



Urbanization and plant invasion alter the structure of litter microarthropod communities

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Abstract

1. Anthropogenic activity underpins the creation of urban ecosystems, often with introduced or invasive species playing a large role in structuring ecological communities. While the effects of urbanization on charismatic taxa such as birds, bees or butterflies have received much attention, the impacts on small and inconspicuous organisms remain poorly understood.
2. Here, we assess how the community structure of leaf litter-inhabiting microarthropods in city parks varies along an urbanization gradient in Toronto, Canada. At each park, we established paired forest understorey plots which were either dominated by native vegetation or dog-strangling vine *Vincetoxicum rossicum*, an invasive species that is spreading throughout northeastern North America and abundant in urban areas. We compared microarthropod richness, abundance and diversity in ecological traits between invaded and non-invaded plots as well as compositional dissimilarities among plots across the urbanization gradient.
3. We recorded 123 genera and found (a) there was a negative effect of urbanization on microarthropod richness and abundance but only in invaded plots; (b) richness and abundance increased continuously with urbanization in non-invaded plots, but peaked at intermediate urbanization levels in invaded plots and (c) there was significant turnover with increasing urbanization, with distinct communities represented in highly urbanized areas compared to less urbanized areas, regardless of whether invaded. We also found litter microarthropod richness and abundance increased with soil ammonium and decreased with nitrate. These trends were especially strong for fungivorous microarthropods; however, there was no relationship between soil nutrients and urbanization or invasion.
4. Urbanization and biological invasion drive biodiversity change, and there is a need to disentangle these effects on ecological communities and related ecosystem processes. We show microarthropod communities change with urbanization, with the effects of invasion most prominent in non-urban areas. Here, there is high richness and abundance but low ecological trait diversity, possibly because certain feeding traits are excluded and others overrepresented.

5. Understanding of urban ecological systems must include knowledge of the microarthropods that interact widely across food webs, form distinct communities in highly urban areas and drive many of the important ecological functions upon which people in cities depend.

KEYWORDS

beta diversity, community assembly, dog-strangling vine, ecological traits, functional diversity, mites, soil mesofauna, urban forests

1 | INTRODUCTION

Urbanization results in fragmented green spaces that vary in size, dimension and disturbance (Forman, 2014; Lepczyk et al., 2017). Plant communities and soil conditions are influenced by a myriad of anthropogenic factors which alter available resources that drive patterns in animal diversity and abundance (Aronson et al., 2017). Urban forests are particularly susceptible to human impacts, including litter and soil habitats (Sharma & Sharma, 2004). Microarthropods are extremely diverse (Young, Proctor, deWaard, & Hebert, 2019) and abundant (Ducarme, André, Wauthy, & Lebrum, 2004) in litter and soil, and major contributors to multiple functions including decomposition and nutrient cycling (Kaneko & Salamanca, 1999; Seastedt, 1984; Yang, Wagg, Veresoglou, Hempel, & Rillig, 2018). The impacts of land-use change on microarthropod diversity are well studied in agriculture (Cortet et al., 2002) and forestry (Seastedt & Crossley, 1981), and only recently in urban areas (Joimel et al., 2017; Rzeszowski & Sterzyńska, 2016; Santorufo, Van Gestel, & Maisto, 2012).

Few studies have considered the interactive effects of urbanization on these communities with other major drivers of biodiversity loss such as biological invasion (but see Trentanovi et al., 2013), but it is becoming increasingly appreciated that these two drivers of diversity change interact (Cadotte, Yasui, Livingstone, & Maclvor, 2017). Biological invasions are pervasive in urban green spaces and impact a range of animal species including microarthropods which have been shown to be negatively impacted in several studies (Rusterholz, Salamon, Ruckli, & Baur, 2014; St. John, Wall, & Hunt, 2006). However, the impacts of plant invasion on soil biodiversity are not well understood and particularly in relation to the potential synergistic impacts of invasion interacting with urbanization. Cities are home to many invasive plant species as a result of human activity and require significant attention to curb economic impacts and spillover into nearby natural areas (Gaertner et al., 2017). Microarthropods are rarely considered in invasive species management despite the critical role these animals contribute to litter and soil food web dynamics. As a result, understanding how urban plant invasion impacts diversity and abundance is necessary to sustain urban green spaces and the important ecosystem services provided (Aronson et al., 2017).

