sized logs, 100 cm in length and 25 ± 3 cm in diameter, for five subsequent harvests. Given that the "habitat-heterogeneity" effect and "habitat-amount" effect are often intertwined (Seibold et al., 2016, 2017), this standardization guaranteed that the logs used contained a similar amount of volume while minimizing the variation in internal heterogeneity among logs at the outset. Each site hosted five plots of 12 × 12 m, with at least 20m wide buffer zones between each other to reduce the interactions to a bare minimum. In Schovenhorst sites were fenced to keep wild animals from wandering in. The five logs of each individual tree were placed in a separate plot and the incubation commenced in 2012. Logs were positioned c. 30 cm apart within a plot.

2.2.1. Log harvest, isopod extraction and identification, and beetle hole counting

In February 2020, after eight years of incubation, one random log out of five in each replicate plot was sawn into two equal halves in the field, so in total 40 logs of these two species were harvested. One half was taken for other analyses. The other half was kept intact and carefully placed back exactly where it was taken from. This part was sampled 2 months later, i.e., in April, assuming the deadwood community had recovered from any chainsaw disturbance by then. These harvested (half) logs were individually bagged and transported (with minimal disturbance) to the laboratory at Vrije Universiteit Amsterdam for isopod extractions. All logs were stored at 4 °C and aired weekly until processing. During extraction, each log was put in a large tray with tall enough edges to prevent animals from escaping. We first painstakingly searched bark and moss for isopods, and then carefully peeled off the bark layer to collect isopods hiding beneath it. A large number of isopods were present in wood cavities and galleries; we therefore slowly dissected the entire log to sample the isopods therein. All isopods collected were transferred to a coded vial filled with 70% ethanol, and later were counted and identified to species-level under a stereomicroscope. Before we destructively sampled a log, we counted the holes created by wood borers (mostly wood-boring beetle larvae) in the 50 cm long log. We also used a screwdriver to detect holes that had been clogged by wood frass or mud by poking around the log surface. Only

some hard inner-wood sections that could impossibly have hosted any isopods were left untouched. The diameter of each beetle hole was measured to determine its area. In the case of non-circular ellipses, we measured the longest and shortest radii. We identified six isopod species from incubation site F: *Oniscus asellus* (Linnaeus) (*O. asellus*), *Porcellio scaber* (Latreille) (*P. scaber*), *Philoscia muscorum* (Scopoli) (*P. muscorum*), *Armadillidium vulgare* (Latreille) (*A. vulgare*), *Trachelipus rathkii* (Brandt) (*T. rathkii*), and *Trichoniscus pusillus* (Brandt) (*T. pusillus*). Four isopod species were found in incubation site S: *O. asellus*, *P. scaber*, *P. muscorum*, and *T. pusillus*. A total of 2203 isopods belonging to six species were collected from 39 out of 40 logs (as one of them had no isopods).

2.2.2. Stable isotope analysis

To determine isotopic variability of potential food sources derived from or associated with deadwood, we measured δ^{13}C and δ^{15}N values of various substrate types, i.e., bark, moss, wood "top" (upper log section in horizontal field position) and wood "bottom" (lower section touching the soil), highly decomposed wood materials (which could be easily removed by hand), and frass. The number of samples varied per log since some logs did not have moss, bark, frass or because of their decomposition status is relative homogenous within dead logs. Samples were dried at 70 °C for 48h for moss samples, and about two weeks for bark, frass and woody samples until constant mass. After being fully dried, samples were finely ground in a ball mill and then weighed (to the nearest ug) and sealed into tin capsules. Since the natural isotope composition of substrates differ significantly, in several trial runs the weight of sample required for isotope analysis was determined, and ranged between 1.5 mg and 10 mg. Samples were stored in a desiccator until analysis of the stable isotopes. In total 874 of 2203 individuals from both incubation sites were analyzed for δ^{13}C and δ^{15}N values. The sample size for each isopod species within each log was roughly proportional to the abundance of that species within the specific isopod community associated with that particular log (Table S1). To incorporate as much intraspecific trophic variation as possible within a confined spatial scale, we selected samples from both juvenile and adult groups of each isopod species in approximately proportional representation within each log (Table S1). After drying at 70 °C for 48h, all selected isopod individuals were ground in a ball mill (MM400 Retsch, Haan, Germany) and 1–2 mg of the powder samples were weighted into tin capsules. Samples were stored in a desiccator until analysis of stable isotopes.

Stable isotope of isopods and food sources were determined using an elemental analyzer (NC 2500, Carlo Erba, Milano; Italy) in tandem with a stable isotope ratio mass spectrometer (Delta Plus; ThermoFinnigan, Bremen, Germany). Samples were calibrated against USGS 40 and USGS 41 standards. The working standard used for δ^{13}C and δ^{15}N analysis was NIST 1577c (powdered bovine liver), and the standard deviations of δ^{15}N and δ^{13}C values of this standard (n = 3) were ≤0.3‰ and 0.15‰, respectively. Isotopic signatures were expressed using the δ notation: δ X (‰) = $(R_{sample} - R_{standard})/R_{standard} \times 1000$, with X representing the target isotope and R the ratio of heavier to lighter isotope. Vienna PeeDee Belemnite (VPDB) served as standard for δ^{13}C and atmospheric air as standard for δ^{15}N.

