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Small urban fragments maintain complex food webs of litter-dwelling arthropods in a subtropical city in China

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ABSTRACT

Urbanization-induced environmental changes such as habitat fragmentation impact arthropod assemblages and food web-related ecosystem functions, such as nutrient cycling and energy fluxes. Yet, we lack insight into how arthropod food webs are structured along urban fragmentation gradients. Here, we investigated the community composition and food web structure of litter-dwelling arthropods along fragmentation gradients (green median strip, i.e. green fragments in the middle of roads, urban park, urban forest and natural forest) in Xiamen City, southeast China. We found the density of litter-dwelling arthropods in median strips and urban parks to be two to four times higher than in urban and natural forests, with, as indicated by literature-based stable isotope values, 67%–68% of the individuals comprising primary consumers (trophic level I). Consequently, more complex food webs were found in small urban fragments (i.e., green median strip and urban park) than in the other fragments studied, including higher linkage density and higher energy flux. The biomass of litter on the floor was significantly correlated with the density of arthropods of trophic levels I, III and IV, and each trophic guild positively correlated with each other pointing to the dominance of bottom-up forces. Overall, our results suggest that small urban fragments maintain a high density of arthropods forming complex food webs and thereby may contribute to maintaining high energy fluxes and providing important ecosystem functions in urban areas.

1. Introduction

The global urban area rapidly expanded in the last 40 years and is expected to form the home of 5 billion people by 2030, i.e. about 60% of the world's population (United Nations, 2019; Liu et al., 2020). Rapid urbanization entails a corresponding increase in resource supplies from surrounding ecosystems, resulting in more green lands being merged during urban expansion and more natural habitats being transformed into smaller functional blocks for inhabitants of cities (Zhou et al., 2017; Lin et al., 2019). On the other hand, areas not suited for development, such as hills and wetlands, are increasingly transformed into urban forests, recreation parks or other types of green infrastructures, which is expected to alleviate environmental problems, maintain the ecological functions of urban ecosystems (Jia et al., 2018). Yet, the isolation of greenspaces due to constructions, roads and other paved urban areas is a global threat to soil organisms and results in biotic homogenization (Cane et al., 2006; Fujita et al., 2008; Joimel et al., 2019; Piano et al., 2020b), with stronger habitat fragmentation resulting in stronger effects on soil biodiversity (Malaysiä et al., 2003). These changes likely also affect ecosystem functioning and services of urban greens (Zhu et al., 2004; Liu et al., 2019; Hong et al., 2022) due to the simplified food web structure (Buchholz et al., 2018; Piano et al., 2020a). However, the consequences of fragmentation and isolation of greenspaces on arthropod food webs and the energy they process remain poorly understood.

Soil and litter layers perform a wide range of ecosystem functions

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and services, for example, as refugia for wildlife, by regulating microclimate and nutrient cycling, and by sequestering carbon (Wang and Tong, 2012; Melliger et al., 2018; Malloch et al., 2020). Soils in urban areas often are artificially formed, e.g. by refilling with excavated deep soil and construction residues, and exposed to novel environmental conditions, such as increased temperature and input of pesticides (Wei et al., 2014; Nero and Anning, 2018; Ulpiani, 2021). Further, litter materials forming an important resource for soil food webs often are removed in urban greenspaces (McKinney, 2008; Milano et al., 2017; Kotze et al., 2022). These changes likely result in soil arthropod communities diverging from surrounding natural systems (Malloch et al., 2020). However, not all urban greenspaces are strongly managed, e.g. urban forests may remain close to natural systems.

Arthropods comprise the largest and most diverse phylum on Earth and account for approximately 85% of known animal species (Giribet and Edgecombe, 2012). In terrestrial ecosystems, arthropods colonize virtually any habitat from tropical forests to cold arctic regions (Stevens and Hogg, 2002; Basset et al., 2012). They inhabit a wide array of ecological niches and provide a variety of ecosystem services such as nutrient recycling and carbon sequestration, maintaining soil fertility, pollination and pest control (Isaacs et al., 2009; Wang et al., 2021). Arthropod species can be classified into different trophic groups according to their trophic position in the green and brown food web, e.g. primary consumers/decomposers (phytophages, detritivores, coprophages), secondary consumers/decomposers (omnivores, fungivores) and predators (carnivorous, scavengers) (Scheu and Falca, 2000; Maguire et al., 2016; Lagerlöf et al., 2017). While a number of studies documented that environmental changes shape the composition of arthropod assemblages as well as their trophic position (Lagerlöf et al., 2017; Geldenhuys et al., 2022; Zhou et al., 2022), the role of urbanization processes in shaping the composition of arthropod communities received little attention.

Arthropod food webs are vertically structured with nodes (taxon groups), node positions as well as edge features (predator-prey relationships) and energy fluxes. Stable isotope ratios of nitrogen ($^{15}N/^{14}N$) in consumer tissue allow to identify the trophic niche of consumers (Post, 2002; Oelbermann and Scheu, 2010; Potapov et al., 2019a), and, combined with biomass data, the calculation of energy fluxes through soil food webs (Gauzens et al., 2019; Li et al., 2023).

This study aimed at investigating how the fragmentation of urban greenspaces affects the abundance, body mass and biomass of litter-dwelling arthropods, and their food web structure in Xiamen City, one of the most greening cities in China, as a model area. We hypothesized that (i) soil and litter conditions are harsher in urban fragments compared to natural forest (i.e., lower concentrations of soil nutrients, lower litter quality and quantity), resulting in lower abundance and biomass of litter-dwelling arthropods, with the effects being strongest in the smallest fragments, and (ii) food web structure is more simple in small urban fragments compared to forests, with this being most pronounced in the smallest fragments.

2. Material and methods

2.1. Study area

The study was conducted in Xiamen city, which is located in south-eastern China (117°53' −118°26′ E, 24°23′-24°54′ N, Fig. 1). The region has a subtropical marine climate with an annual average air temperature of 22.8 °C and annual average precipitation of 1078 mm; the rainy season spans from May to August. Textures of soils in Xiamen city are mostly silt loam and loamy sand, which are generally poor in soil organic matter and nutrients (Wang et al., 2017). The city is one of the most developed cities in Fujian province and the urban area has rapidly expanded during the last 40 years. Xiamen city is the most densely populated city in Fujian province with 9153 inhabitants km^{-2}, but also the city with the highest urban green area (45%) compared to the other cities with at least 1 million inhabitants in China; each citizen in Xiamen city shares 14.8 m^2 of public greenspace (China, 2021). Natural forests

