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Artificial tree holes as a tool to assess spatial and temporal diversity of cavity-dwelling invertebrates in urban forests

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Abstract

Tree cavities form over long periods of wood decay and represent important microhabitats that support diverse invertebrate assemblages in forest ecosystems. However, the structure and diversity of cavity-dwelling invertebrate communities in urban environments remain poorly understood. In this study, multiple artificial tree holes were installed in two types of urban forests that differed in size and structure, and the spatial and temporal patterns of cavity-dwelling invertebrate communities were analysed. Invertebrates inhabiting each artificial tree hole were periodically collected and recorded. We compared the community composition and α, β, and γ diversity while evaluating environmental factors influencing community assembly. Invertebrate communities in small urban forests exhibited slightly higher local within-cavity diversity (α diversity) and were dominated by a limited number of species adapted to urban environments. In contrast, large urban forests showed higher regional diversity (γ diversity) and greater among-cavity diversity (β diversity), with predators and omnivores contributing substantially to spatial community heterogeneity. Invertebrate communities within tree cavities changed dynamically over time following installation, and the abundance of xylophagous and omnivorous taxa increased with time after the installation of artificial tree holes. Although species richness and abundance were positively correlated with air temperature, invertebrate abundance was negatively correlated with tree density and diversity. These results demonstrate that artificial tree holes are an effective tool for assessing the diversity of cavity-dwelling invertebrate communities in urban forests and provide important insights into the effects of urbanisation on cavity ecosystems, with implications for the conservation and management of cavity resources.

1. Introduction

Tree cavities are formed through excavation by bird species or long-term decay processes in trees infected with wood-decaying fungi (Cockle et al. 2012; Zheng et al. 2016). They function as habitats for a wide range of animals and provide important tree-related microhabitats (i.e., tree-related microhabitats [TreMs]; Bütler et al. 2024) in forest ecosystems (Goldingay 2009; O'Connell and Keppel 2016; Ranius et al. 2024). Invertebrate communities inhabiting tree cavities are influenced by the physical characteristics, surrounding landscape structure, and forest management practices (Ranius 2002; Quinto et al. 2014; Gossner et al. 2016; Bartel et al. 2025). However, as the dynamics of deadwood and tree cavities vary widely depending on regional environmental conditions (Traylor et al. 2025), cross-regional comparative studies and an integrated understanding of ecological responses under diverse environmental conditions are required. Cavity-dwelling invertebrates contribute to forest ecosystem function through nutrient cycling and wood decomposition (Ulyshen and Šobotník 2018), pollination outside cavities during their adult stages (Ulyshen et al. 2023), and potential pest control by serving as prey for predators (Williams et al. 2017). Despite their ecological importance, large, old trees suitable for cavity formation are exposed to multiple threats, including drought, pests, diseases, logging, land development, landscape fragmentation, and climate change, making their conservation a global challenge (Lindenmayer and Laurance 2017).

Urbanisation causes habitat loss and fragmentation, and is a major factor in reducing the abundance of large old trees. Concurrently, remnant forests and trees within urban landscapes serve as important patch habitats for diverse organisms and help maintain biodiversity and ecosystem services (Paudel and States 2023; Koji et al. 2024). In recent years, tree-related microhabitats in urban environments, including tree cavities, have attracted increasing attention, and their ecological value and conservation importance have been suggested to be underestimated compared to those in forested landscapes (Peuhu et al. 2019). Urbanisation generally leads to habitat fragmentation and reduction, resulting in community homogenisation and biodiversity loss (Piano et al. 2020). Highly specialised saproxylic species are particularly sensitive to landscape changes because of their strong dependence on specific habitat conditions and resources (Gossner and Müller 2011; Henneberg et al. 2025), suggesting that urbanisation poses a threat to cavity-dwelling invertebrates. Conversely, urbanisation can increase the abundance of certain species adapted to urban environments (Hahs et al. 2023). Despite the contrasting positive and negative effects of urbanisation, few studies have examined in detail how invertebrate community structures within tree cavities are assembled in urban landscapes.

Tree-hole bird nests accumulate diverse organic materials, including nesting materials, faeces, food remains, feathers, and carcasses, creating resource-rich environments within the cavities (Hanzelka et al. 2023). Such resource subsidies provided by birds increase invertebrate population densities, and the input of resources such as carcasses and feathers promotes not only keratin feeders and scavengers but also omnivorous and predatory taxa (Sugiura et al. 2013; Sugiura and Ikeda 2013; Sugiura and Masuya 2015). Understanding the invertebrate communities associated with tree-hole bird nests helps elucidate symbiotic relationships with birds and provides insights into biotic interactions within nest webs. Previous studies on treehole bird nests have primarily focused on the effects of parasites on avian reproductive success (Wesołowski and Stańska 2001; Hund et al. 2015). However, interest in the ecological functions of nonparasitic invertebrates has increased in recent years. For example, saprophagous fly larvae have been reported to improve nest hygiene, thereby improving health (Krištofík et al. 2017). These findings suggest that tree-hole bird nests are not merely breeding sites for birds, but also represent important resource bases that influence the structure and ecological functions of invertebrate communities.

Although the importance of tree-hole bird nests and their associated invertebrate communities in forest ecosystems has been widely recognised, field surveys targeting natural cavities have several limitations. Tree cavities are relatively rare, and surveys can disturb them. In addition, natural cavities vary greatly in shape, entrance size, internal deposits, and decay stage, resulting in substantial variations in invertebrate assemblages among cavities (Schauer et al. 2018; Cuff et al. 2021; Ranius et al. 2024). These factors make it difficult to conduct standardised comparisons and evaluate diversity patterns and environmental responses on a regional scale. As an alternative approach, the use of wooden boxes mimicking tree-hole bird nests (i.e., artificial tree holes) has been proposed and has attracted attention as a habitat for cavity-dwelling invertebrates (Jansson et al. 2009; Carlsson et al. 2016). Artificial tree holes allow for standardisation of shape, internal conditions, installation height, and replication, thereby facilitating comparative studies that are difficult to conduct using natural cavities. Moreover, by manipulating

internal resources, artificial tree holes can partially reproduce the characteristics of invertebrate communities associated with natural cavities, and the introduction of poultry carcasses can promote the use of artificial tree holes by invertebrates associated with tree-hole bird nests, including keratin feeders, scavengers, omnivores, and predators (Jansson et al. 2009).