2.2.3. Statistical analysis

We used generalized linear mixed-effects models to detect possible effects of isopod species, host wood species, and origin of log on the isotopic variability of isopods in each incubation site, where log origin and host species identity were fixed factors, and LogID and isopod species identity were treated as two independent random factors. Ontogeny had a minor influence on isotopic signatures (Fig. S1). Consequently, to streamline model structures, we omitted age status as a random factor. The R package 'lme4' was applied for generalized linear mixed effect model construction. To assess model performance, we used the package "MuMIn" to calculate the marginal and conditional R^2, which quantified the proportions of model variation explained by fixed

effects (marginal R^2) and the combination of fixed and random effects, respectively (conditional R^2). Explanatory power of each factor was calculated with variance decomposition in the model (Nakagawa and Schielzeth, 2013). We used the ranges (the differences between the highest and lowest values) of the isotope values of food sources to represent deadwood resource heterogeneity (Layman et al., 2007; Potapov et al., 2018). To test for facilitation of isopod trophic niche diversity (niche breath) by wood-boring beetles, we calculated the area occupied by each community using the δ^{13}C and δ^{15}N values of individual isopods in isotopic biplots. This metric is widely used to represent the trophic niche of a community or specific group(s) within the community (Newsome et al., 2007). To better account for the influences of sample size sensitivity and extreme values over the metric, which, in turn, compromise its comparability across communities, we calculated the area based on the standard ellipse (SEA, Standard Ellipse Area) (Jackson et al., 2011). Finally, SEA calculated using Bayesian estimation (SEA.B) with the R package 'SIBER' (Jackson et al., 2011) was chosen as a proxy for trophic niche diversity of isopod communities (n = 39). Diversity indices (Shannon and Simpson) were also calculated for each isopod community using the R package 'vegan'. Linear regression was employed to test the responses of the food axis of deadwood and isopod diversity (abundance, Shannon index and Simpson index) and isotopic niche diversity to wood-boring beetle facilitation. Considering the variability in sizes of holes left by different wood-boring beetle species, we conducted a linear regression analysis to examine the correlation between beetle hole density and the total beetle hole area per log surface. This analysis aimed to determine whether beetle hole density could accurately reflect the impact of beetles. All data used to run linear regression models were checked for normality and heterogeneity. All statistical procedures were run in R (version 4.2.1; R Core Team, 2022).

3. Results

3.1. Isotope values of isopods and their food

Overall, out of 874 isopod individuals measured for their isotopic values, 368 belonged to six species collected from 19 logs in site F. Their δ^{13}C values varied between −27.9‰ and −22.0‰ (mean ± SD = −24.9‰±1.2‰) and δ^{15}N values varied between −1.3‰ and 8.7‰ (mean ± SD = 4.3‰±1.8‰). The difference in δ^{15}N values among species was significant (one-way ANOVA following GLM, $F_{5, 362}$ = 12.13, $P < 0.001$, Fig. S2a), with *T. rathkii* showing the highest values and *P. scaber* the second lowest followed by *A. vulgare* (two individuals). The δ^{13}C values were also significantly different among isopod species (one-way ANOVA following GLM, $F_{5, 362}$ = 79.75, $P < 0.001$, Fig. S2c), with *O. asellus* being the most enriched in ^{13}C, *P. muscorum* being the lowest. The other 506 individuals belonging to four species were collected from 20 logs in site S. The range of their δ^{13}C values was −27.1‰ to −21.9‰ (mean ± SD = −24.8‰±1.0‰) and the range of their δ^{15}N values was −8.1‰ to −0.5‰ (mean ± SD = −4.4‰±1.5‰). Both isotopic signatures differed significantly among isopod species (one-way ANOVA following GLMs, $F_{3, 502}$ = 81.7, $P < 0.001$ (δ15N); $F_{3, 502}$ = 49.7, $P < 0.001$ (δ^{13}C), Figs. S2b and d), *T. pusillus* had the highest δ^{15}N value and the lowest δ^{13}C value, and *P. scaber* had the second lowest δ^{13}C and δ^{15}N values. *A. vulgare* had the lowest δ^{15}N value (three individuals). Generalized linear mixed effect analyses showed δ^{15}N values of isopods in site F were influenced by host tree species and log origin (Table 1), but not by the interaction between these two factors (Table 1). δ^{15}N values of isopods in site S were only marginally affected by their host tree species (Table 1), while δ^{13}C values of isopods in both sites were not affected by host tree species and log origin (Table 1).

Out of 217 potential food (bark, wood, frass and moss) samples measured for isotope values, 103 were collected from 19 logs harvested from site Flevoland. Their δ^{13}C values varied between −31.3‰ and −24.8‰ (mean ± SD = −27.5‰±1.8‰) and δ^{15}N values varied between −5.3‰ and 3.9‰ (mean ± SD = −0.7‰±2.3‰). The other 124

Table 1

Overview of the generalized linear mixed effect models examining the effects of host log origin, host wood species on δ^{13}C and δ^{15}N values of isopods extracted from 39 logs in site Flevoland and Schovenhorst. The model used for isotopic signatures for both sites is Isotope value ~ Origin_site × Host_species + (1| LogID) + (1|Isopod_species), with LogID and Isopod_species being the random effects. Significant estimates are indicated in bold ($P < 0.05$). Host logs were collected from site Flevoland and Schovenhorst prior to incubation, and they belong to *P. abies* and *Q. robur*.