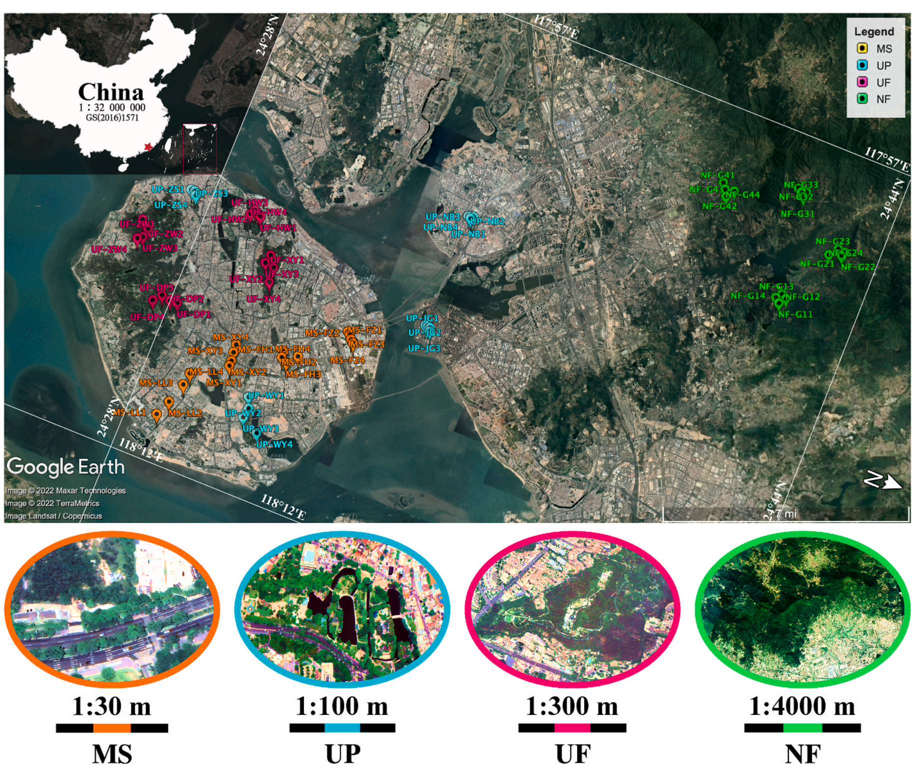

Fig. 1. Map of sampling plots in Xiamen city, China. Median strip (MS, orange), urban park (UP, blue), urban forest (UF, red), and natural forest (NF, green). The map of China was downloaded from http://bzdt.ch.mnr.gov.cn/index.html, the satellitic map of Xiamen city is a screen capture from Google Earth Pro (version 7.3.4.8248).

and urban forest remnants are dominated by *Acacia confusa*, *Schima superba*, *Pinus massoniana* and *Cunninghamia lanceolata* in the canopy layer, and *Ilex pubescens*, *Brucea javanica*, *Dicranopteris dichotoma* and *Rosa bracteate* in the shrub layer. The vegetation in urban green infrastructures mostly consists of exotic ornamental species, such as *Bauhinia variegata*, *Ceiba speciosa*, *Ficus elastica*, and other foliage and flowering plants.

2.2. Experimental design and sampling

We selected four fragment types including three urban fragments, i.e. green median strips (MS), urban parks (UP) and urban forests surrounded by human constructions (UF), and continuous natural forests located outside of the city (NF; representing the least fragmented and most natural habitat) forming a gradient of increasing fragment size (Fig. 1). For each fragment type, we set up four replicate sites spaced >2 km from each other. In each site we set up four plots of 20 m × 20 m at least 100 m apart from each other, except for median strips, resulting in a total of 64 plots. Tree and shrub species within plots were recorded. Within each plot, a subplot of 5 m × 5 m was set up from which litter and soil samples were taken. Litter samples were taken using a frame (20 cm × 20 cm, height 12 cm) which was randomly placed in the subplot. Soil samples were taken at the same site where the litter samples were taken using a steel corer (5 cm diameter and 10 cm depth). Samples were taken on June 22, 2021.

2.3. Trophic level of arthropods

We searched for published data on nitrogen stable isotope (δ^{15}N) values of arthropods using "nitrogen stable isotope*" and "arthropod*" as search terms in ISI Web of Science (https://www.webofscience.com/wos/). The search resulted in 2,904 hits from which we filtered 94 studies that matched the following eligibility criteria: (i) the study reported at least one species included in our arthropod groups (see below) and (ii) the δ^{15}N values given were calibrated to the local litter material (δ^{15}N values). A maximum of ten references were used for each arthropod group. In total, 3065 data were retrieved and compiled (Fig. 2). Based on Minagawa and Wada (1984), and Potapov et al. (2019b), the assumption of an enrichment of 3.4‰ per trophic level, the taxonomic groups in our study were ascribed to four trophic levels: (I) Phycophages/plant-sucking insects (−3.4-0‰) feeding mainly on lichens and algae, (II) primary decomposers/herbivores (0–3.4‰) feeding on plant litter/detritus but also on living plant tissue, (III) secondary decomposers and first-order predators (3.4–6.8‰) predominantly feeding on microorganisms, in particular fungi, but also living as predators and omnivores, and (IV) second-order predators (6.8–10.2‰) feeding on other arthropods or living as scavengers or parasites (Scheu and Falca, 2000; Lafferty et al., 2006; Maraun et al., 2011; Potapov et al., 2019c).

2.4. Extraction and classification of arthropods

Soil and litter samples were transported to the laboratory, and then, the fresh litter samples were weighed and transferred to Berlese funnels for animal extraction. The temperature was gradually increased to ~30 °C using incandescent lamps over an extraction period of 7 days (Wang et al., 2021; Qiao et al., 2022). Animals were collected in plastic vials filled with 70% ethanol (Macfadyen, 1961). During extraction, the funnels were covered with 1 mm mesh to prevent the escape of arthropods. Arthropods were picked under a stereomicroscope and sorted into taxonomic groups at levels allowing assignment to trophic groups. The grouping of the taxa was based on two criteria, the ability to identify them and the availability of δ^{15}N values in published papers. In total, 35 taxonomic groups were distinguished and ascribed to four trophic groups (Tables 1, S1, Fig. 2).

Adult arthropods were measured for body length and maximum body width using the software S-gauge (Nikon SMZ745T, Tokyo, Japan). Length and width were used in a set of group-specific body size - body mass power equations to estimate individual fresh body mass (Jochum et al., 2017; Potapov et al., 2019b). The total biomass of arthropods in each plot was calculated as the sum of individual body masses. Predator-prey relationships between arthropod groups were searched and filtered using GloBI (https://www.globalbioticinteractions.org). A network binary adjacency matrix was built based on predator-prey relationships. In cases where the description of prey was overly vague the link was removed; this was also done for cannibalistic loops.

2.5. Soil and litter analysis

Soil and litter moisture content was determined gravimetrically after drying at 105 °C for 24 h. Soil pH was analyzed using a pH meter (PHS–3C, Shanghai, China) in an aqueous suspension (soil: water of 1:5). The remaining soil samples were air-dried, ground, sieved (0.16 mm mesh) and stored at room temperature until further analysis.