Evaluating how microarthropod community composition is altered by urbanization and invasion can provide fundamental conceptual and

applied insights into biodiversity patterns. Delineating taxa by ecological traits supports information about community-level change that is independent of taxonomic diversity (Blaum, Mosner, Schwager, & Jeltsch, 2011). For example, two communities could have similar richness and abundance, but the species that make up each community are unique (having different properties and interactions; e.g. feeding guilds in mite communities in Mori et al., 2015), leading to different outcomes for ecosystem functioning. The dissimilarity in the ecological attributes present in microarthropod communities, but not richness, has been shown to drive litter decomposition and soil respiration (Heemsbergen et al., 2004). Identifying shifts in ecological traits across gradients of urbanization provides additional insights beyond taxonomic diversity since they provide a much more direct link to different ecosystem properties and multi-trophic interactions, thus influencing ecosystem function (Cadotte, Carscadden, & Mirotchnick, 2011; Seibold, Cadotte, Maclvor, Thorn, & Müller, 2018).

Furthermore, beta diversity can resolve the extent of compositional dissimilarity associated with urbanization or invasion. Dissimilarity among communities in different locations can be additively partitioned into nestedness and turnover components (Baselga, 2010). Nestedness can quantify the extent to which species loss accounts for the dissimilarity among communities subjected to different levels of urbanization or invasion. Turnover reflects the role of species replacement in driving compositional changes among communities. These two components allow us to ask whether litter microarthropod communities in city centres are subsets of those in less urban areas, or if they consist of distinct sets of species. Characterizing communities in terms of their dissimilarity both in taxonomic and functional diversity along an urbanization gradient and in interaction with invasive species can inform where to target and prioritize environmental management to support different ecological outcomes (Socolar, Gilroy, Kunin, & Edwards, 2016).

This study aims to determine the significance of urbanization and plant invasion on litter microarthropod communities in urban parks. As a study system, we selected Toronto, Canada, where an invasive plant, the dog-strangling vine *Vincetoxicum rossicum* [(Kleopow) Barbar.; 'DSV' hereafter] is widespread. DSV is native to Ukraine and Russia (DiTommaso, Lawlor, & Darbyshire, 2005) but has now established in cities across Northeastern North America (Sheeley & Raynal, 1996). Its tendency to overgrow native species allows it to form virtual monocultures, dramatically reducing the richness and altering functional diversity of plant

communities (Sodhi, Livingstone, Carboni, & Cadotte, 2019). It is also tolerant of both high- and low-light environments, and resistant to herbivory (Milbrath, 2010) which facilitates its dominance across vast areas of urban green spaces (Kricsfalussy & Miller, 2010). DSV invasion has been shown to reduce richness and diversity of other trophic levels such as adjacent macroinvertebrate (Ernst & Cappuccino, 2005), microbial (Bugiel, Livingstone, Isaac, Fulthorpe, & Martin, 2018) and fungal communities (Day, Antunes, & Dunfield, 2015). These changes have been speculated to occur in part due to potential antibiotic properties of its root (-) antofine exudates (Bongard, Butler, & Fulthorpe, 2013) but invaded plots also have high volumes of DSV leaf litter which would affect the spatial structure of leaf litter of non-DSV species, and thus food availability for litter-inhabiting species. In this study, we evaluate the impact of urbanization and invasion on the taxonomic and ecological trait diversity of litter microarthropod communities and quantify beta diversity to determine the relative importance of nestedness and turnover in describing resulting patterns. We measure soil nutrient properties to determine the relationship to urbanization and invasion, and whether there are ramifications for microarthropod communities. We hypothesize that microarthropod richness, abundance and ecological trait diversity will all be negatively correlated with urbanization, and that these would all be significantly lower in invaded understorey habitats compared to non-invaded. Additionally, we hypothesize that there would be significant turnover in litter microarthropod communities with urbanization.

2 | MATERIALS AND METHODS

2.1 | Study design

This study was conducted in 16 urban parks distributed across the Greater Toronto Area and three non-urban locations near Toronto at the Koffler Scientific Reserve at Joker's Hill near King City, Ontario (Table S1) in late July 2017. All urban parks were more than 1 km apart and selected based on the proportion of urbanization surrounding each park within a 500 m radius. These properties were calculated using R (R Core Team, 2019; hereafter, all analyses conducted using this program) and the 'land.metric' function in the *SPATIALECO* package (Evans, 2016). Landscape data were obtained from the 2007 Forest and Land Cover dataset (0.6 m raster pixel resolution) which contains eight landscape cover classes, from which we estimated urbanization as the sum of 'buildings', 'roads' and 'other paved surfaces' (City of Toronto, 2009). Urbanization ranged from 0% to 55.4% across all 19 parks (Table S1).