Flevoland	δ^{15}N ($R^2_m = 0.15$, $R^2_c = 0.75$)			δ^{13}C ($R^2_m = 0.00$, $R^2_c = 0.52$)		
Factors	F value	P	η^2	F value	P	η^2
Origin_site (O)	15.1	**<0.01**	0.51	0.05	0.44	0.04
Host_species(H)	7.10	**<0.05**	0.32	0.52	0.81	0.00
O × H	0.43	0.44	0.04	0.00	0.90	0.00
Schovenhorst	δ^{15}N ($R^2_m = 0.02$, $R^2_c = 0.52$)			δ^{13}C ($R^2_m = 0.00$, $R^2_c = 0.37$)		
Factors	F value	P	η^2	F value	P	η^2
Origin_site (O)	0.63	0.44	0.04	0.91	0.36	0.06
Host_species(H)	2.63	0.12	0.14	0.48	0.50	0.03
O × H	1.70	0.21	0.09	0.34	0.57	0.02

Notes: R^2_m is marginal R^2, R^2_c is conditional R^2. η^2 (partial) is the proportion of the total variance in isotopic signatures explained by each factor and their interactions.

samples were collected from 20 logs harvested from site Schovenhorst. Their range of δ^{13}C values was −31.0‰ to −24.5‰ (mean ± SD = −27.3‰±1.5‰) and the range of δ^{15}N values was −8.9‰–0.1‰ (mean ± SD = −5.1‰±2.0‰). Both δ^{13}C and δ^{15}N values of potential food were significantly different, and were influenced by all three main factors namely substrate type ($F_{4, 97}$ = 34.3, $P < 0.001$ (δ^{15}N, F); $F_{4, 97}$ = 46.6, $P < 0.001$ (δ^{13}C, F); $F_{4, 108}$ = 38.6, $P < 0.001$ (δ^{15}N, S); $F_{4, 108}$ = 47.9, $P < 0.001$ (δ^{13}C, S)), log origin ($F_{1, 101}$ = 270.5, $P < 0.001$ (δ^{15}N, F); $F_{1, 112}$ = 188.6, $P < 0.001$ (δ^{15}N, S); $F_{1, 112}$ = 22.6, $P < 0.001$ (δ^{13}C, S)), and host deadwood species ($F_{1, 96}$ = 6.6, $P < 0.05$ (δ^{15}N, F); $F_{1, 96}$ = 46.6, $P < 0.001$ (δ^{13}C, F); $F_{1, 107}$ = 54.4, $P < 0.001$ (δ^{15}N, S); $F_{1, 107}$ = 24.3, $P < 0.001$ (δ^{13}C, S)) except for δ^{13}C ($F_{1,101}$ = 0.4, $P > 0.05$) in Flevoland (Three-way ANOVA after GLMs results in Fig. S3). The δ^{15}N values of potential food were significantly affected by the interactions of log origin with substrate type ($F_{4, 92}$ = 17.4, $P < 0.001$ (δ^{15}N, F); $F_{4, 103}$ = 12.1, $P < 0.001$ (δ^{15}N, S)) and host wood species ($F_{1, 91}$ = 9.1, $P < 0.01$ (δ^{15}N, F); $F_{1, 102}$ = 6.0, $P < 0.05$ (δ^{15}N, S)) in both sites (Three-way ANOVA after GLM result in Fig. S3). The δ^{13}C values of potential food in site S were significantly affected by the interaction between host wood species and substrate type ($F_{4,98}$ = 8.7, $P < 0.001$. Three-way ANOVA after GLM result in Fig. S3). Almost all isopod species were enriched in ^{13}C and ^{15}N relative to their potential food sources in site F; however, in site S the enrichment in ^{15}N of isopods relative to woody samples (wood, bark and frass) was low (Fig. 1).