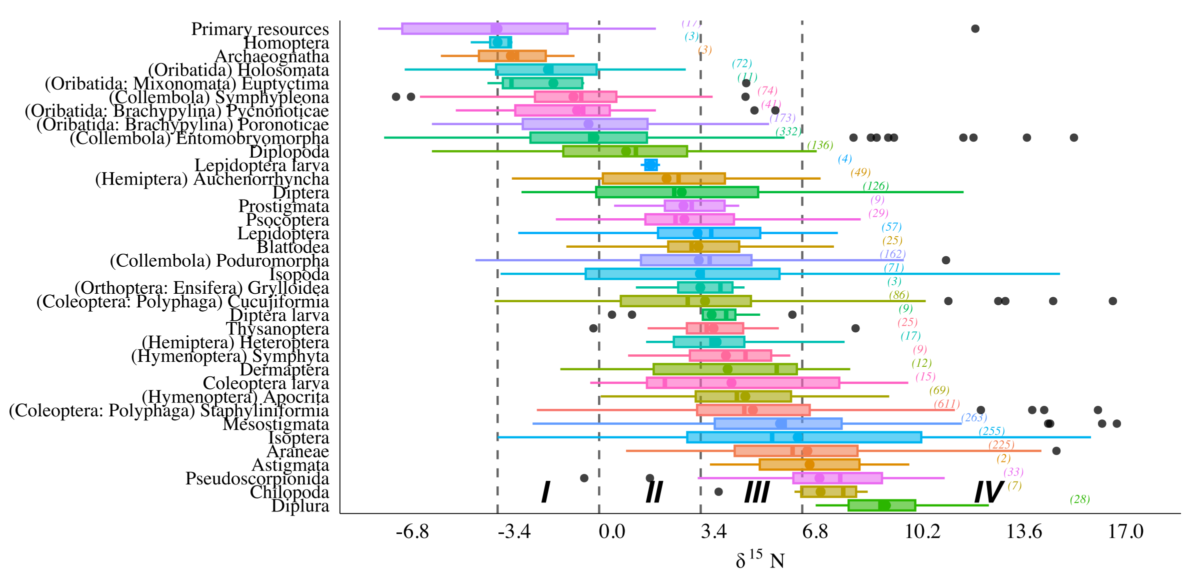

Fig. 2. Published δ^{15}N values of arthropod groups; points in boxplots represent mean values; I, II, III, and IV represent trophic levels, assuming an enrichment in δ^{15}N by 3.4‰ per trophic level.

Litter materials were sorted into three components, woody debris (branches, twigs), non-woody debris (flowers and leaf litter) and decomposed litter (can easily pass through a sieve with 5 mm × 5 mm mesh size but remained in a sieve with 1 mm × 1 mm mesh size). Non-woody debris were identified to genus or species level if possible. The three litter components were weighed and their relative contribution to the total litter was calculated. Prior to chemical analyses, the litter components were pooled and ground into powder using a centrifugal mill (SBYF-2500A, Guangzhou, China). The powder was combusted at 1150 °C using an elemental analyser (Vario MACRO cube CNS, Elementar, Germany) to measure soil organic carbon (SOC, assuming that carbonate carbon can be neglected) and total nitrogen (TN) content. The total content of phosphorus (TP) was measured using an inductively coupled plasma spectrometer (ICPS-7500, Kyoto, Japan) after digestion with H_2SO_4–HClO (Qiao, et al., 2022). Lignin and cellulose contents were determined using acid detergent fiber analysis (Vitale et al., 2019).

2.6. Statistical analysis

The statistical analysis of community structure followed the approach used by Potapov et al. (2019b) and Yin et al. (2022). All of the analyses were performed in R version 4.2.1 (R Core Team, 2022), and results were visualized using the *ggplot2* package (v3.3.6).

Physicochemical properties of soil and litter: Mean differences in soil physicochemical properties (soil moisture, soil pH, soil TC, TN and TP content, and C-to-N ratio) and litter chemical characteristics (TC, TN, TP, lignin, cellulose content, and lignin-to-N ratio) between fragment types (median strip, urban park, urban forest and natural forest) were analyzed by a one-way ANOVA using the general linear model procedure. Litter physical and biological variables (litter moisture content, litter species richness, and biomass of woody, non-woody, decomposed litter and total biomass of plant residues) were analyzed via mixed-effects linear models ('*lmer*' function of the '*lme4*' package) with 'Site code' as a random factor. The data were log10 transformed to improve normality and homoscedasticity. Differences between means were inspected using post hoc Tukey's HSD.

Arthropod communities: To characterize the trophic structure of arthropod communities and their habitat conditions (composition of the litter layer), we used the *vegan* package (v2.6–2) to calculate taxa density (number of taxa per square meter). Mean differences in density of all arthropods between fragment types were tested via mixed-effects linear model with 'Site code' as a random factor. For each taxonomic group, the mean differences in arthropod density, biomass and body mass were analyzed using general liner models. We then employed Principal Coordinate Analysis (PCoA) and non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity to analyze the species composition of litter and community structure of arthropods, respectively (*vegan* package, v 2.6–2). Significant differences in connectivity and multivariate homogeneity of group dispersion of arthropod structure between fragment types were determined using permutational multivariate analysis of variance (PERMANOVA, *adonis2* function with 999 permutations) and *betadisper* models (*betadisper* function with 999 permutations) (Anderson, 2005).

Food web structure: To structure the food web of litter-dwelling arthropods, the *fluxing* function in the *fluxweb* package was used (v0.2.0; Gauzens et al., 2017). Predator-prey relationships, the biomass of arthropod groups, metabolic losses and feeding efficiencies were included in the calculations according to Gauzens et al. (2019). *A priori* conceptual food webs were constructed based on published $\delta^{15}N$ values and predator-prey relationships (Fig. 3). First, arthropod groups were ordered according to published mean $\delta^{15}N$ values. The vertical position of arthropod taxa in the food web (V_υ) was calculated as $V_\upsilon = \delta^{15}N * l + \kappa$ where l is the classified trophic level (range 1–4), κ is a constant that generally equals to the enrichment of ^{15}N per trophic level (3.4‰). The horizontal position of arthropod taxa in the food web (H_υ) was calculated by square-rooting the difference of the $\delta^{15}N$ values of an arthropod group between the arthropod group ranked ahead according to the mean