All parks contained DSV. Paired sample plots (~50 m apart) were selected from understorey habitat beneath mature deciduous tree cover (predominantly *Acer* and *Quercus*), and that were either invaded (>75% DSV cover within 2 m²) or not invaded (>75% non-DSV cover). Plots were selected to be as similar as possible in their canopy cover and tree composition and so the biggest difference in litter

composition was between invaded and non-invaded plots. Each plot was 1 m² and from which litter was collected and stored in coolers.

2.2 | Microarthropod sampling and traits

Within each 1 m² plot, we split the area into four equal quadrants and from each collected approximately 200 ml of litter directly from the soil surface and combined. We retrieved litter samples from all plots except one which was lost (i.e. $n = 37$ in total; invaded plot at KSR track; Table S1). In the laboratory, microarthropods were extracted from a subsample of the combined leaf litter from each plot via Berlese extraction using 40 W incandescent bulbs over a period of 4 days. Each subsample was approximately 200 ml based on the maximum volume that could fit in the Berlese funnel and exact weights were not obtained because of slight variation in wetness and to minimize disturbance to microarthropods. Raw extractions were stored in scintillation tubes in 95% ethanol. Microarthropod taxa considered included Acari, Collembola, Protura, Symphyla, Pauropoda and Pseudoscorpionida. Small-bodied insects such as Thysanoptera and some Hymenoptera were somewhat regularly encountered but these were excluded from the present study. Adult specimens were identified morphologically to the genus level. Immature stages for many microarthropods, particularly in the Acari, are often not identifiable even to the family level due to the poor ontogenetic understanding of most taxa and so were also omitted from the analyses. The taxonomic literature used for generic identification included Krantz and Walter (2009), Gilyarov (1975, 1977, 1978), Dindal (1990), Balogh (1972), as well as more specialized treatments at the family level or lower for groups that have since received taxonomic revision. All specimens were stored in 95% ethanol in 1.7 ml microcentrifuge tubes and curated in the zoology collections at the New Brunswick Museum's zoology collections (NBM-MNB), Saint John, New Brunswick, Canada.

Once identified, a literature review was conducted to determine the ecological traits of each genus (see Table S2 for a complete list of genera, traits and supporting literature). Not using the term 'trait' *sensu stricto* (Violle et al., 2007), we were able to define six 'ecological traits': fungivory, phytophagy, nematophagy, arthropodphagy, phoresy and parthenogenesis. The first four traits are associated with the diet of each genus (i.e. feeding preference). Each variable was defined to take the value of either 0 or 1; for example, if a given genus fed on fungi, it was assigned the value 1 for the trait 'fungivory'. The four guilds were defined as separate binary variables, rather than one categorical variable with four categories (fungivory, phytophagy, nematophagy and arthropodphagy) to account for the fact that some genera had more than one diet type. The feeding guilds were assigned to the genera for which information was available in published literature. Phytophagy was used as an umbrella dietary trait and included taxa that feed on algae, pollen, moss/liverworts, wood, as well as phloem of vascular plants. The fifth trait, phoresy, represents a dispersal strategy whereby microarthropods migrate via attachment to larger animals. The phoretic genera were

assigned the value 1, while others were assigned 0, and were determined based on either published reports of behaviour or the presence of an instar specialized for phoresy (e.g. phoretic hypopi in the Astigmata). Phoresy rarely occurs in microarthropod taxa other than the Acari (mites), so this was the only taxon included for this trait. The sixth trait, parthenogenesis, represents the ability of asexual reproduction. The genera with this ability were assigned the value 1, while others were assigned 0. This reproduction strategy is common in the Acari, and this variable was recorded for acarine genera that have been observed to exhibit this character. The two main modes of parthenogenesis in the Acari are thelytoky, which results in the production of haploid females, and arrhenotoky, producing haploid males. Both strategies usually result in strongly female-biased sex ratios (Norton & Palmer, 1991). This allows all these reproductive strategies to be represented by a single qualitative trait of either bisexual or female-biased populations. For many taxa, asexual reproduction is plastic at the subgeneric level. As we only identified microarthropods to genus, we could not assign reproductive strategy to a genus with absolute certainty. We considered a genus as female biased as long as the behaviour was reported for at least one species in the genus. All plot-level taxonomic richness, relative abundances and ecological trait data are available in the Dryad Digital Repository (Malloch, Maclvor, Tatsumi, Seibold, & Cadotte, 2020).