3.2. Heterogeneity in host logs with different levels of beetle infestation

In total 40 logs had decomposed in site Flevoland (20; one without isopods was excluded from the analyses) and site Schovenhorst (20) for eight years before harvest, and these logs had sustained varying degrees of beetle attack. The number of wood-boring beetle holes per 50 cm log length ranged between 0 and 120 and was positively correlated to total beetle hole area for both host species. The percentages of explained variance ranged between 72% and 95% (Fig. S4). Holes were mostly positioned in the top (air-exposed) half and cut side of logs. On average, *P. abies* logs had more holes than *Q. robur* logs in both sites ($F_{1, 17}$ = 19.4, $P < 0.001$ (site F); $F_{1, 18}$ = 6.3, $P < 0.05$ (site S), Fig. S5). Both δ^{13}C and δ^{15}N range in woody material sampled from the two host wood species were significantly correlated with the number of holes in both sites, with the percentages of variance explained ranging between 43% and 78% (Fig. 2). However, the relationships disappeared when including bark and moss samples (Fig. S6).
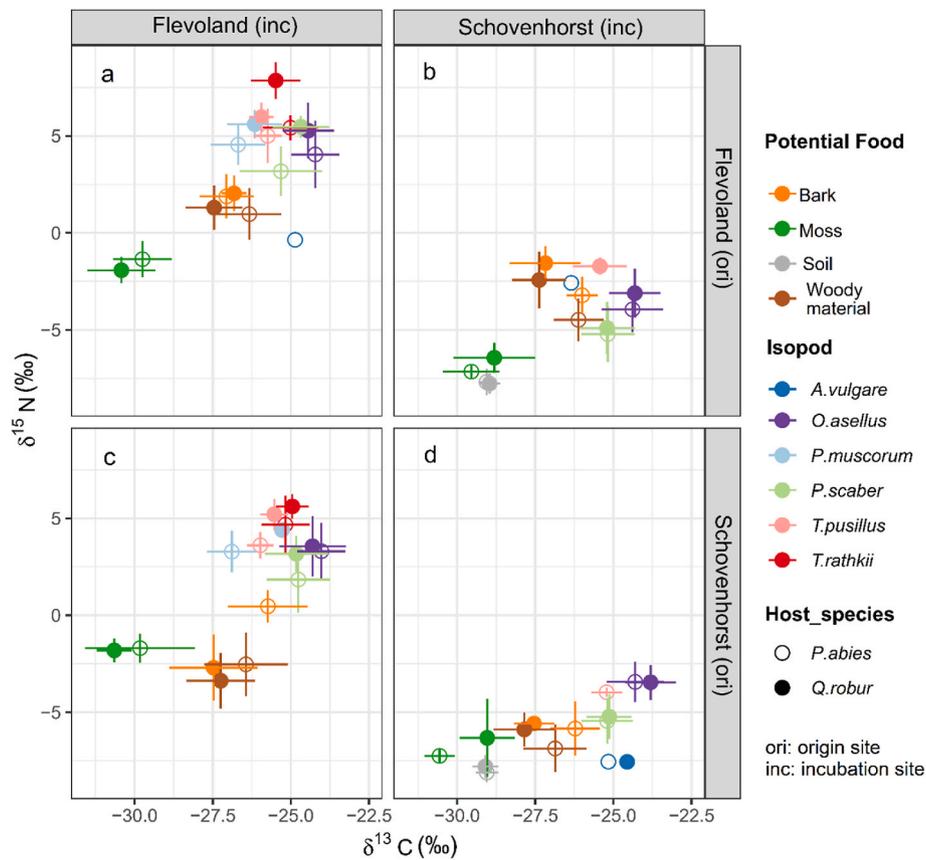
Fig. 1. Mean (+ standard deviation) δ^{13}C and δ^{15}N values of isopods and their potential food items from sites Flevoland and Schovenhorst. Open circles represent isopods and food materials (moss, bark and wood) from *P. abies* logs. Filled circles from *Q. robur* logs. SD is shown for all isopod species and potential food items with three or more samples. inc, the incubation site where tree logs had been incubated; ori, the origin site where tree logs were collected. (a) logs were collected and incubated in site F; (b) logs were collected in site F but incubated in site S; (c) logs were collected in site S but incubated in site F; (d) logs were collected and incubated in site S. The soil isotope data used in panel b, d were obtained from (Fujii et al., 2023).

3.3. Facilitation of isopod diversity by wood holes

In both sites, the trophic niche diversity of isopods increased significantly with the number of holes in host wood logs, for both host wood species from both sites of origins (Fig. 3). The overall abundance of isopod in each log did not differ between the two species (Fig. S7). However, it was significantly and positively related to the number of wood holes, and it generally explained between 43% and 70% of variation in isopod abundance for the two host species across the two sites (Fig. 4a and b). In terms of other taxonomic diversity indices, there were only significant relationships between both Shannon and Simpson indices and number of wood holes for *P. abies* logs in both sites (Fig. 4c, d, e, f).

4. Discussion

In line with our expectation, isotope measurements revealed heterogeneity in food items within logs varied among individual logs of *P. abies* and *Q. robur*. Specifically, high isotopic variabilities within logs coincided with strong signs of wood-boring beetle infestation (higher hole density) in both experimental sites. We demonstrated that hole density had significantly positive effects on isopod abundance inhabiting deadwood, suggesting wood-boring beetles expanded the living space for isopods in deadwood. The diversity indices of isopod communities responded to hole densities in *P. abies* but not in *Q. robur* logs. We also found that higher hole densities enhanced the trophic niche diversity of isopod communities across the two wood species in both sites. This suggests that the observed expansion of isopod communities'

niches is associated with the facilitation of food resource availability by wood-boring beetles. In addition, the outcomes of our reciprocal treatment indicate that isopods made different use of deadwood, with isopods using deadwood merely as shelter in site S and both shelter and food in site Flevoland. This finding suggests the trophic diversity of isopods was driven by both habitat and food components of heterogeneity in deadwood.