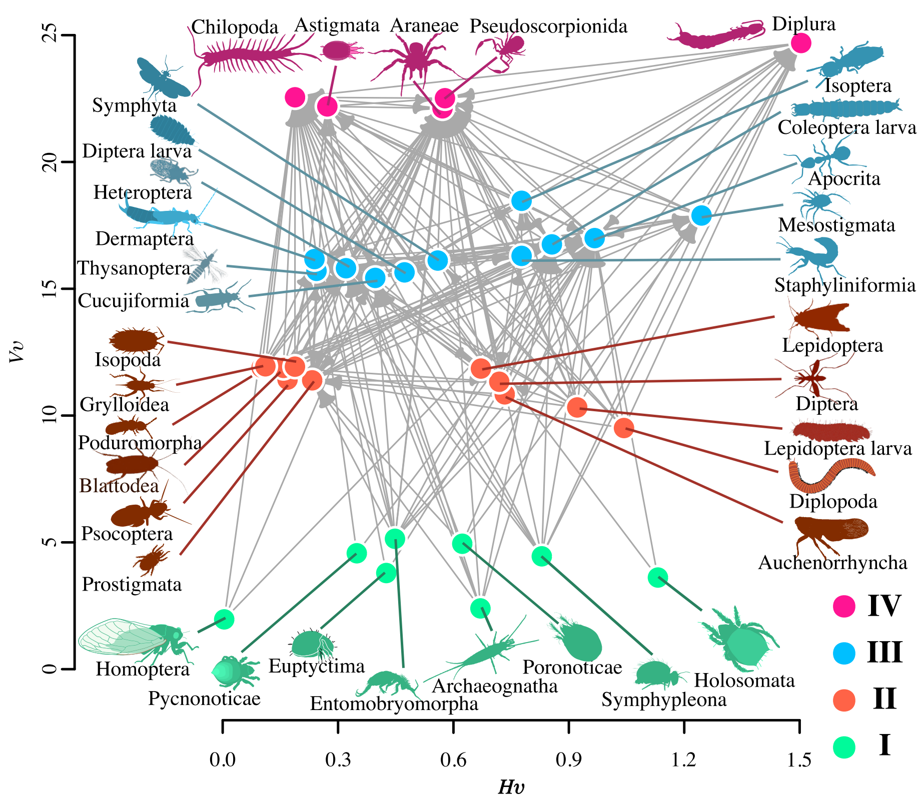

Fig. 3. *A priori* conceptual representation of the food web structure used based on $\delta^{15}N$ values retrieved from literature (see Fig. 2). Green, orange, blue and deep-pink circles and silhouettes indicate trophic levels I, II, III and IV, respectively. Silhouettes were downloaded from http://phylopic.org.

δ^{15}N values in Fig. 2: $H_v = \sqrt{(\delta^{15}N_i - \delta^{15}N_{i-1})}$, where $\delta^{15}N_i$ and $\delta^{15}N_{i\text{-}1}$ are the mean δ^{15}N values of the *i*th and the (i-1)th arthropod taxon, *i* is the ranking of arthropod groups in Fig. 2.

Food web traits: To assess differences in food web structure among fragment types, we structured network analyses with taxonomic groups as nodes (*N*) and predator-prey relationships as edges (*E*). Food web nodes were calculated based on mean body mass and biomass of individual fragment types. The food web structure was assessed based on the number of edges ($E_p = C_N^2$), linkage density ($d = \frac{E}{E_p}$), directed connectance ($C = \frac{E}{N^2}$) and the sum of weight (Martinez, 1991; Atmar and Patterson, 1993; Tamaris-Turizo et al., 2018). The mean path length and the longest food chain in fragments was identified using the '*pathways*' and '*longest.chain*' function in the *loop* package, respectively (version 1.1, Chen, 2013). The complexity of the food web was evaluated by a combination of indicators, i.e. linkage density, mean path length and sum of weight for each food web.

Correlations: To identify potential drivers of the abundance of each trophic group across fragment types, we inspected correlations between soil and litter physicochemical properties, and the abundance of arthropod trophic groups (I - IV) using the Mantel test (*mantel_test* function in the *ggcor* package with 999 permutations, v0.9.7). Further, Pearson's regression test was performed to evaluate correlations (considered significant if $P < 0.05$) between trophic levels I, II, III and IV.

3. Results

3.1. Soil and litter physicochemical properties

Soil pH, moisture content and C-to-N ratio varied significantly among fragment types ($P < 0.01$); they were generally higher in median strips than in urban and natural forests (Table S2, Fig. S1A). Among the measured litter biological and physical traits, litter species richness, biomass of woody debris and litter moisture content varied significantly with fragment type ($P < 0.01$). Litter species richness and litter moisture content were highest in natural forests (Table S2, Fig. S1B), while the amount of non-woody debris on the soil surface was higher in urban forests than in green median strips (Table S2). Among the measured litter chemical traits, TP and cellulose content in the green median strip was significantly higher, but TC, lignin and lignin-to-N ratio were significantly lower than in the other fragment types ($P < 0.05$).

3.2. Arthropod communities

A total of 13,842 arthropod individuals, representing 35 taxonomic groups (32 genera and 3 larval groups), were recorded. Entomobryomorpha, Poronoticae, Holosomata and Mesostigmata were the most abundant groups accounting for 34%, 15%, 12%, and 10% of the total individuals, respectively. The average densities of arthropods in the litter layer were 2025 ± 1714 ind. m^{-2} in the urban forest, 4162 ± 2456 ind. m^{-2} in the natural forest, 5456 ± 5118 ind. m^{-2} in the median strip, and 9345 ± 8867 ind. m^{-2} in the urban park (Fig. 4A). Arthropod density varied significantly with fragment type ($F_{3,12} = 4.46$, $P = 0.025$); it was the highest in urban parks and lowest in urban forests with that in median strips and natural forests being intermediate (Fig. 4A). Further, arthropod community composition in urban forest differed from that in the other three fragment types (Fig. 4D, PERMANOVA: $F_{3,59} = 4.35$, $P <$ 0.001). Neither arthropod biomass nor body mass varied significantly with fragment type (Fig. 4B C).

Compared to natural forests, the density of 63% and 71% of the taxonomic groups was lower in median strips and urban forests, respectively (Fig. S2 A-C). By contrast, the density of 68% of taxonomic groups was higher in urban parks than in natural forests. Specifically, the density of Euptyctima, Poduromorpha, Symphypleona and Thysanoptera were significantly lower in green median strips and urban forests, whereas the density of Entomobryomorpha and the body mass of Isopoda was higher compared to natural forests (Fig. S2 A, B, H, I). Moreover, the density of Araneae, Coleoptera larva, Cucujiformia, Dermaptera, Isopoda and Poronoticae was significantly higher in urban parks than in natural forests. Further, Pseudoscorpionida were absent in urban fragments, whereas Dermaptera were only found in urban fragments.

3.3. Trophic groups of arthropods

The average density of arthropods of trophic levels I, II, III and IV were 3653 ± 562, 652 ± 106, 964 ± 165 and 244 ± 34 ind. m^{-2} across fragment types, respectively. By contrast, arthropod biomass was highest in trophic level II (232 ± 103 mg dry mass m^{-2}) and arthropod body mass was highest in trophic level IV (256 ± 106 μg dry mass ind.$^{-1}$). The density, biomass and body mass of arthropods differed significantly between trophic levels (Table S3; $P < 0.001$). Trophic level I arthropods contributed most to total arthropod density (Fig. 5A), but their density varied with fragment type and was lowest in urban forests ($F_{3,60} = 4.55$, $P = 0.006$). By contrast, the body mass of trophic level I arthropods was generally lowest across fragment types (Fig. 5C). The biomass of trophic level II arthropods also varied significantly with fragment type ($F_{3,60} =$

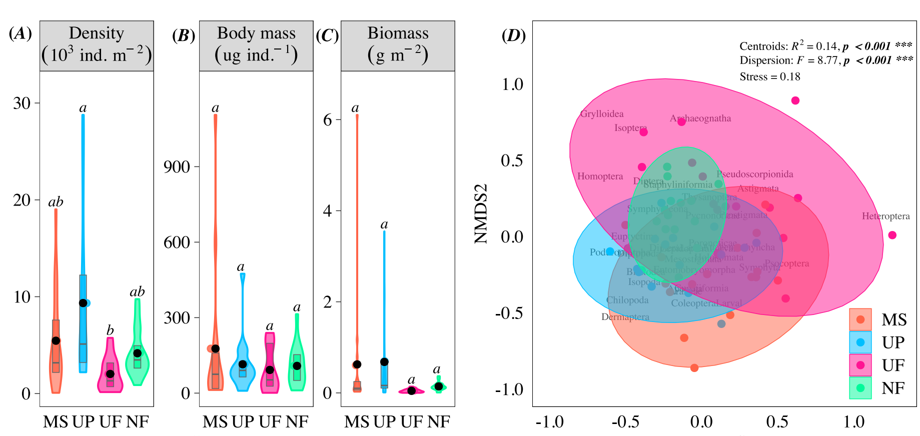

Fig. 4. Variations in arthropod density (A), body mass (B), biomass (C) and community composition (D) with urban fragment type (green median strip, urban park, urban forest, natural forest). Lowercase letters and represent significant differences between fragment types as indicated by Tukey's HSD tests at $P < 0.05$. Variations in arthropod community composition are based on Bray-Curtis distance. Ellipses represent 95% confidence ranges.