In this study, we aimed to clarify how the diversity and community structure of invertebrates inhabiting artificial tree holes mimicking tree-hole bird nests differ across forest environments with varying degrees of urbanisation. We installed artificial tree holes to simulate tree-hole bird nests by adding chick carcasses to remnant urban forests and suburban forests, and periodically collected and recorded the invertebrate communities inhabiting the cavities. Specifically, we addressed the following objectives: (1) to compare the diversity (α, β, and γ diversity) and community structure of invertebrates using artificial tree holes between small and large urban forests, and (2) to evaluate environmental factors influencing community assembly. We hypothesised that the species composition, including cavity-dependent species, would differ between small and large urban forests. We expected a limited number of tolerant species to dominate communities in small urban forests, whereas more diverse species assemblages would use artificial tree holes in large urban forests. Consequently, we predicted that communities in small urban forests would be composed of fewer species, with lower within-cavity (α), among-cavity (β), and within-forest (γ) diversity and simplified community structure. Furthermore, we expected that artificial tree holes, which provide high-quality resource environments by adding bird carcasses, would increase the abundance and frequency of invertebrates associated with bird nests and scavengers.

2. Materials and Methods

2.1. Study area

Field surveys were conducted at two sites in Tokyo, Central Japan (Fig. 1): the Field Museum of Tama Hills, Tokyo University of Agriculture and Technology, located in the southern part of the Tama Hills (35.63842° N, 139.37822° E; Site A), and the Fuchu Campus of the same university, located in an urbanised area of Fuchu City (35.684997° N, 139.485764° E; Site B). The mean annual temperature and annual precipitation in this region are 15.4°C and 1598.9 mm, respectively (Japan Meteorological Agency 2026). The region falls within the Asian monsoon climate zone, and its potential climax vegetation is an evergreen broadleaf forest. However, due to historical human use, much of the area is currently covered by secondary deciduous broadleaf forest.

Site A (large urban forest) was located within a forested area of approximately 49.5 ha. The elevation of the study area ranges from 140 to 180 m a.s.l. and consists of a valley running from northwest to southeast and two adjacent hills. Most ridge and slope areas were dominated by broadleaf forests composed mainly of *Quercus serrata* and *Quercus acutissima*, with small areas of experimental plantations of *Cryptomeria japonica* and *Chamaecyparis obtusa*. Site B (small urban forest) was a green space of approximately 3 ha located within a university campus at an elevation of approximately 50 m

a.s.l. The dominantly planted tree species were *Zelkova serrata*, *Chamaecyparis pisifera*, and *Pinus densiflora*.

2.2. Construction and installation of artificial tree holes

Previous studies have shown that artificial tree holes filled with a basic substrate consisting of oak sawdust, oak leaves, hay, and alfalfa powder, combined with various attractants, can reproduce approximately 70% of the species observed in natural tree cavities when limited to cavity-dwelling, nest-associated, and saproxylic species (Jansson et al. 2009). In this study, artificial tree holes mimicking tree-hole bird nests were constructed from *Cryptomeria japonica* wood as rectangular wooden boxes with a thickness of 12 mm, a height of 40 cm, and a width and depth of 21 cm (Fig. 2a). A circular entrance hole with a diameter of 8.5 cm was created on the front side to allow invertebrate access. The entrance was covered with a wire mesh (2 cm mesh size) to prevent the intrusion of birds and mammals. The roof was designed to be open for periodic inspection of the interior. Five drainage holes (5 mm in diameter) were drilled at the bottom to prevent water accumulation.

Each artificial tree hole was filled with 3 L of hardwood chips (Bio Breeding Mat for Beetles, MARUKAN Co., Ltd., Osaka, Japan) to simulate a decomposing wood environment within the cavities. In addition, to reproduce the high-quality resource conditions characteristic of bird nests, a chicken chick carcass (*Gallus gallus domesticus*; 40.1 ± 3 g) was placed inside each artificial tree hole. This design attracted keratin feeders, scavengers, and other invertebrates associated with tree-hole bird nests. It allowed us to examine the effects of resource input on community composition (Fig. 2b). Artificial tree holes were attached to tree trunks at a height of approximately 1.5 m above ground using palm fiber rope during March 2024 (Fig. 2c), and wood chips and chick carcasses were introduced on April 8, 2024. Within each Site A, artificial tree holes were spaced at least 20 m apart, with 35 holes installed at Site A and 5 at Site B.

2.3. Invertebrate sampling

To examine temporal changes in the species composition of invertebrate communities inhabiting artificial tree holes, surveys were conducted approximately every two weeks from April 8 to October 21, 2024. During each survey, 29 of the 35 artificial tree holes installed at Site A and all five artificial tree holes at Site B were inspected. Vertebrates observed visually within each artificial tree hole were recorded. Individuals that were clearly identified in the field were counted and recorded, whereas those that were difficult to identify were collected, placed in plastic containers, and transported to a laboratory.

Individual counts were not conducted for ants (Formicidae) forming colonies within the artificial tree holes; instead, colony presence or absence was recorded. Dipteran larvae obtained from chick carcasses during the surveys were reared indoors using chicken meat as food, and species identification was conducted after adult emergence. Based on feeding habits closely associated with tree cavities and bird nests, all collected invertebrates were classified into five trophic groups: predators, detritivores, carrion feeders, xylophages, and omnivores (Quinto et al. 2014; Hanzelka et al. 2023; Ranius et al. 2024). Species with unknown feeding habits and invertebrates primarily associated with living plants or tree sap

were excluded from analyses and categorised as “others.” Voucher specimens were deposited in the laboratory at Shiraume Junior College.

2.4. Environmental factors

In the present study, five environmental factors potentially affecting cavity-dwelling invertebrate communities were examined: species richness, abundance, total basal area (TBA), crown openness, and diameter at breast height (DBH). For trees located within an approximately 10 m radius around each artificial tree hole, tree species and girth at breast height (GBH) were recorded for trees with a DBH > 10 cm. The total basal area (TBA; cm^2) was calculated by first estimating each tree's basal area (BA) from its GBH and then summing these estimates. On September 9, 2024, hemispherical photographs were captured using a fisheye lens from a position approximately 1.5 m in front of each artificial tree hole. The crown openness was estimated from these hemispherical images using CanopOn 2 (http://takenaka-akio.org/etc/canopon2/).

2.5. Statistical analysis

All statistical analyses were conducted using R version 4.5.1 (R Core Team 2025). The invertebrate species richness in each artificial tree hole was calculated as the total number of species recorded across the 14 survey occasions and used to compute diversity indices.

Hill numbers with q = 0 (species richness) were used as diversity measures. Mean species richness per artificial tree hole was defined as α diversity, whereas total species richness observed at each study site was defined as γ diversity. For γ diversity, rarefaction and sample coverage–based standardisation were applied using the iNEXT package to correct for differences in sample size and sampling completeness. To evaluate species turnover among artificial tree holes, β diversity was calculated based on α and γ diversity using both additive ($\beta_{+} = \gamma - \alpha$) and multiplicative ($\beta_{\times} = \gamma / \alpha$) approaches.