4.1. Heterogeneity in deadwood and wood holes

It is widely accepted that deadwood enrichment increases forest spatial heterogeneity, which influences species diversity and community composition (Sandström et al., 2019; Heidrich et al., 2020; Vogel et al., 2020). However, deadwood-related heterogeneity for invertebrates has been mostly quantified at forest stand level or above, while the cryptic variation within single logs has been largely overlooked in understanding deadwood functionality with regard to biodiversity conservation and biochemical cycling (Seibold et al., 2016; Harmon, 2021). We used the variabilities (as ranges) in δ^{13}C and δ^{15}N as proxies for the food axis of heterogeneity in logs (wood, bark and the moss layer covering them). Our results confirm the expectation that isotopic signatures differ significantly among substrate types (Fig. S3), leading to high within-deadwood food diversity after eight years of decomposition. The heterogenization of deadwood during decomposition is partly attributable to the substantial differences in quality among tissues (Harmon, 2021). These differences can lead to the disparity in microbial activities these tissues host and hence the varying levels of isotopic enrichment in different parts of deadwood (Potapov et al., 2018). This is consistent
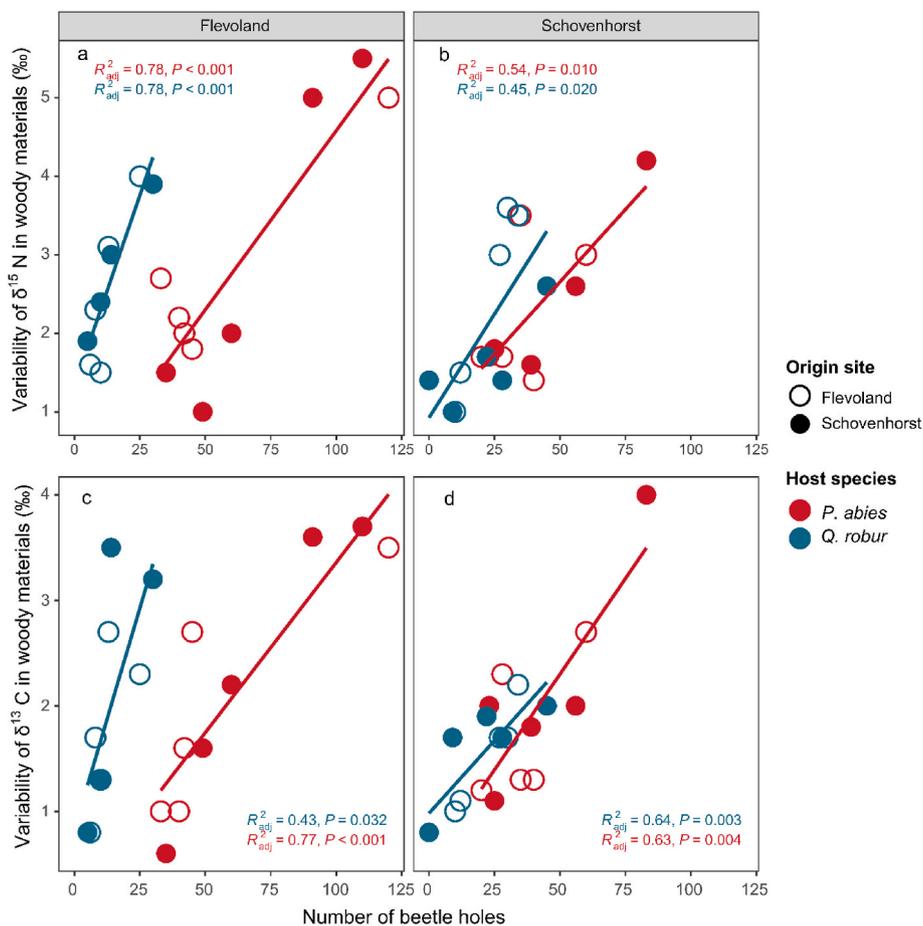
Fig. 2. Relationships between number of wood-boring beetle holes per 50 cm log length and isotopic variabilities of δ^{15}N (a, b) and δ^{13}C (c, d) in woody materials collected from different parts of logs (wood top half, bottom half and frass) for both incubation sites, i.e., site Flevoland (a, c) and site Schovenhorst (b, d). Host species *P. abies* is coded in red and *Q. robur* is coded in blue. Open circles and filled circles represent logs collected from site Flevoland and Schovenhorst, respectively before incubation. Solid lines represent significant relationships.
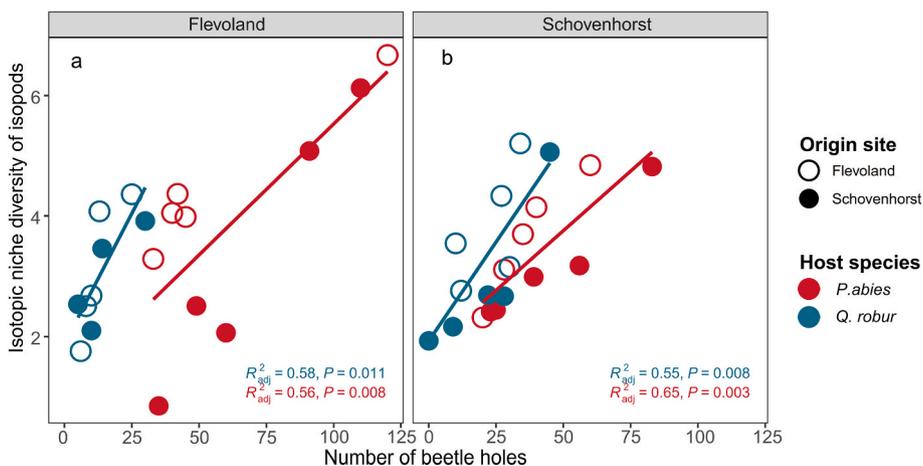
Fig. 3. Relationships between number of wood-boring holes per 50 cm log length and trophic niche diversity of isopods (Bayesian standard ellipse area) for both incubation sites, i.e., site Flevoland (a) and site Schovenhorst (b). Host species *P. abies* is coded in red and *Q. robur* is code in blue. Open circles and filled circles represent logs collected from site Flevoland and Schovenhorst, respectively before incubation. Solid lines represent significant relationships.