We acknowledge that, ideally, not only interspecific but intraspecific trait variations should be taken into account to reflect individual-level fitness (Violle et al., 2007), and that there are a number of frameworks and methodologies to incorporate such variation (e.g. Carmona, de Bello, Mason, & Lepš, 2019). However, measurements of individual-level traits are practically challenging especially for small-bodied organisms like the mites and Collembola examined here. Additionally, the use of trait-based approaches for soil microarthropods has only begun recently and there is still no consensus about which traits should be used in community assembly analyses (Mori et al., 2015). Since it is not known precisely which traits contribute to which function, we use the term 'ecological trait'; however, to stick to the framework, 'ecological trait' diversity is called functional diversity even though we do not know about the functional role of the traits used. The ecological traits selected best reflect what is known of microarthropod life strategies and environmental niches in the literature to date (see Table S2).

To quantify ecological trait diversity of microarthropod communities, we calculated functional dispersion (FDis; Laliberté & Legendre, 2010). Although the ecological trait groupings used in this analysis are not 'functional traits' in the strictest sense (Garnier et al., 2017), such functional groupings have been used to calculate FDis in studies on invertebrates (ground beetles: Schirmel, Blindow, & Buchholz, 2012; dung beetles: Barragán, Moreno, Escobar, Halffter, & Navarrete, 2011; mites: Mori et al., 2015) and other animal groups (Devictor et al., 2010; Mazel et al., 2014; Wilman et al., 2014). Among a number of available trait diversity indices, FDis was preferable over others because it is a multi-trait index and can account for species relative abundances (which was measured by the number of mite individuals in our study; Laliberté & Legendre, 2010).

First, intergeneric trait distances were quantified based on the six microarthropod traits and using Gower's distance which allows for binary data (Laliberté & Legendre, 2010). Although Gower's distance can accept missing trait values to some extent, we excluded genera for which fewer than four traits were available from the analyses because the calculation did not converge. This left us with 112 out of 123 genera (91.1%) and 3,221 out of 3,396 individuals (94.8%). Then, FDis was calculated using the intergeneric trait distances and the generic abundances in each plot.

2.3 | Soil nutrient and moisture analysis

We quantified soil nitrate and ammonium content using 2 g of fresh soil collected in each plot. Each soil sample was mixed with 20 ml of 2 M potassium chloride for 30 min using an automated shaker. Activated charcoal was added to clay-rich soils. Samples were then filtered, and the filtrate was analysed with a Lachat QuikChem 8500 Series 2 Flow Injection Analyzer. For soil carbon and nitrogen content, fresh soil was homogenized with a RETSCH ball mill for 30 s, and ~200 mg was placed inside a LECO 628 Series H/C/N determinator. Soil moisture content was measured as a ratio (%) by first weighing fresh soil, then placing it in an oven at 105°C for at least 48 hr, then weighing the dried soil, taking the difference and dividing by the dry weight.

2.4 | Statistical analysis

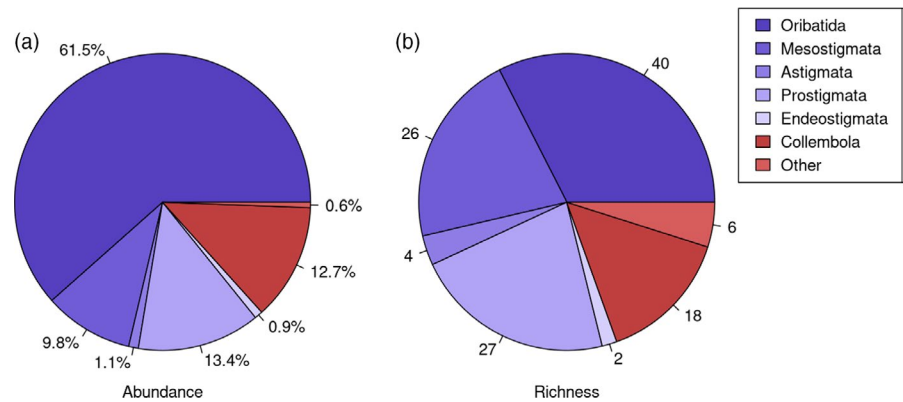
The effects of urbanization and plant invasion on microarthropod richness and abundance were tested by means of GLMMs. Microarthropod richness and abundance were defined as the number of genera and individuals in each plot, respectively. Poisson distribution was used to describe the variation in richness, which is a count variable. For abundance, which is also a count variable, negative binomial distribution was used because it showed a wide range in values. All linear and quadratic models used included log link functions. Urbanization, DSV invasion and their interaction were included as explanatory variables:

$$\log(y) = \beta_0 + \beta_1 Inv + \beta_2 Urb + \beta_3 Inv \cdot Urb + \epsilon_{Park}, \quad (1)$$