The patterns of species composition among artificial tree holes were examined using non-metric multidimensional scaling (nMDS) based on Bray–Curtis dissimilarity. The nMDS ordination was performed in two dimensions using the metaMDS function in the R package vegan, and the reliability of the ordination was assessed using stress values. To improve analytical robustness, taxa represented by three or fewer individuals and taxa that could not be reliably identified and that may have included multiple species were excluded from the analyses. Statistical differences in species composition between sites were tested using permutational multivariate analysis of variance (PERMANOVA) implemented using the Adonis function. In addition, a similarity percentage (SIMPER) analysis was conducted using the same adjusted dataset as the nMDS to identify the taxa contributing most to differences between sites.

Species richness and abundance of invertebrates recorded during each monitoring period were used as response variables to evaluate the effects of environmental factors and feeding guilds (predators, detritivores, carrier feeders, xylophages, and omnivores). Generalised linear mixed models (GLMMs) were constructed assuming a Poisson distribution for species richness and a negative binomial

distribution for abundance. Explanatory variables included the study site (Sites A or B), cumulative days since the installation of artificial tree holes (days), mean air temperature during each monitoring interval (mean temperature), presence or absence of ant colonies, DBH of the host tree, TBA, tree species richness, tree abundance, and crown openness. Study site, feeding guild, and ant presence were treated as categorical variables. Interactions between feeding guilds and sites, as well as between feeding guilds and days, were also evaluated. Prior to model construction, multicollinearity among the explanatory variables was assessed using the VIF function in the car package, and variables were selected to ensure that the variance inflation factors (VIFs) were below 5.

3. Results

Comparisons of environmental factors between Site A (large urban forest) and Site B (small urban forest) are shown in Table 1. Crown openness (Mann–Whitney U test, $p < 0.05$), tree species richness ($p < 0.001$), tree abundance ($p < 0.01$), and TBA ($p < 0.001$) were all significantly higher at Site B. In contrast, the diameter at breast height (DBH) of the trap trees was significantly larger at Site A ($p < 0.001$).

Table 1
Comparison of Environmental Factors Between Study Sites

Variables	Site A (mean)	Site B (mean)	p value
Crown openness	27.0	32.9	< 0.05
Tree species richness	4.3	10.8	< 0.001
Tree abundance	11.5	31.8	< 0.01
TBA	7996.2	16928.6	< 0.001
Trap tree DBH	113.4	33.5	< 0.001

p-values were calculated using the exact Wilcoxon rank-sum test (Mann–Whitney U test) for independent groups.

A total of 1,618 individuals belonging to 41 invertebrate species were recorded from the artificial tree holes during the survey period. Of these, 38 species and 1,276 individuals were recorded at Site A, whereas 17 species and 342 individuals were recorded at Site B (Table S1). In terms of species richness by feeding guild, predators were relatively more abundant at Site A, whereas detritivores were the most species-rich group at Site B, indicating differences in the dominant feeding guilds between sites (Fig. 3a). Patterns of abundance by feeding guild also differed markedly between sites. At Site A, omnivores and predators accounted for a relatively large proportion of the individuals, whereas at Site B, carrion feeders and detritivores were dominant (Fig. 3b).

The composition of the feeding guilds within the artificial tree holes changed over time following installation (Fig. 4). Carrion feeders were abundant during the early survey period, but declined rapidly and were no longer recorded after the fourth survey. Predators and detritivores increased during the

middle phase of the survey and subsequently declined during the later phase. In contrast, omnivores steadily increased over time and became the most abundant feeding guild during the middle phase of the survey. Xylophagous species were rarely recorded during the early phase, but appeared from the seventh survey onwards and were consistently recorded at low abundance during the later phase.

Alpha diversity (mean species richness per artificial tree hole) was lower at Site A (4.55) than at Site B (6.20), whereas gamma diversity (total species richness at the Site A level) was higher at Site A (23.5) than at Site B (15.2) (Table 2). Both additive (β□dd) and multiplicative (β□ult) beta diversity were higher at Site A (β□dd = 18.9, β□ult = 5.16) than at Site B (β□dd = 8.99, β□ult = 2.45), consistent with the pattern observed for gamma diversity. Vertebrate community composition differed significantly between sites A and B (PERMANOVA, $R^2 = 0.142$, $F = 5.30$, $p < 0.001$; Fig. 5). SIMPER analysis identified six species, *Armadillidium vulgare*, *Porcellio scaber*, *Plesiophthalmus spectabilis*, *Amphipyra monolitha*, *Meghimatium bilineatum*, and *Lehmannia valentiana*, as major contributors to the compositional differences between the sites, all of which occurred more frequently at Site B (Table 3).

Table 2
Species richness–based diversity indices of invertebrate communities at Sites A (large urban forest) and B (small urban forest)

Site	α	γ	βadd	βmult
A	4.55	23.5	18.9	5.16
B	6.20	15.2	8.99	2.45

α indicates mean local (within-trap) species richness; γ represents total species richness across all traps within each site; β_add is calculated as γ − α (additive β-diversity); and β_mult is calculated as γ / α (multiplicative β-diversity).

Table 3
Species contributing significantly to community dissimilarity between Sites A (large urban forest) and B (small urban forest) based on SIMPER analysis.

Species	Average	SD	Ratio	Site B	Site A	p value
Armadillidium vulgare	0.121	0.035	3.45	0.472	0.050	< 0.001
Porcellio scaber	0.060	0.057	1.05	0.226	0.020	< 0.05
Plesiophthalmus spectabilis	0.039	0.018	2.17	0.162	0.023	< 0.001
Amphipyra monolitha	0.034	0.041	0.82	0.126	0.011	< 0.01
Meghimatium bilineatum	0.019	0.025	0.75	0.072	0.000	< 0.001
Ambigolimax valentianus	0.011	0.022	0.50	0.042	0.000	< 0.01

Only species with $p < 0.05$ are shown.