with our results that bark had higher isotopic value compared with woody material. We did not find that both C and N isotopic signatures were notably enriched in wood bottom relative to wood top in most cases (Fig. S3).

This research offers compelling evidence that wood-boring beetles play a significant role in promoting this fine-scale heterogeneity. Their facilitation not only expands living space but also impacts the food aspect of wood heterogeneity. Specifically, frass produced by wood-boring beetle larvae generally has higher isotopic signatures and much lower C to N ratio than unprocessed wood (Fig. S3, Fig. S8), which
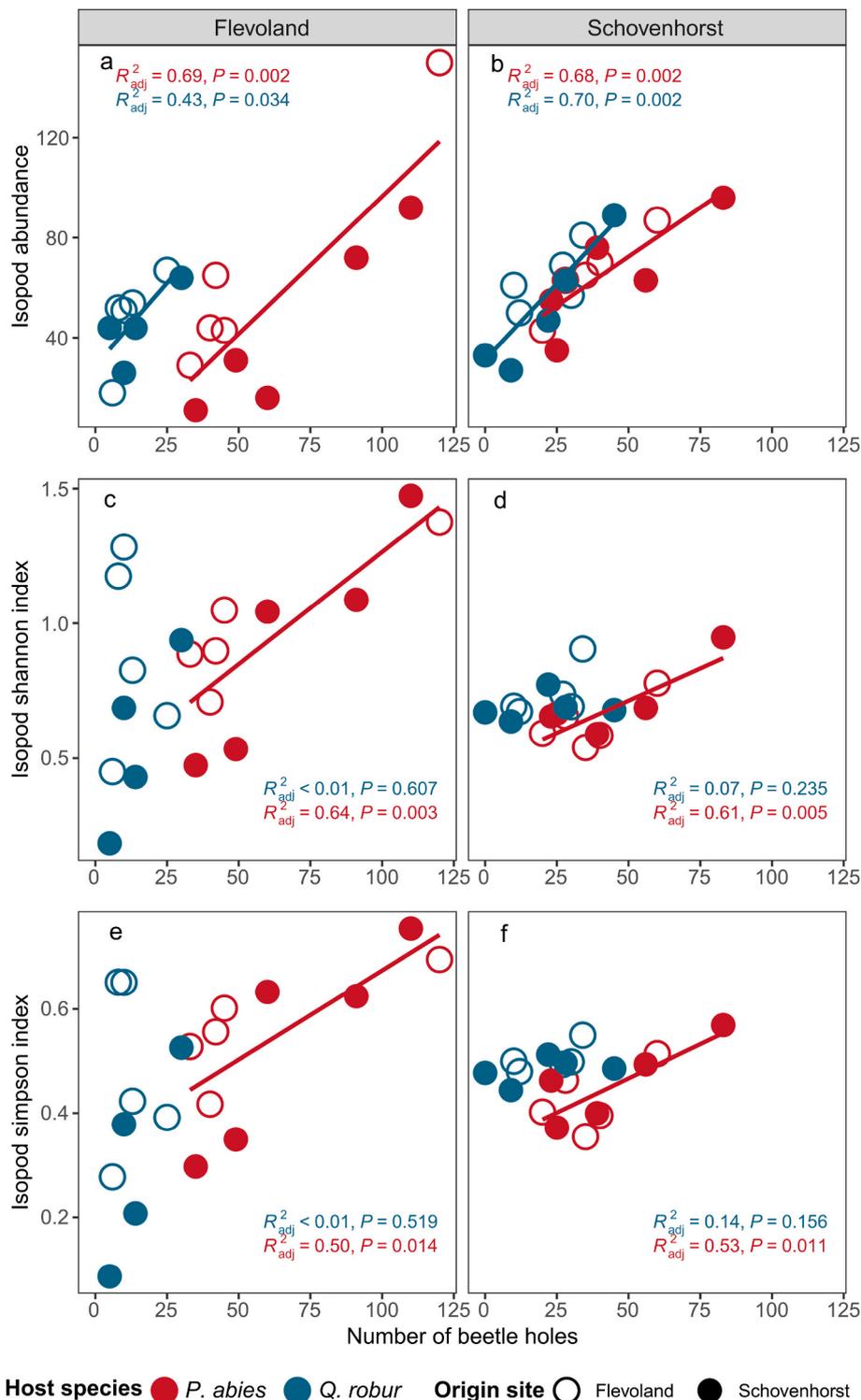
Fig. 4. Relationships between number of wood-boring holes per 50 cm log and diversity indices of isopods for both incubation sites, i.e. site Flevoland (a, c, e) and site Schovenhorst (b, d, f). These indices are isopod abundance (a, b), isopod Shannon index (c, d) and isopod Simpson index (e, f). Host species *Picea abies* is coded in red and *Q. robur* is coded in blue. Open circles and filled circles represent logs collected from site Flevoland and Schovenhorst, respectively before incubation. Solid lines represent significant relationships.