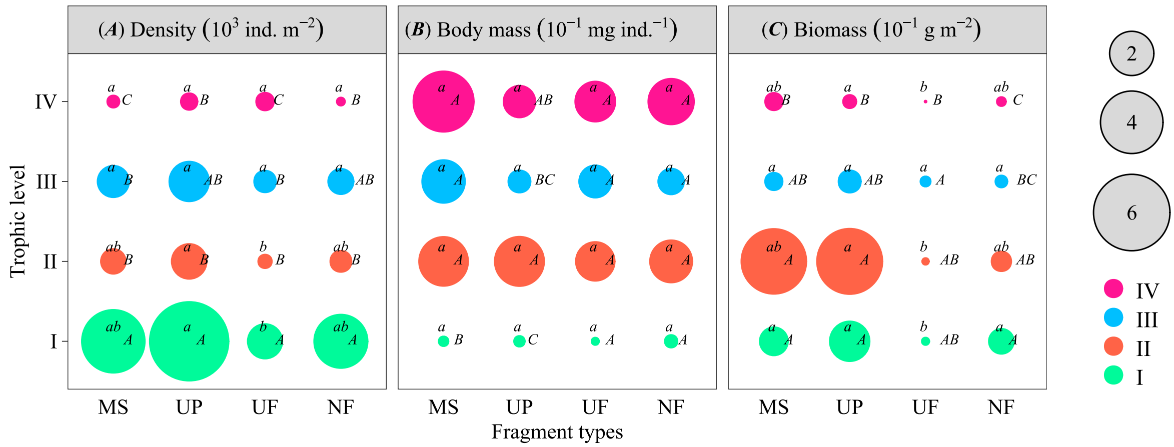

Fig. 5. Density (*A*), body mass (*B*) and biomass (*C*) of arthropods of four trophic levels in median strip (MS), urban park (UP), urban forest (UF) and natural forest (NF). Trophic levels were classified based on published $\delta^{15}N$ values (see Fig. 2). Different lowercase letters denote significant differences among fragment types within the same trophic level; different capital letters denote significant differences among trophic levels in the same fragment type (Tukey's HSD pairwise comparisons at $P < 0.05$).

4.53, $P = 0.006$); it was particularly high in median strips and urban parks (Fig. 5B).

Arthropods of medium size, such as Holosomata, Poronoticae and Entomobryomorpha, ranged between 15% (in urban parks) and 57% (in urban parks and median strips) of the total number of trophic levels I arthropods. While the biomass mostly comprised Entomobryomorpha and ranged between 77% (in urban forests) and 99% (in median strips and urban parks) of the total biomass of trophic level I arthropods. Prostigmata, Lepidoptera larva and Poduromorpha made up most of trophic level II arthropods in each of the four fragment types. Diplopoda

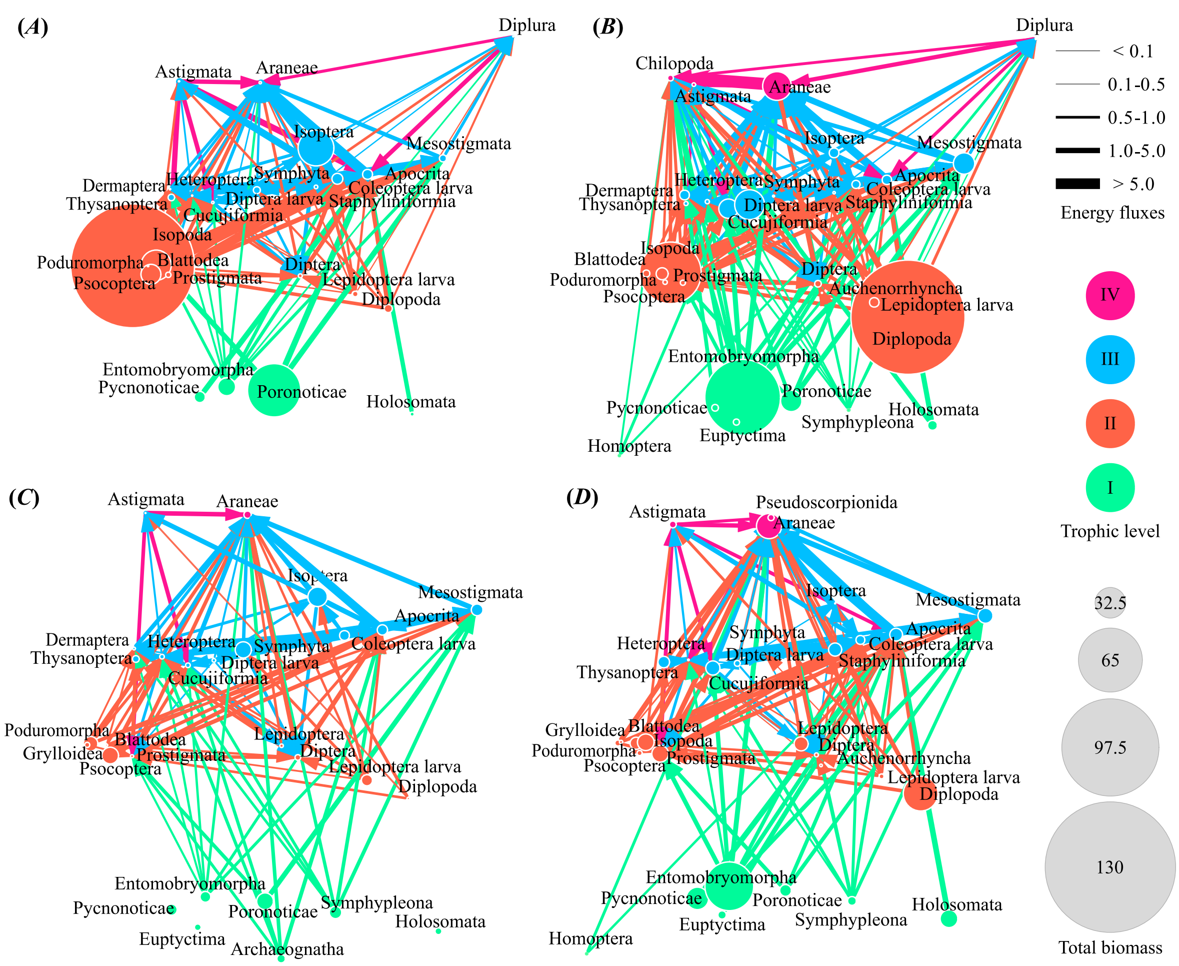

Fig. 6. Food web structure in median strip (A), urban park (B), urban forest (C) and natural forest (D). Food webs were constructed based on predator-prey relationships. The position of nodes was based on published $\delta^{15}N$ data (for more details see Methods and Fig. 2). Width of edges scaled with the $\log_{10}$ of energy fluxes (calculated using biomass, metabolic rates and feeding efficiencies; see Methods). The size of nodes corresponds to the total biomass of arthropod groups.

and Isopoda comprised 76% and 95% of the total biomass of trophic level II in urban parks and median strips, respectively. Mesostigmata comprised 51% of total trophic level III arthropod density, while Cucujiformia comprised most of trophic level III biomass in each of the four fragment types. Trophic level IV arthropods had the highest body mass in each of the fragment types except urban park (Table S3; $F_{3,902} = 11.18$, $P < 0.001$), but both density and biomass were considerably lower than that of arthropods of trophic level I and II. Across fragment types, Araneae on average contributed 48% of total density and 98% of the total biomass of trophic level IV arthropods.