The results of the GLMM analysis are presented in Tables 4 and 5. Both species richness and abundance were significantly higher for predators (species richness: Estimate = 1.70, $p < 0.001$; abundance:

Estimate = 1.38, $p < 0.001$) and omnivores (species richness: Estimate = 1.63, $p < 0.001$; abundance: Estimate = 2.31, $p < 0.001$) than for detritivores, whereas carrion feeders showed significantly lower values for both species richness (Estimate = − 3.96, $p < 0.001$) and abundance (Estimate = − 3.91, $p < 0.001$). In contrast, the xylophagous species did not differ significantly from the detritivores in terms of species richness ($P = 0.395$). For the interaction between feeding guild and study site, species richness and abundance of all feeding guilds other than detritivores were relatively lower at the small urban forest (Site B) than at the large urban forest (Site A) (e.g., predators: Estimate = − 3.59, $p < 0.001$; omnivores: Estimate = − 2.07, $p < 0.001$), indicating a biased community structure at Site B. Regarding temporal effects, species richness and abundance of xylophagous (species richness: Estimate = 1.16, $p < 0.001$; abundance: Estimate = 1.80, $p < 0.001$) and omnivorous species (species richness: Estimate = 0.61, $p < 0.001$; abundance: Estimate = 1.30, $p < 0.001$) increased over time since installation, whereas carrion feeders showed a decreasing trend (species richness: Estimate = − 4.09, $p < 0.001$; abundance: Estimate = − 4.68, $p < 0.001$). Among environmental factors, mean temperature had a positive effect on both invertebrate species richness (estimate = 0.26, $p < 0.001$) and abundance (estimate = 0.32, $p < 0.001$) within the artificial tree holes. In contrast, tree density (TBA; abundance: Estimate = − 0.56, $p = 0.001$) and tree species richness (abundance: Estimate = − 0.40, $p = 0.010$) had negative effects on invertebrate abundance.

Table 4
Generalized linear mixed model results for species richness across feeding guilds and environmental variables.

Variables	Estimate	Std. Error	z	p value
Main effects				
Intercept	-3.02	0.22	-13.66	< 0.001
Predators	1.70	0.23	7.31	< 0.001
Carrion feeders	-3.96	1.05	-3.79	< 0.001
Xylophagous	-0.30	0.35	-0.85	0.395
Omnivorous	1.63	0.24	6.89	< 0.001
Site B (Detritivores)	2.64	0.38	6.99	< 0.001
Days (Detritivores)	-0.07	0.15	-0.48	0.631
Mean temperature	0.26	0.06	4.09	< 0.001
Crown openness	-0.12	0.07	-1.60	0.109
Tree species richness	-0.13	0.08	-1.51	0.131
Tree abundance	0.05	0.07	0.69	0.489
TBA	-0.16	0.09	-1.73	0.084
Trap tree DBH	-0.03	0.09	-0.33	0.745
Ant colony	-0.09	0.15	-0.62	0.533
Interaction effects:				
Feeding guild × Site B				
Predators × Site B	-3.59	0.53	-6.73	< 0.001
Carrion feeders × Site B	-1.73	0.51	-3.41	< 0.001
Xylophagous × Site B	-1.95	0.53	-3.70	< 0.001
Omnivorous × Site B	-2.07	0.35	-5.89	< 0.001

1. Results are based on a generalized linear mixed model (GLMM) with a Poisson distribution (log link). Trap ID was included as a random effect. Model fit: AIC = 1909.9, BIC = 2042.7, − 2 × logLik = 1863.9; random effect SD = 0.152.

2. Feeding guild was treated as a categorical variable with Detritivores as the reference level. The main effects of Site B and Days represent values for Detritivores only. Interaction terms (Feeding guild × Site B, Feeding guild × Days) indicate the relative effect of Site B or Days for each feeding guild compared to Detritivores.

Variables	Estimate	Std. Error	z	p value
Main effects				
Interaction effects: **Feeding guild ×Days**				
Predators × Days	-0.15	0.18	-0.85	0.395
Carrion feeders × Days	-4.09	0.71	-5.78	< 0.001
Xylophagous × Days	1.16	0.29	3.95	< 0.001
Omnivorous × Days	0.61	0.18	3.39	< 0.001
1. Results are based on a generalized linear mixed model (GLMM) with a Poisson distribution (log link). Trap ID was included as a random effect. Model fit: AIC = 1909.9, BIC = 2042.7, − 2 × logLik = 1863.9; random effect SD = 0.152.				
2. Feeding guild was treated as a categorical variable with Detritivores as the reference level. The main effects of Site B and Days represent values for Detritivores only. Interaction terms (Feeding guild × Site B, Feeding guild × Days) indicate the relative effect of Site B or Days for each feeding guild compared to Detritivores.				

Table 5
Generalized linear mixed model results for invertebrate abundance across feeding guilds and environmental variables.

Variables	Estimate	Std. Error	z value	p value
Main effects				
Intercept	-2.74	0.24	-11.54	< 0.001
Predators	1.38	0.25	5.59	< 0.001
Carrion feeders	-3.91	0.82	-4.76	< 0.001
Xylophagous	-0.85	0.38	-2.20	< 0.05
Omnivorous	2.31	0.24	9.79	< 0.001
Site B (Detritivores)	4.25	0.62	6.90	< 0.001
Days (Detritivores)	-0.25	0.18	-1.41	0.159
Mean temperature	0.32	0.09	3.70	< 0.001
Crown openness	-0.11	0.13	-0.82	0.415
Tree species richness	-0.40	0.16	-2.59	< 0.01
Tree abundance	0.11	0.14	0.80	0.424
TBA	-0.56	0.17	-3.25	< 0.01
Trap tree DBH	-0.08	0.17	-0.49	0.624
Ant colony	-0.25	0.19	-1.29	0.197
Interaction effects:				
Feeding guild × Site B				
Predators × Site B	-4.30	0.63	-6.84	< 0.001
Carrion feeders × Site B	-1.20	0.56	-2.13	< 0.05
Xylophagous × Site B	-2.55	0.65	-3.91	< 0.001
Omnivorous × Site B	-3.11	0.46	-6.72	< 0.001

1. Results are based on a generalized linear mixed model (GLMM) with a negative binomial distribution (nbinom2). Trap ID was included as a random effect. Model fit: AIC = 3018.1, BIC = 3156.7, -2 × logLik = -1485.1; random effect SD = 0.468; dispersion parameter = 0.288.

2. Feeding guild was treated as a categorical variable with Detritivores as the reference level. The main effects of Site B and Days represent values for Detritivores only. Interaction terms (Feeding guild × Site B, Feeding guild × Days) indicate the relative effect of Site B or Days for each feeding guild compared to Detritivores.

Variables	Estimate	Std. Error	z value	p value
Main effects				
Interaction effects: **Feeding guild ×Days**				
Predators × Days	0.02	0.22	0.10	0.917
Carrion feeders × Days	-4.68	0.61	-7.68	< 0.001
Xylophagous × Days	1.80	0.35	5.17	< 0.001
Omnivorous × Days	1.30	0.22	6.04	< 0.001
1. Results are based on a generalized linear mixed model (GLMM) with a negative binomial distribution (nbinom2). Trap ID was included as a random effect. Model fit: AIC = 3018.1, BIC = 3156.7, -2 × logLik = -1485.1; random effect SD = 0.468; dispersion parameter = 0.288.				
2. Feeding guild was treated as a categorical variable with Detritivores as the reference level. The main effects of Site B and Days represent values for Detritivores only. Interaction terms (Feeding guild × Site B, Feeding guild × Days) indicate the relative effect of Site B or Days for each feeding guild compared to Detritivores.				