$$\log(y) = \beta_0 + \beta_1 Inv + \beta_2 Urb + \beta_3 Inv \cdot Urb + \beta_4 Urb^2 + \beta_5 Inv \cdot Urb^2 + \epsilon_{Park}, \quad (2)$$

where y is either microarthropod richness or abundance, Inv is a binary variable (0 = without invasion; 1 = with invasion), Urb is the urbanization rate (%), ϵ_{Park} is a random effect for park and β_0 - β_5 are parameters. The random effect ϵ_{Park} was included to account for the non-independence of the paired plots within each park. We compared the Akaike's information criterions (AIC) of the two models, and the one with lower AIC was considered a better model. The same GLMM analyses were repeated for the richness and abundance of each of the six ecological trait guilds. To infer the assembly mechanisms of microarthropod communities, we calculated the standardized effect

FIGURE 1 Proportion of total sample represented by major taxa in terms of (a) relative abundance, and (b) generic richness. The major subgroups of the Acari are represented in blue. Low-abundance taxa were agglomerated into the 'Other' category including Pseudoscorpionida, Pauropoda, Symphyla and Protura



sizes (SES) of FDis. While the original FDis could be influenced by species richness, we can remove such an influence by calculating its SES (Mason, de Bello, Mouillot, Pavoine, & Dray, 2013). For the calculation, we used an individual-based null model proposed by Kraft et al. (2011). This null model randomly shuffles individuals among plots while preserving the relative abundance of each genus across plots and the number of individuals and species per plot. The SES of each community was defined as $(x - \mu_{null}) / \sigma_{null}$, where x is the observed FDis, μ_{null} is the mean expected FDis and σ_{null} is the standard deviation of the expected FDis. The μ_{null} and σ_{null} were determined based on 999 randomized communities. The SES that are higher and lower than expected by chance indicate trait overdispersion and clustering, respectively (Weiher & Keddy, 1995). The effects of urbanization and plant invasion on observed FDis and SESFDis were tested by means of linear mixed models (LMMs). We used the same linear and quadratic models as indicated by Equations 1 and 2, except that $\log(y)$ were replaced with y which represent the observed and SESFDis. Urbanization, plant invasion and their interaction were included as fixed effects, and park as a random effect. The model with lower AIC was considered better over another.

Effects of urbanization and plant invasion on microarthropod generic composition were tested by means of PERMANOVA using distance matrices (Anderson, 2001). Compositional dissimilarities (i.e. beta diversity) among community pairs were quantified using Bray–Curtis and Jaccard indices which are abundance- and presence/absence-based measures, respectively. To analyse whether the potential compositional changes resulted from either replacement or loss of genera, we further additively partitioned the Jaccard index into spatial turnover and nestedness components (Baselga, 2010). PERMANOVA included urbanization rate, plant invasion (with vs. without) and their interaction as explanatory variables. All R functions and packages used for the analyses are listed in Table S3.

3 | RESULTS

Across 39 litter samples, 5,840 individuals were extracted. Of these, 3,396 were adults that represented 123 genera. Abundance of adults per plot ranged from 6 to 291 and richness from 6 to 33

genera (Table S4). The Acari were the most abundant group with 2,944 individuals (86.7%), represented by 100 genera. The next most abundant microarthropod group were the Collembola with 432 individuals (12.7%) from 18 genera. The Pauropoda, Pseudoscorpionida, Symphyla and Protura had very low abundance, with only 20 individuals combined (0.6%), representing six genera (Figure 1). The most common microarthropods recorded were predatory Mesostigmatid mites in the genus *Pergamasus* (Berlese 1903, Family: Parasitidae; 84.2% of plots, all parks) and oribatid mites including the xylophagous *Phthiracarus* (Perty 1841, Family: Phthiracaridae; 81.5% of plots, 18/19 parks), the herbofungivorous grazer *Tectocepheus* (Berlese 1895, Family: Tectocepheidae; 78.9% of plots, all parks) the fungi and wood feeding *Acrotritia* (Jacot 1923, Family: Euphthiracaridae; 65.8% of plots, 17/19 parks) and the fungivorous oribatid mite, *Galumna* (68.4% of plots, 16/19 parks). Litter microarthropod richness and abundance were significantly positively correlated (Figure S1).

Among the soil properties, moisture ranged from 11.6% to 48.7%, ammonium from 0.518 to 71.994 mg/kg, nitrate from 0.148 to 70.070 mg/kg, nitrogen from 1.286 to 4.015 mg/kg and carbon from 22.52 to 72.77 mg/kg (Table S1). Pairwise correlation tests between soil properties showed ammonium and nitrate were negatively correlated, nitrogen positively correlated with carbon and soil moisture positively correlated with ammonium. There was no significant correlation between urbanization or invasion and the different soil inorganic parameters (Figure S1).