3.4. *Food web structure of litter-dwelling arthropods*

There were 126, 169, 111 and 143 edges for the arthropod food web in median strips, urban parks, urban forests and natural forests, respectively (Table 2, Fig. 6). The food web structure in urban forests was the simplest, whereas that in urban parks was the most complex among the four fragment types (Fig. 6B and C). Total energy flux in median strips, urban parks, urban forests and natural forests was 266.4, 591.9, 185.2 and 305.8 kJ ha^{-1} year^{-1}, respectively (Fig. S3). Urban forests and natural forests had similar food web structure as indicated by similar edge density, directed connectance and sum of weight (Table 1). The food webs in median strips and urban parks had a similar structure and the longest food chains, but lower mean path length compared to natural forests (Table 1, S4). Diplura had the highest trophic position in green median strips and urban parks, while Araneae formed the apex predator in median strips, urban forests and natural forests, whereas in urban parks Chilopoda formed the apex predator receiving 85% of the

Table 1
Taxonomic composition of litter-dwelling arthropods in this study.

Subphylum	Class	Order	Suborder	Infraorder[1]/Superfamily[2]	Trophic level	Illustration
Chelicerata	Arachnida	Pseudoscorpionida	–	–	IV	
Chelicerata	Arachnida	Astigmata	–	–	IV	
Chelicerata	Arachnida	Oribatida	Brachypylina	Poronoticae[1]	I	
Chelicerata	Arachnida	Oribatida	Brachypylina	Pycnonoticae[1]	I	
Chelicerata	Arachnida	Oribatida	Holosomata	–	I	
Chelicerata	Arachnida	Oribatida	Mixonomata	Euptyctima[1]	I	
Chelicerata	Arachnida	Prostigmata	–	–	II	
Chelicerata	Arachnida	Mesostigmata	–	–	III	
Chelicerata	Arachnida	Araneae	–	–	IV	
Myriapoda	Chilopoda	–	–	–	IV	
Myriapoda	Diplopoda	–	–	–	II	
Crustacea	Malacostraca	Isopoda	–	–	II	
Hexapoda	Entognatha	Collembola	Entomobryomorpha	–	I	
Hexapoda	Entognatha	Collembola	Poduromorpha	–	II	
Hexapoda	Entognatha	Collembola	Symphypleona	–	I	
Hexapoda	Entognatha	Diplura	–	–	IV	
Hexapoda	Insecta	Archaeognatha	–	–	I	
Hexapoda	Insecta	Dermaptera	–	–	III	
Hexapoda	Insecta	Orthoptera	Ensifera	Grylloidea[2]	II	
Hexapoda	Insecta	Blattodea	–	–	II	
Hexapoda	Insecta	Isoptera	–	–	III	
Hexapoda	Insecta	Thysanoptera	–	–	III	
Hexapoda	Insecta	Hemiptera	Heteroptera	–	III	
Hexapoda	Insecta	Hemiptera	Homoptera	–	I	
Hexapoda	Insecta	Hemiptera	Auchenorrhyncha	–	II	
Hexapoda	Insecta	Psocoptera	–	–	II	
Hexapoda	Insecta	Hymenoptera	Symphyta	–	III	
Hexapoda	Insecta	Hymenoptera	Apocrita	–	III	
Hexapoda	Insecta	Coleoptera	Polyphaga	Staphyliniformia[1]	III	
Hexapoda	Insecta	Coleoptera	Polyphaga	Cucujiformia[1]	III	
Hexapoda	Insecta	Coleoptera larva	–	–	III	
Hexapoda	Insecta	Lepidoptera	–	–	II	
Hexapoda	Insecta	Lepidoptera larva	–	–	II	
Hexapoda	Insecta	Diptera	–	–	II	
Hexapoda	Insecta	Diptera larva	–	–	III	

Note: Taxa were ordered according to phylogeny (Regier et al., 2010; Misof et al., 2014). Trophic level I: Phycophages (green, δ^{15}N < −3.4‰); trophic level II: Primary decomposers and herbivores (dark red, −3.4‰ < δ^{15}N < 0.0‰); trophic level III: Secondary decomposers and first-order predators (dark blue, 0.0‰ < δ^{15}N < 3.4‰); trophic level IV: Second-order predators (rose red, δ^{15}N > 3.4‰), seeing Fig. 2 for more details.

Table 2
Indicators of arthropod food web structure (number of nodes and edges, linkage density, connectance, mean path length, longest food chain and sum of weight) in the four types of urban fragments studied.

Indicator	MS	UP	UF	NF
Number of nodes	26	31	28	31
Number of edges	126	169	111	143
Linkage density	0.39	0.36	0.29	0.31
Directed connectance	0.19	0.18	0.14	0.15
Mean path length	5.83	6.44	5.03	5.52
Number of nodes in longest food chain	16	17	15	16
Sum of weight	17.57	33.85	9.24	13.48

energy from Araneae (Fig. 6B).

3.5. Correlation between trophic groups and properties of soil and litter

Of the studied soil and litter properties only litter moisture and TP content and biomass of decomposed litter significantly correlated with the density of arthropods of at least one trophic level (Fig. 7A). The biomass of decomposed litter correlated with each the density of arthropods of trophic level I ($r = 0.24$, $P = 0.02$), III ($r = 0.40$, $P < 0.001$) and IV ($r = 0.19$, $P = 0.05$). Further, the density of arthropods of trophic level III arthropods significantly correlated with litter TP ($r = 0.26$, $P = 0.04$), and trophic level IV was significantly correlated with litter moisture content ($r = 0.21$, $P = 0.05$).

In addition to environmental factors, Pearson's correlation test indicated that arthropods in urban fragments were significantly influenced by trophic interactions, and the correlation analysis between the density of each trophic level consistently revealed positive correlations (Fig. 7B). Additionally, the trophic level I was significantly correlated with the trophic level II ($r = 0.67$, $P < 0.001$), but gradually weakening among higher levels (r values between trophic level I and III, and I and IV were 0.53 and 0.35, respectively).