4. Discussion

Comparisons of invertebrate communities utilising artificial tree hollows between the small urban forest (Site B) and the large urban forest (Site A) revealed clear differences in community composition, as well as differences in within-hollow (α), among-hollow (β), and stand-level (γ) diversity. Urbanisation generally leads to habitat loss and fragmentation, resulting in community homogenisation and reduced biodiversity (Piano et al. 2020), while simultaneously increasing the abundance of a limited number of species adapted to urban environments (Hahs et al. 2023). Studies examining invertebrate communities inhabiting artificially installed water-filled tree-hole microhabitats in urban settings have shown that cosmopolitan species tend to dominate under certain urban conditions (Srivastava et al. 2023). Similarly, in the artificial tree hollows examined in this study, six species adapted to urban environments—*Armadillidium vulgare*, *Porcellio scaber*, *Plesiophthalmus spectabilis*, *Amphipyra monolitha*, *Meghimatium bilineatum*, and *Lehmannia valentiana*—contributed disproportionately to the community structure in the small urban forest (Site B). These species are commonly recorded in urban environments and remnant green spaces (Magura et al. 2008; Akita and Masumoto 2016; Nakano 2017; Waki 2017), suggesting that urbanisation promotes the dominance of specific urban-adapted species within cavity-dwelling invertebrate communities. Consequently, the utilisation of artificial tree hollows by urban-adapted species may have resulted in higher within-hollow diversity (α diversity) in the small urban forest (Site B).

When species richness was compared among feeding guilds, detritivores showed significantly higher species richness in the small urban forest (Site B). In contrast, predators, carrion feeders, xylophagous species, and omnivores all exhibited lower species richness at Site B than in the detritivores. This pattern

is likely attributable to the fact that predators, carrion-feeding beetles, and xylophagous species are particularly prone to a decline in species richness with increasing urbanisation (Ulrich et al. 2007; Rocha and Fellowes 2020; Meyer et al. 2021; Hahs et al. 2023). Consequently, reductions in these feeding guilds likely contributed directly to the observed decreases in between-tree-hole (β) and within-forest-stand (γ) diversity in the small urban forest (Site B). In addition, in tree-hole environments, the presence of predators can limit the use of tree holes by non-predatory taxa (Ranius et al. 2024). In the small urban forest (Site B), where predator abundance was lower, reduced predation pressure may have facilitated the use of tree holes by non-predatory invertebrates. This, in turn, may have contributed to shifts in feeding guild composition and community structure, as well as to increased within-tree-hole (α) diversity. The structure of invertebrate communities inhabiting tree holes varies in response to multiple interacting environmental factors, including landscape context, light availability, moisture content, and substrate density (Cuff et al. 2021). Even within standardised artificial water-filled tree-hole microhabitats, differences in installation environments can generate variations in temperature, aquatic nutrient availability, leaf litter input, and exposure conditions, all of which influence invertebrate species richness and abundance (Srivastava et al. 2023). Accordingly, in the present study, despite the use of artificial tree holes with standardised designs and contents, microhabitat heterogeneity arising from differences in installation environments likely affected between-tree-hole community heterogeneity (β diversity). In particular, in the large urban forest (Site A), the larger forest stand size was expected to generate greater environmental heterogeneity among artificial tree holes, which may have promoted differentiation in community composition among tree holes and been reflected as higher β diversity. In contrast, in the small urban forest (Site B), even with some degree of microhabitat variation, reductions in the regional species pool and the dominance of urban-adapted species associated with urbanisation may have limited the expression of environmental differences, such as community differentiation. As a result, tree-hole communities in Site B likely became more homogeneous, resulting in lower β diversity.

Effects of abiotic environmental factors (mean temperature, tree species richness, and TBA) and installation duration were detected in invertebrate communities inhabiting the tree holes. Mean temperature had positive effects on both species richness and invertebrate abundance. Invertebrates, particularly insects, are highly dependent on seasonal increases in temperature, with higher temperatures generally leading to increased activity and diversity (Wardhaugh et al. 2018; Tang et al. 2025). Temperature plays an important role in the establishment and maintenance of invertebrate communities, even within tree holes, which are largely enclosed systems isolated from external conditions and supported by woody substrates. In contrast, TBA and tree species richness negatively affected invertebrate abundance. Many saproxylic invertebrates prefer relatively dry microclimatic conditions within tree holes (Schauer et al. 2018). In general, forest structural attributes strongly regulate forest microclimates, and open environments with lower tree density and canopy cover tend to experience higher atmospheric dryness (Mwamulima et al. 2025). In addition, dryness within tree holes is influenced by entrance size, with larger entrances promoting drier conditions and, consequently, higher species diversity (Schauer et al. 2018). In the present study, because the entrance size was standardised across artificial tree holes, the microclimatic conditions within the tree holes were likely primarily

determined by the external forest structure. Specifically, in forest stands with higher TBA, increased canopy closure likely reduces light availability and atmospheric dryness, leading to more humid conditions within tree holes. This may have suppressed the abundance of invertebrates that prefer drier conditions. The negative effect of tree species richness on treehole invertebrate communities further suggests that higher tree species richness does not necessarily reflect forest maturity but rather indicates younger forest stands dominated by small-diameter trees. In young stands with smaller trunks, tree-hole formation is often limited (Zawadzka et al. 2016), reducing the availability of suitable tree-hole resources and consequently lowering local species richness and abundance.

In addition to the overall effects of installation duration, the interaction between feeding guild and days since installation revealed distinct temporal responses among guilds. Xylophagous and omnivorous taxa exhibited increasing trends in both species richness and abundance over time, whereas predators showed no clear temporal change compared to detritivores, and carrion feeders exhibited a declining trend. Saproxylic communities inhabiting tree holes are known to form complex food webs that change over time and across seasons (Carlsson et al. 2016; Conca-Esquembre 2024). In tree-hole assemblages composed of saproxylic hoverflies and beetles, nested community structures have been reported during summer in certain tree species (Conca-Esquembre 2024), likely reflecting sequential colonisation processes in which newly dispersing species are progressively incorporated into pre-existing communities as adult activity and dispersal increase seasonally. The observed increase in xylophagous individuals in the present study may similarly be associated with such seasonal dispersal and colonisation dynamics. Moreover, the majority of individuals classified as omnivorous were represented by a single species, *Periplaneta japonica*. In this species, adult emergence is followed by a reproductive period concentrated from summer to autumn (Tsuji 1985). In cockroaches, behavioural traits differ across life-history stages, with adults often exhibiting active movement related to shelter selection, resource exploration, and mating behaviour (Schal et al. 1984). Therefore, the temporal increase observed in omnivorous individuals may reflect not only gradual establishment following installation but also seasonal dispersal and recruitment associated with adult activity and reproduction.