highlights that they change not only the physical properties of dead-wood microhabitats, as suggested by previous studies (Priest et al., 2021; Seibold et al., 2022), but also the chemical properties that determine the palatability of deadwood to other consumers. Moreover, in line with our first hypothesis, the isotopic ranges (both for $\delta^{13}C$ and $\delta^{15}N$) of woody and wood-derived material (wood-top and

wood-bottom, frass) increased significantly along with the number of wood holes, irrespective of deadwood species (Fig. 2). This positive relationship may be explained by the facilitated colonization of various microorganisms and the conversion of woody material by wood-boring beetle larvae (Hyodo, 2015; Makipaa et al., 2017; Potapov et al., 2022). However, the isotopic variabilities in deadwood, when including bark

and moss, did not respond to the number of wood holes (Fig. S6), suggesting the wood-boring facilitative effects were limited to the woody parts of the logs. Considering the presence of various wood-boring beetles and other saproxylic insects, we established strong correlations between the number of wood holes and the total hole area per log surface for both wood species in both sites (Fig. S4), suggesting that the simple index could effectively capture their collective effect.

4.2. Wood-boring beetle facilitation of isopod diversity

Aligned with our second hypothesis, we found that the abundance of isopods was positively correlated with the number of wood holes, independently of deadwood host species (Fig. 4a and b), as was previously shown for bark beetles and their bark holes and galleries (Zuo et al., 2016b). This suggests that there is a sequence from facilitation of invertebrates including isopods by bark beetles followed by facilitation by wood-boring beetles. This way, wood-boring beetles supplant early-colonizing bark beetles as a subsequent force to lessen the environmental filtering effect for deadwood community assembly in the mid to late decomposition stage by increasing living space in deadwood. Intriguingly however, we found average isopod abundance in *P. abies* logs was on par with that in *Q. robur* logs, despite *P. abies* logs having more wood holes (Fig. S5). A possible explanation is that, contrary to *P. abies* logs, most *Q. robur* logs were still loosely covered with a thick layer of outer bark even after eight years of decomposition, which supplemented the living space of isopods (Zuo et al., 2016a). This result also implies that interactions between tree identity and keystone invertebrate species such as wood-boring beetles should be considered when predicting deadwood-associated biodiversity. In addition, we found that isopod diversity was significantly and positively correlated with numbers of wood holes for *P. abies* in both sites, but this relationship did not hold true for *Q. robur* and only weak trends were detected in site S (Fig. 4). It is likely that, when the xylem parts of logs became new colonization sites for deadwood consumers after their bark was depleted of nutrient, the outer bark still influenced the deadwood community (Zuo et al., 2016a; Chang et al., 2022; Lin et al., 2022). Another possible explanation for the weak relationships for *Q. robur* logs could be that they only varied narrowly in the numbers of wood holes (Fig. S5).

4.3. Wood-boring beetles drive the expansion of isopod trophic diversity and underlying mechanisms

Agreeing with the third hypothesis, we found strong and positive correlations between isotopic niche diversity of isopods and numbers of holes in logs for two deadwood host species in both sites (Fig. 3); this correlation was likely driven by the increase of heterogeneity in food sources (Fig. S9). These results provide direct evidence for wood-boring beetles facilitating the trophic aspect of deadwood-associated biodiversity. Consistent with previous studies, most isopod species showed differences in $\delta^{15}N$ and $\delta^{13}C$ values regardless of host species, indicating that this group required a wide variety of resources (Fig. 1, Fig. S2). Assuming a $\delta^{15}N$ enrichment of 3–4‰ per trophic level, ^{15}N values of most isopod species roughly ranged within one trophic level in the two sites (Fig. S2), which supports the view that isopods are generalist detritivores, their diet consisting of leaf litter, rotting wood, fungi, animal tissue and feces. For example, saprotrophic fungi are known to be a major food source for *O. asellus*, while *P. scaber* exhibits coprophagous behavior, whereas small-sized isopod species such as *T. pusillus* feed predominantly on microorganisms (Potapov et al., 2022). Moreover, isopods in different developmental stages may select different food sources due to strong variability in body size, although the ontogenetic effect on isotope signatures is usually not pronounced (Klarner et al., 2013; Potapov et al., 2018, also see Fig. S1). Therefore, deadwood logs heavily infested by beetles are more likely to fulfill the requirements of the diverse coexisting isopods (Fig. 4) by enhancing the food aspect of deadwood resource.