Microarthropod richness and abundance declined significantly with urbanization, but only in invaded plots (Figure 2; Table S5). Invaded, non-urban plots had the highest taxonomic richness and abundance, with significant representation by fungivorous taxa (Figure S2). Functional dispersion in microarthropod communities increased significantly with urbanization, but there was no independent effect of plant invasion (Figure 3a). For both FDis and SESFDis, there were strong interaction effects, whereby invaded plots exhibited a concave relationship and non-invaded plots a convex relationship with urbanization (Figure 3). We also show invasion independently had a significant effect on SESFDis with invaded plots having more clustered microarthropod communities than non-invaded plots (Figure 3; Table S5). Richness of fungivorous taxa and abundance of nematophagous, phytophagous and fungivorous taxa were all significantly greater in invaded plots (Figure S2).

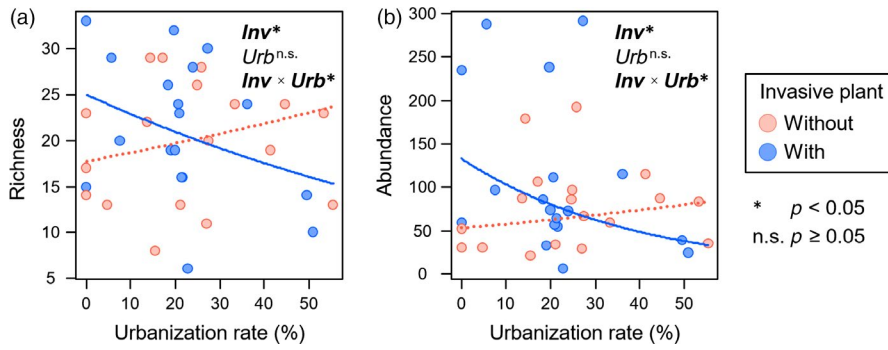


FIGURE 2 Urbanization and invasion impact on (a) taxonomic richness and (b) abundance. Taxonomic richness and abundance declined significantly with urbanization, but only in invaded plots (as indicated by the blue line). Non-invaded plots buffered against the effects of urbanization (as indicated by the dotted red line)

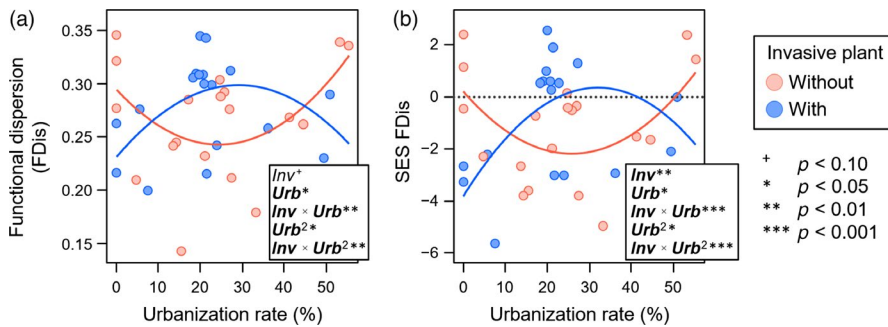


FIGURE 3 Scatterplots illustrating the parabolic relationship between urbanization with (a) functional dispersion (FDIs) and (b) the standard effect size of FDIs (SESFDis) for invaded and non-invaded understorey habitat