In raptor breeding nests, carrion-feeding (necrophagous) beetles are established through prey remains and carcasses brought in during nesting activities (Cosandey et al. 2021). In the present study, carrion feeders also appeared intensively during the initial phase following the placement of chick carcasses; however, both species richness and abundance rapidly declined as resources were consumed. This pattern is consistent with previous findings that carcasses are highly nutritious but transient resources that decompose rapidly and are consumed, leading to short-term increases in carrion-feeding invertebrates in response to resource availability (Dawson et al. 2022). In contrast, raptor nests have been reported to support carrion-feeding assemblages, including beetles that exploit dried remains and keratin-based resources, over extended periods after breeding (Cosandey et al. 2021). Similarly, experiments using artificial tree holes captured multiple necrophagous invertebrates following the introduction of chicken carcasses, although the amount of resources was not specified (Jansson et al. 2009). The chick carcasses used in the present study likely represent a more limited resource than those

used in previous experiments. As a result, invertebrates typically associated with the later stages of carrion decomposition were scarcely detected, and only a single keratin-feeding individual was recorded.

This study had several limitations. First, the study was conducted within a specific region and at a limited number of sites. To generalise the patterns of tree-hole use across different regions or forest structures, broader spatial sampling is required. Second, this study did not include direct comparisons of invertebrate communities that inhabit natural treeholes. Artificial microcosms are widely recognised as effective model systems for controlling spatial and temporal conditions, enabling experimental replication and testing of ecological theories. However, artificial systems inevitably represent simplified environments compared to natural systems and are subject to general limitations in fully reproducing large-scale environmental variability and complex biotic interactions (Srivastava et al. 2004; Benton et al. 2007). Although artificial tree holes have been reported to compensate for the scarcity or uneven distribution of natural tree holes and provide temporary habitats or dispersal stepping stones for cavity-dwelling invertebrates, they are not effective for all tree-hole-dependent species (Jansson et al. 2009). Therefore, the results of the present study should be interpreted as observations that characterise the general tendencies of cavity-dwelling invertebrate communities across sites and environmental conditions, as revealed by the use of artificial tree holes.

Declarations

Competing Interests

The authors declare no conflicts of interest.

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Author Contribution

R.A. collected and analysed the data, prepared the figures, and drafted the manuscript. T.Y. supervised the study and contributed to writing and revising the manuscript.

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Data availability

The datasets generated and/or analysed in the current study are available from the corresponding author upon reasonable request.

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Figures

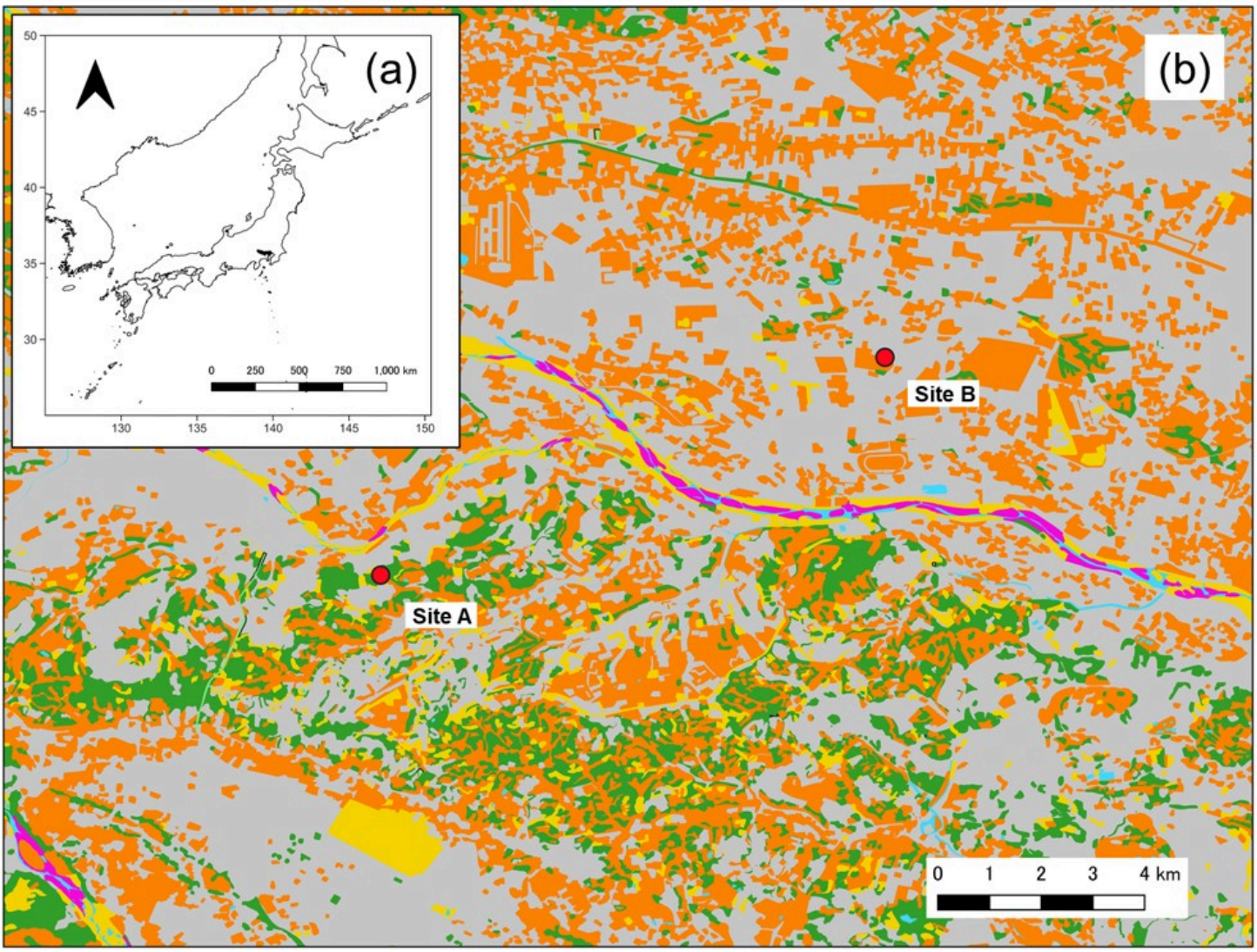


Figure 1

Study sites in Tokyo, Japan. (a) Location of Tokyo (black) in Japan and (b) locations of Site A (large urban forest) and Site B (small urban forest) within Tokyo. The background map was created in QGIS using the Vegetation Map (scale 1:50,000, Tokyo, updated June 17, 2025, dataset name: moe_bp_ntttx) published by the Biodiversity Center, Nature Conservation Bureau, Ministry of the Environment, Japan.