4. Discussion

We investigated how urban greenspace fragmentation drives the community composition and food web structure of litter-dwelling arthropods in a subtropical city. Our results showed that arthropod density in urban parks was five times higher than in urban forests. Further, the density, biomass and body mass of most trophic groups of arthropods were higher in more fragmented habitats (median strips and urban parks) than in urban forests. In particular, the density and biomass of trophic level I and II arthropods were considerably higher in urban parks than in urban forests. Also, food web structure (as indicated by indexes, such as, linkage density, connectance, mean path length and sum of weight) was more complex in heavily fragmented habitats (median strip and urban park) than in less fragmented habitats (natural and urban forest). On the contrary, however, the taxonomic composition of arthropods was consistently less complex in fragmented habitats than in natural forest. Among the studied environmental factors, the biomass of litter on the floor was significantly correlated with the density of trophic levels I, III and IV arthropods. In addition, each trophic guild consistently positively correlated with each other, with the correlation between trophic levels I, III and IV being weaker compared to the correlation between trophic levels I and II.

4.1. Density and biomass of litter-dwelling arthropods in fragments

In contrast to our first hypothesis, edaphic conditions (higher soil moisture, pH, TC and C-to-N ratio) and litter quality (lower lignin-to-N ratio) in small urban fragments (median strips) were favorable for arthropods and resulted in higher density and biomass of arthropods than in urban forests. Edaphic conditions, such as soil moisture content and pH, were important environmental factors driving arthropod communities. Previous research showed that the abundance of arthropods is generally higher in humid and alkaline soils, as soil moisture reduces the desiccation risk of arthropods and many soil arthropods do not tolerate low pH conditions (Stenchly et al., 2017; Manu et al., 2021). Due to greenspace management practices, soils in green median strips and urban parks received more irrigation water than urban forests resulting

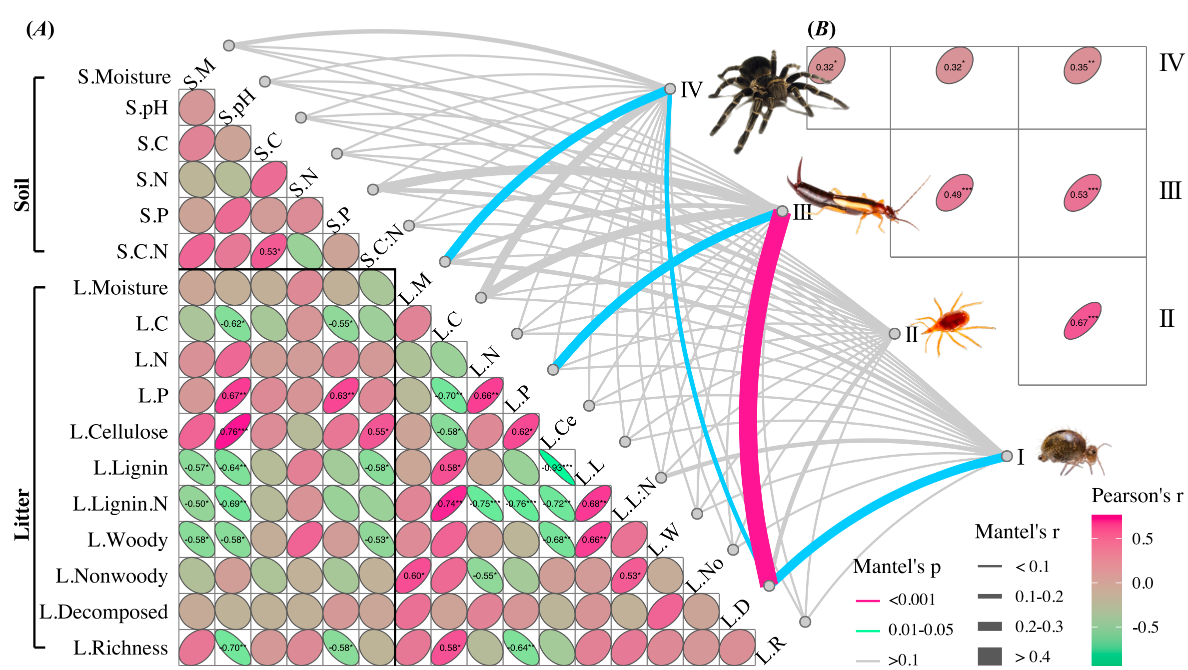

Fig. 7. Correlation matrix between trophic levels and physicochemical properties (A) of soil (S.) and litter (L.) and correlations between density of trophic levels (B). Non-significant correlations were omitted from the graph. Values and gradient ramp (from green to pink) on ellipses indicate negative or positive correlation between soil and litter parameters or between trophic groups. Blue and deep-pink links between soil and litter parameters and trophic groups indicate significant correlations at $0.01 < P < 0.05$ and $P < 0.001$, respectively. Asterisks indicate significance levels: *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

in a humid soil environment for arthropods. Further, soil pH was significantly higher in median strips and urban parks than in forests also contributing to favorable soil conditions for soil invertebrates. These favorable edaphic conditions contributed to small urban green spaces hosting complex soil food webs.

Plant residues play an essential role in soil processes, vegetation regeneration and maintaining soil ecological functions by providing favorable microhabitat conditions and nutrient resources (Hättenschwiler et al., 2005; Berg et al., 2010; Trentini et al., 2018). Notably, litter material was also present in green median strips and in particular areas of limited access in urban parks. Further, in little-managed areas in urban parks, there was a similar amount of woody and non-woody debris on the floor compared to natural forests providing food resources for primary consumers. On the other hand, according to the intermediate disturbance hypothesis, moderate management of plants in urban green infrastructures might unintentionally assist arthropods to overcome hostile environmental conditions. For example, irrigating plants likely alleviates drought stress, applying fertilizers stimulates the growth of plants thereby improving microclimatic conditions for arthropods, and frequent cutting of plants in median strips and urban parks may provide high-quality litter for detritivore soil arthropods (Parsons et al., 2004). Overall, this suggests that the litter layer in median strips and urban parks provides sufficient habitat and high-quality food material resulting in high density and biomass of soil arthropods (Loranger-Merciris et al., 2008; Dray et al., 2014; Sauvadet et al., 2017; Reis et al., 2018).

Among the soil and litter physicochemical properties studied, the biomass of litter was significantly correlated with the density of trophic level I, III and IV arthropods. The highly porous structure and humid environment (Wang et al., 2016), and carbon resources in litter provide favorable habitat conditions for fungi and detritivore arthropods (Neris et al., 2013; Joseph et al., 2015; de Smedt et al., 2016; Wang et al., 2021). In our study, the amount of litter in particular favored the density and biomass of decomposer taxa such as Entomobryomorpha, Poronoticae, Isopoda and Diplopoda. However, also taxa of higher trophic groups benefitted from the increased amount of litter such as Diptera larva, Astigmata and Araneae. In addition to environmental factors, biological interactions may shape arthropod food webs in urban fragments as supported by the consistent positive correlation of the density of trophic groups. The positive correlation between arthropods of lower and higher trophic levels is in line with the results of Yin et al. (2022). Overall, it points to the dominance of bottom-up control with the density of arthropods of trophic level I propagating up to top predators (Walton et al., 2006).