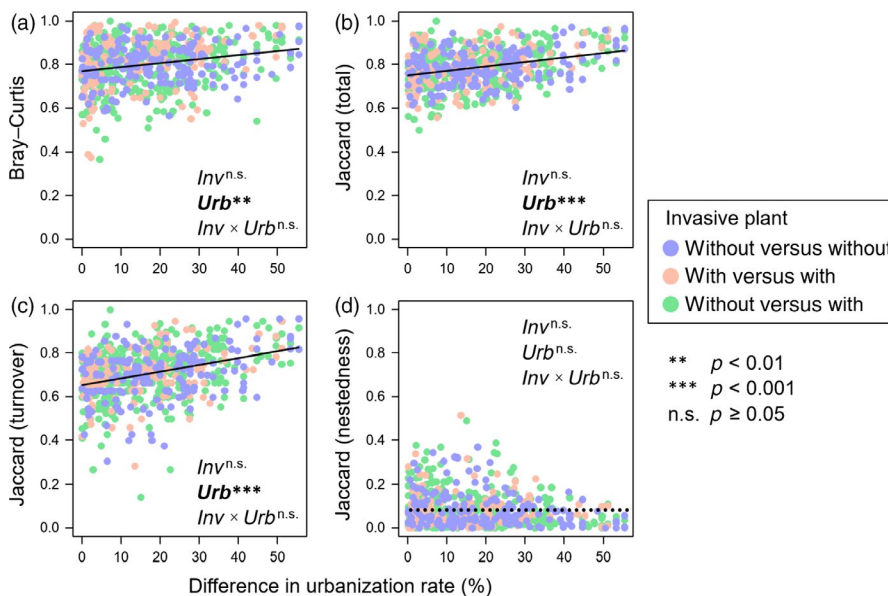


FIGURE 4 Scatterplots indicating relationships between urbanization and beta diversity metrics, including Bray-Curtis dissimilarity (a), Jaccards index (b) and with Jaccards decomposed into turnover (c) and nestedness (d)

Microarthropod richness and abundance increased significantly with ammonium, decreased significantly with nitrate and was not correlated to soil moisture, carbon or nitrogen (Figure S1). The abundance of fungivorous, phytophagous and nematophagous mites, as well as species richness of fungivorous and phytophagous mites and those reproducing via parthenogenesis were negatively correlated with available nitrate (Table S6). Abundances of fungivorous and phytophagous mites and those dispersing via phoresy, as well as species richness of fungivorous and parthenogenetic mites were positively correlated with ammonium (Table S6).

There was a significant increase in community dissimilarity (as measured using the Bray-Curtis distance) with increasing differences

in urbanization rates, but there was no difference between invaded and non-invaded plots, nor was there was an interaction effect (Figure 4a). The same patterns were demonstrated using the Jaccard index (Figure 4b). When the Jaccard index was partitioned into community turnover and nestedness to assess beta diversity, we found a strongly significant effect of urbanization in driving turnover, indicating that the compositional changes were mostly explained by replacement of microarthropod genera (Figure 4c). We found no effect of urbanization or invasion on nestedness (Figure 4d) indicating that communities in invaded understorey habitat were not truncated versions of the non-invaded plots, nor were more highly urban parks compositionally a subset of less urban parks.

4 | DISCUSSION

Microarthropod communities are extremely diverse and support a range of critical ecosystem functions in forest leaf litter and surface soils. Despite this, these taxa have received only recent attention in community ecological research, and especially in regard to anthropogenic pressures such as urbanization and biological invasions. Here we evaluate the microarthropod community structure in urban forest understorey environments in pairs of invaded and non-invaded plots. We found a negative effect of urbanization on microarthropod richness and abundance, but only in invaded plots, giving us partial support for our hypotheses that urbanization would be correlated with decline in both parameters. As well we demonstrate synergistic effects manifesting in taxonomic decline resulting from the interaction between urbanization and invasion. We also found microarthropod richness and abundance, especially of fungivorous taxa, increased with soil ammonium and decreased with nitrate. However, these soil nutrient properties were not explained by urbanization or plant invasion.

Invaded and uninvaded understorey plots exhibited contrasting concave and convex patterns in FDis with increasing urbanization. FDis was highest at the most urban, non-invaded plots, and in invaded plots it peaked at intermediate levels of urbanization. As a result, we reject our hypotheses that ecological trait diversity would decline with urbanization and be lower in invaded plots. The functional ecology of litter microarthropods is poorly known, and only a few broad ecological traits could be considered. Nevertheless, our approach provides much needed inference about the ecological influences on these microarthropod communities and we acknowledge that more quantitative traits might reveal more nuanced patterns. Fundamental aspects of the biology of the vast majority of free-living microarthropods have yet to be learned, where for example, feeding traits for many are understood at the kingdom or phylum level (Walter, 1988). Feeding traits within phyla have been determined from laboratory experiments, particularly for fungi, where mites, for example, are allowed to choose between a small selection of food items (Schneider, Renker, & Maraun, 2005). We also found that there was significant community turnover with increasing urbanization such that there were distinct communities represented in high urban areas compared to low urban areas, regardless of whether plots were invaded. This result supports our final hypothesis that beta diversity in litter microarthropod communities would be significantly correlated with urbanization. Altogether, our findings illustrate the role of urbanization and plant invasion in structuring microarthropod communities, and the need to better understand these highly diverse communities which drive important ecosystem functioning in cities.