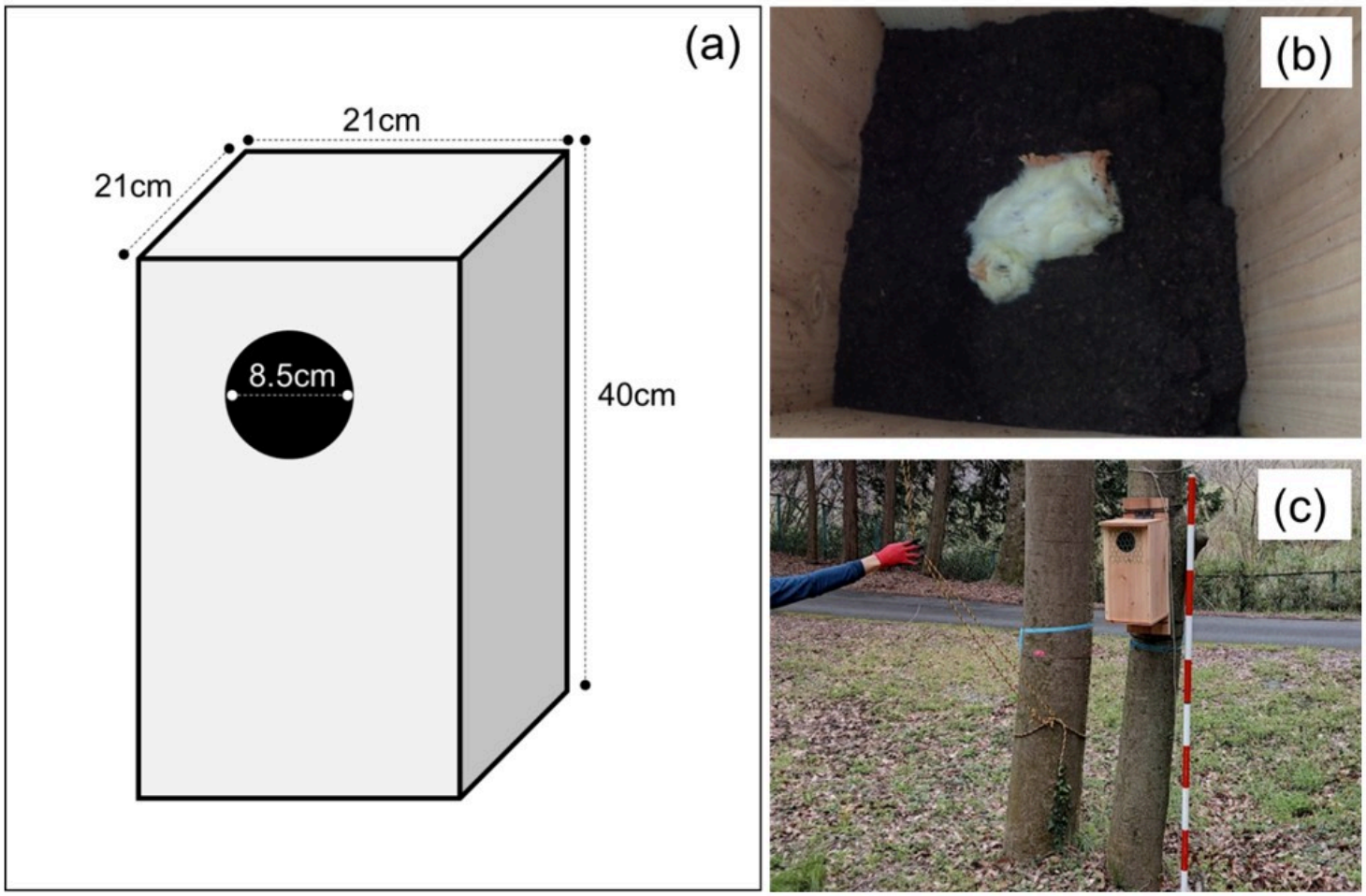


Figure 2

Traps used in this study. (a) Sketch of the trap structure, (b) inside view of the trap at the initial stage, and (c) trap installed on a tree.

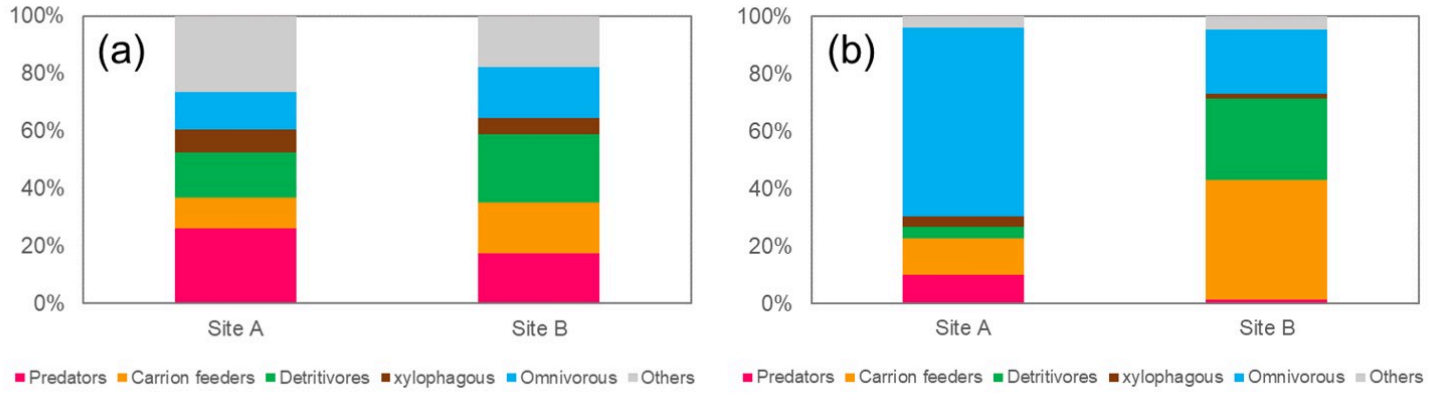


Figure 3

Number of Species and Individuals by Feeding Guild. (a) Species Richness, (b) Abundance.