4.2. Community structure of litter-dwelling arthropods in fragments

Soil organisms in urban ecosystems are declining because of environmental changes and habitat fragmentation during urbanization processes (Piano et al., 2020a, 2020b; Szabó et al., 2023). Contrary to these studies and our first hypothesis, the density and biomass of soil arthropods were higher in urban parks compared to urban forests. Most of the parks in urban areas had been established in or near coastal areas next to lakes or sea bays, characterized by a high density of arthropods because of favorable habitat conditions (Kowarik, 2011). Therefore, high arthropod density in urban parks likely contribute to the maintenance of soil ecological functions such as biogeochemical cycling (Kostrakiewicz-Gierałt et al., 2022). In particular, the high density of Entomobryomorpha, the most dominant taxon, in median strips and urban parks might contribute to litter decomposition and nutrient transfer to higher trophic groups.

Green median strips are established as green barriers to increase the green cover in urban areas and reduce headlight disturbances of cars on the other side of the road. Here, we found that these isolated green fragments in the middle of roads are a valuable component of urban habitats, the density and biomass of arthropods in median strips were even higher than in natural forests although only slightly. However, the low number of taxonomic groups of arthropods in median strips suggests that their contribution to arthropod conservation in cities is limited. Median strips are isolated by road lanes and traffic, hampering colonization by wingless arthropods such as Diplopoda (Noordijk et al., 2006; Martin et al., 2019). Despite winged arthropods may easily reach median strips, the airflow created by cars may hamper colonization and this may explain why the composition of winged arthropods (including their larva) in median strips was much lower than in urban parks. Further, adverse microclimatic conditions in median strips may detrimentally affect arthropods and contribute to the observed low number of taxonomic groups (Richards and Edwards, 2017; Luo et al., 2022). Moreover, the widespread planting of ornamental plants, such as *Excoecaria cochinchinensis*, *Ficus microcarpa* and *Schefflera arboricola*, producing litter with low food quality for soil arthropods also may contribute to a low number of taxonomic groups of soil arthropods in median strips (Wardle et al., 2006; Donoso et al., 2010; Sánchez-Galindo et al., 2021).

Compared to the small fragments in urban areas, urban forests (isolated by constructions) are generally less fragmented and play a pivotal role in maintaining arthropod populations (Chace and Walsh, 2006; Ferreira et al., 2018; Koricho et al., 2022). As stressed earlier (Kantsa et al., 2013; Xie et al., 2016; Liu et al., 2019), soil conditions, coupled with environmental changes in urban areas, are unfavorable for arthropod communities in urban forests, especially for the dominant animals (such as collembolans and mites) and invasive species (such as *Solenopsis invicta*) (Dale and Frank, 2014; Long et al., 2019), and this likely results in altered food web structure and function. For example, high density of *Entomobrya* sp. (Collembola: Entomobryomorpha) in median strips and urban parks may result in accelerated litter decomposition, while high density of predatory mites such as Zerconidae (Acari: Mesostigmata) in urban forests is likely to be associated by high energy flux to predators, potentially reducing litter decomposition by reducing the density of primary decomposer prey (Yan et al., 2021). On the other hand, large urban animals such as birds rely on larger urban fragments such as urban forests (Gunnarsson et al., 2009), where they form apex predators also feeding on arthropod predators such as Araneae and Chilopoda (Braschler et al., 2021; Szabó et al., 2023).

Presumably due to low pH and low litter quality, the abundance of arthropods in natural forests was lower than in urban parks. However, natural forests were colonized by a wider range of taxonomic groups including more decomposers such as Isoptera (Pothula et al., 2019; Marchin et al., 2022). In addition to decomposers, Astigmata, comprising parasitic or commensal species such as feather mites (Bodawatta et al., 2022), were significantly more abundant in urban forests than in urban parks and median strips. Presumably, this reflects higher activity (foraging and nesting) of host animals, such as urban birds and bats (Dietz et al., 2020).

4.3. Food web structure of litter-dwelling arthropods in fragments

We reconstructed food webs of litter-dwelling arthropods of urban fragments by using published $\delta^{15}N$ values. Unexpectedly and in contrast to our second hypothesis, food webs in urban and natural forests were simpler than in urban parks and median strips, with a higher number of edges, edge density, connectance and total energy fluxes, and lower mean path length. Further, these complex food webs were characterized by being bottom-heavy, i.e., high biomass in trophic levels I and II, but low biomass in trophic level IV. Nevertheless, the total energy flux in natural forests was slightly higher than in median strips, but 50% less than in urban parks. Compared to rainforest (1160 kJ ha^{-1} yr^{-1}) investigated by Pollierer et al. (2023), the total energy flux in natural forest (306 kJ ha^{-1} yr^{-1}) was more than three times lower. However, despite less faunal groups were included in our study, the energy flux in the urban park (592 kJ ha^{-1} yr^{-1}) was higher than in rubber and oil palm plantations (293 and 342 kJ ha^{-1} yr^{-1}, respectively) investigated by Pollierer et al. (2023).

The complex food webs in urban parks might, on one hand, relate to the taxa composition of predators, especially macroarthropod predators such as Chilopoda reaching high abundance, being large and having a wide prey spectrum (Bonato et al., 2021; Li et al., 2023). Contrasting other high trophic level predators such as Araneae, Chilopoda were intensively linked to trophic level I arthropods resulting in short mean path length and implying fast energy flux. Although arthropods of trophic levels I and II dominated in median strips and urban parks, apex predators in these habitats received most of their energy from trophic levels III and IV. This likely reflects the feeding preferences of these predators related to predator-prey body size ratios (Potapov, 2022). The preferential consumption of mesopredators by apex predators in median strips and urban parks likely contributed to the high population density of trophic level I and II arthropods in these habitats.

5. Conclusions

Our findings provide new insight into the maintenance of ecosystem functions of litter-dwelling arthropods in urban greens. Decomposing litter on the soil surface of urban greens, rather than litter quality and species richness, shapes litter-dwelling arthropod density and food web structure, particularly favoring arthropods of trophic levels I, III and IV. The density, body mass and biomass of arthropods in small urban fragments were unexpectedly high and exceeded that in urban forests. Arthropods of trophic levels I and II dominated in density and biomass in median strips and urban parks, whereas in urban and natural forests arthropods of trophic levels III and IV were (relatively) more important. The smaller fragments (median strips and parks) had a more complex food web structure with higher linkage density and length of the longest chain but lower mean path length than urban forests, where the food web structure was the simplest. Overall, our results indicate that fragmentation of urban habitats may be less detrimental than commonly assumed and may even increase the complexity of communities and the food web structure of litter-dwelling arthropods, contributing substantially to energy fluxes. If the litter layer is managed appropriately, these urban fragments therefore may promote arthropod communities and contribute to major ecosystem functions and services such as nutrient cycling and energy fluxes.

Author contributions

BW and XS conceived the idea and designed the experiment, and all authors substantially contributed to refining it. BW, SZ, ZQ, and QY conducted the arthropod sampling and classification. BW, SZ, and ZQ conducted the literature review and extracted $\delta^{15}N$ data. BW conducted the analysis and produced the figures, with support from SS and XS. BW wrote the initial draft of the manuscript, and all authors contributed to the final version of the manuscript.

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.2023.109150.

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