Furthermore, the trophic diversity of isopods was also probably, at least in part, driven by the facilitated habitat aspect of deadwood heterogeneity, meaning some isopods may inhabit deadwood for shelter without necessarily relying on it as a food source. This is evidenced by the relatively low percentage of variation in niche diversity of isopods explained by the food axis of deadwood heterogeneity in site S (Fig. S9). In addition, unlike in site F, $\delta^{15}N$ signatures of most isopod species in site S were not strongly enriched relative to bark and wood, even lower for the reciprocal treatment in site S (Fig. 1), suggesting that some isopod species in site S may feed little or not on food resources derived from deadwood. This is further corroborated by individual-level results which show that the variation in $\delta^{15}N$ values of isopods in site F were significantly influenced by the log origin and deadwood host species (Table 1). Conversely, in site S, only the deadwood host species had a minor impact on the $\delta15N$ values of isopods (Table 1). We hypothesize that this inconsistency may come down to the environmental differences between two sites. In site S, a substantial amount of organic matter has accumulated and been covered by a thick leaf litter layer. Considering that isopods tend to be selective feeders, adapting their diet towards easily decomposable substrates characterized by high nutrient contents and low defenses (Vos et al., 2011; Potapov et al., 2022), it is plausible that isopods favor soil organic matter over deadwood-derived food. This is supported by the enrichment in their $\delta^{15}N$ values compared to the soil (Fig. 1). In contrast, the very thin soil organic and virtually absent litter layer in site F may force deadwood-inhabiting isopods to rely on deadwood for food resources. Thus, it can be inferred that wood-boring beetles can facilitate the trophic diversity of isopods by altering both food and habitat aspects of deadwood heterogeneity, but the relative importance of these two aspects may vary based on the range of other food options present in the environment. It is important to note that species such as *A. vulgare* did not exhibit significant isotopic enrichment and were even depleted in relation to potential food sources, even in site F (Fig. 1). The reduced isotopic enrichment may be linked to the presence of the isotopically depleted isopod carapace influencing the overall isotopic signature of the whole body (Korobushkin and Gongalsky, 2022). Although we have demonstrated that soil biodiversity can benefit from wood-boring beetle facilitation of the deadwood food source, our experimental setup prevents us from teasing apart different components. Therefore, for a more comprehensive generalization of beetle facilitation across environments, we suggest that future studies incorporate additional treatments. This could involve creating artificial holes in various configurations to replicate the impact of wood borers on deadwood habitat heterogeneity while minimizing their influence on the food aspect.

5. Conclusion

We have demonstrated that there is a close association between wood-boring beetle activity and deadwood heterogeneity, i.e., in microhabitat and food for soil fauna, and that this association can significantly impact the abundance, diversity and trophic niche diversity of detritivore groups in the soil subsystem. This finding, which provides empirical support for our main hypothesis, highlights the need to consider positive biotic interactions, especially facilitation in future deadwood and soil biodiversity conservation research. Based on our evidence from stable isotope analysis, we conclude that wood-boring beetles can directly modulate habitat and food facets of heterogeneity in deadwood. Our findings revealed the connection between the food axis of deadwood heterogeneity and isopod trophic diversity, which offers direct support for the proposition that dead plant material provides a 'house made of food' for soil animals (Fujii et al., 2020), thereby adding a fresh perspective on how deadwood sustains soil functional biodiversity. Interestingly, the mechanisms underlying the relationship between functional diversity of isopods and internal deadwood heterogeneity, however, may differ by study area, suggesting the dual functions (food and habitat) of deadwood could change depending on

environmental settings. Hence, future conservation research should focus on the dual functionality of deadwood to better understand how this important source of environmental heterogeneity in forest ecosystems controls soil animal biodiversity; and stable isotope analysis could be a valuable tool to achieve such objectives. Furthermore, most deadwood-associated biodiversity studies in temperate forests have focused on highly mobile invertebrates, such as saproxylic beetles with flight ability. The diversity of (wingless) invertebrates of low mobility, such as isopods and millipedes should be more susceptible to changes in small-scale heterogeneity in habitat and food conditions. Given the important role of isopods in controlling microbial activity and thereby carbon and nutrient cycling (A'Bear et al., 2014; Crowther et al., 2015), future studies should take into consideration within-deadwood heterogeneity to gain a full picture of soil biodiversity conservation status and its role in essential ecosystem functions against the backdrop of rapid global changes.

CRediT authorship contribution statement

Bin Tuo: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Yu-Kun Hu:** Writing – review & editing, Investigation. **Richardus S.P. van Logtestijn:** Writing – review & editing, Project administration, Investigation, Data curation. **Juan Zuo:** Writing – review & editing, Investigation. **Leo Goudzwaard:** Writing – review & editing, Project administration, Investigation, Funding acquisition. **Mariet M. Hefting:** Writing – review & editing, Investigation, Funding acquisition. **Matty P. Berg:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Johannes H.C. Cornelissen:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2024.109353.

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