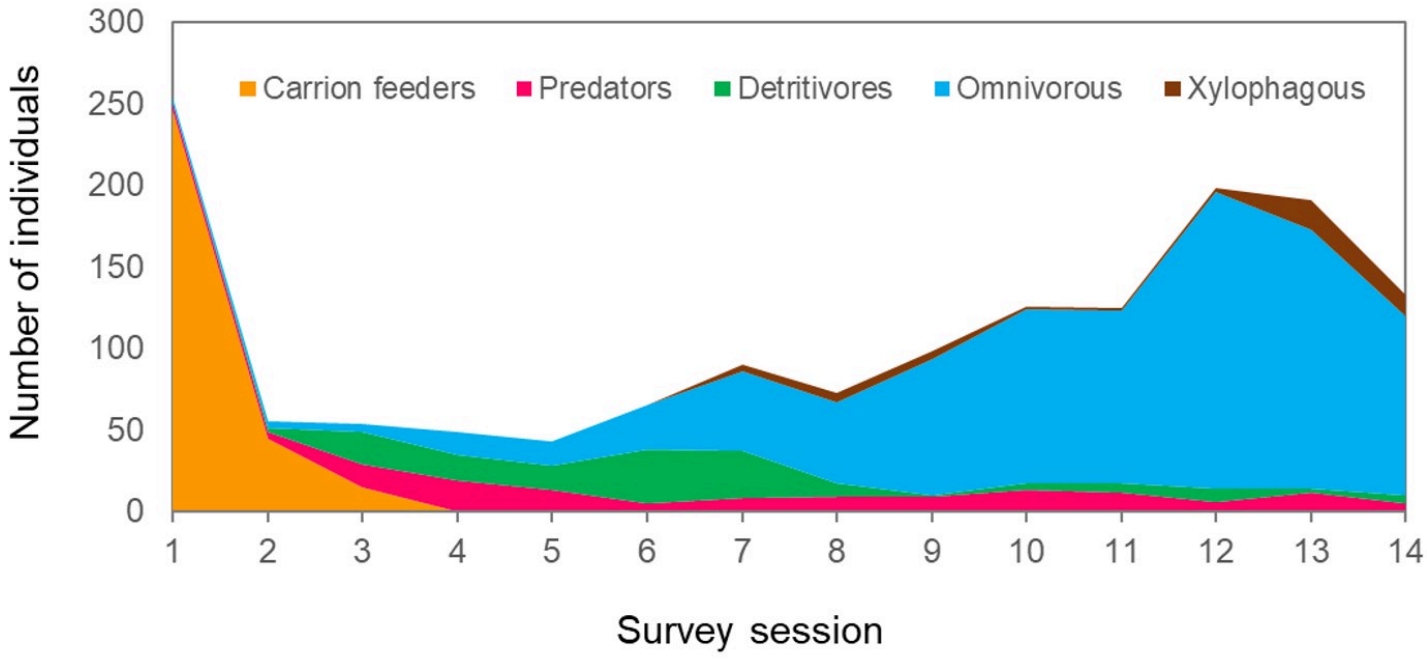


Figure 4

Temporal changes in the abundance of invertebrates by feeding guild during the survey period. Survey sessions were conducted approximately every 14 days.

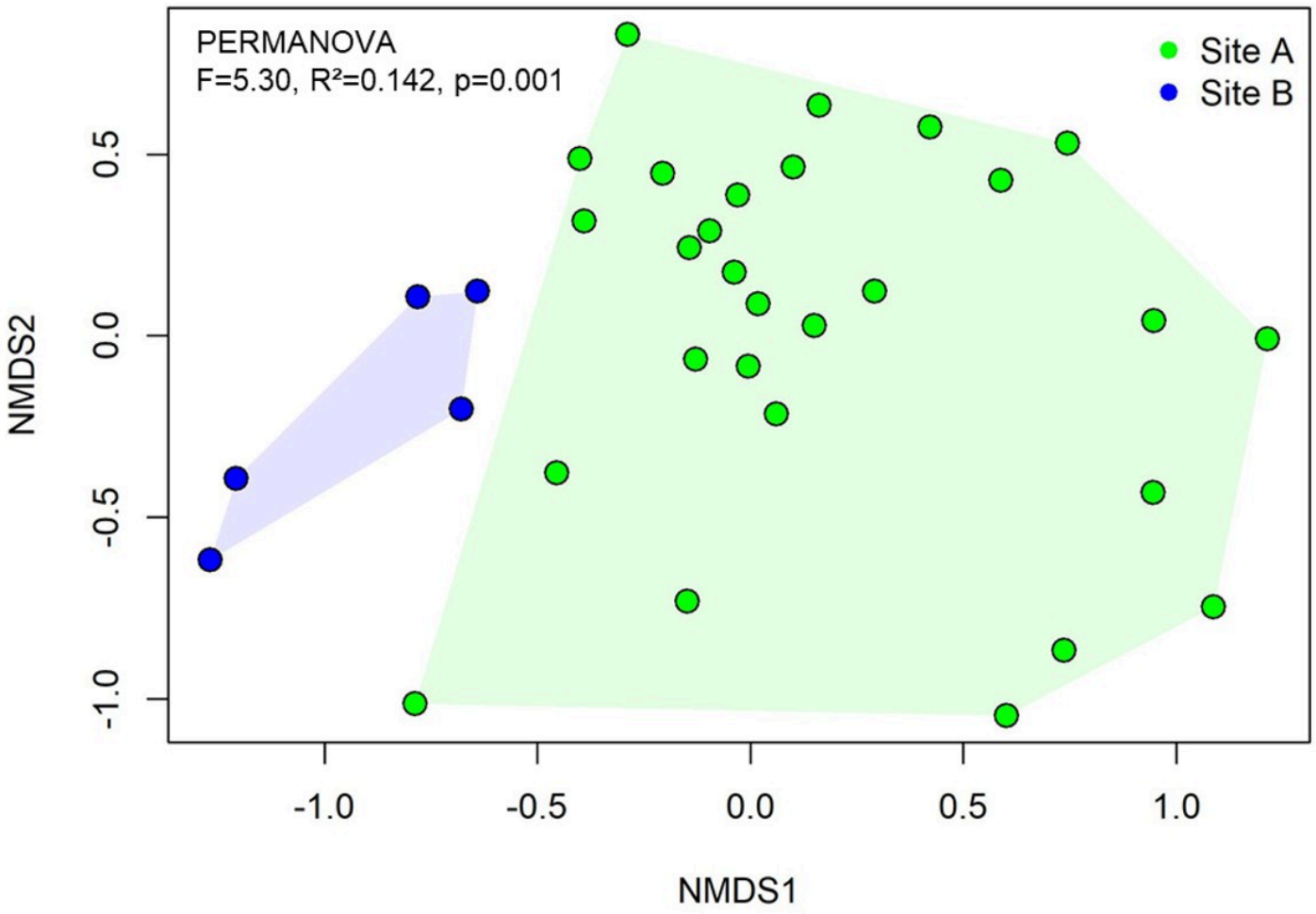


Figure 5

nMDS plots of invertebrate community structure. Stress value = 0.179. Colored convex hulls indicate the outer boundaries of Site A (green) and Site B (blue) samples.

Supplementary Files

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