4.1 | Microarthropod communities along a gradient of urban understorey habitat

Patterns in diversity and community composition in response to urbanization are taxa specific (Faeth, Bang, & Saari, 2011) and often

lead to biotic homogenization (McKinney, 2006). However, we found significant declines in taxonomic richness and abundance with urbanization only in invaded plots, and so it is possible that forest understorey habitat dominated by intact native vegetation could act as a buffer against the negative impacts of urbanization on microarthropod communities. This is reinforced with our results for ecological trait diversity, whereby after a threshold of approximately 30%–35% urbanization, there is a decline, and the inverse relationship was observed in non-invaded plots. Furthermore, urbanization led to significant turnover in the microarthropod community that is independent of invasion, and so variation exists in these poorly studied taxa in terms of their response to the many impacts that are associated with urbanization. How these distinctly urban-tolerant communities lead to changes to key ecosystem services provided including decomposition and nutrient cycling are unknown.

Urban forests support broader ecosystem functions that are desirable including pollution mitigation, carbon sequestration and recreation (Brack, 2002). As a result of the latter, leaf litter of urban forests may see more severe levels of disturbance through trampling, trail creation and the removal of fallen branches and trees (Van Nuland & Whitlow, 2014). We found that the highest abundance of litter microarthropods were found further away from the city centre. Forest litter-inhabiting arthropods decrease in abundance due to alterations in litter quantity and nutritional quality (Bultman & Uetz, 1984) and urban forests are known to exhibit lower canopy density, leading to lower leaf litter thickness (Kostel-Hughes, Young, & Carreiro, 1998). In addition to the physical changes seen in urban forest litter, chemical changes are also commonplace. Urban soils often have high concentrations of heavy metals and exhibit altered pH and salinity levels compared to rural soils, with construction and roadwork leaving a distinct fingerprint in adjacent forest soils (Trammell, Schneid, & Carreiro, 2011). Significantly higher levels of atmospheric carbon dioxide (Idso, Idso, & Balling, 2001), the urban 'heat-island' effect (Peng et al., 2012) and higher atmospheric ozone concentrations can lead to dramatically higher plant growth rates in cities (Gregg, Jones, & Dawson, 2003). Taken together, this suggests urban forests with a high canopy density and relatively low levels of physical disturbance could see higher rates of soil and litter nutrient turnover as a result of higher plant productivity and increased decomposer activity (Pouyat, McDonnell, & Pickett, 1997). We recommend that understorey microarthropod communities be considered when developing criteria and indicators for forest health in urban areas.

4.2 | Plant invasion and litter microarthropod diversity in urban parks

We found that urbanization and invasion interact to have the greatest impact on litter microarthropod communities, whereby richness and abundance at invaded plots steadily declined with increasing urbanization. Urban areas that are hotspots for biological invasions (Cadotte et al., 2017), and along with the altered abiotic

environmental conditions, result in ecosystem types without natural analogues (Hobbs, Higgs, & Harris, 2009). Disturbance by visitors to urban parks for recreation and experiences with nature may unintentionally perpetuate invasive plant species such as DSV. In general, however, the literature on the impacts of plant invasion on litter microarthropods illustrates context dependence and sometimes contrasting patterns. For example, Belnap, Phillips, Sherrod, and Moldenke (2005) found changes to soil nutrients by invasion were not important in structuring microarthropod communities, but that non-invaded plant richness was more important. Similarly, in our study, we found no interaction effect between invasion and soil nutrients on microarthropod communities (Figure S1), and we did see evidence that non-invaded plots buffered against impacts of urbanization (Figure 2). In another study, Lazzaro et al. (2018) show that invasion by black locust trees lowers microarthropod richness even when there is a good-sized litter layer. They suggest allelopathic compounds produced in the leaves or during the decomposition process might be responsible for lowering microarthropod richness. DSV is known to alter soil properties via allelopathy (Douglass, Westin, & DiTommaso, 2009), yet we find that fungivorous taxa were over-represented in invaded plots, in the least urban parks. Functional diversity was highest at invaded parks with intermediate urbanization levels (Figure 3). One difficulty in interpreting these results is that the majority of our parks were in the 20%–30% urbanization range where there was a lot of variation in both the invaded and non-invaded plots, and only 3 of 18 invaded parks were above 30% (Table S1). That said, the concave pattern in FDis could indicate that the intermediate pressure allowed the coexistence of multiple taxa with different environmental tolerance, successional niches and associated traits (Tatsumi, Cadotte, & Mori, 2019).

Invaded plots were not significantly different from non-invaded plots with regard to soil nutrient properties (Figure S1). As a result, trends documented in microarthropod communities are not due to DSV invasion occurring at higher quality plots. Non-invaded plots also exhibited considerable variation which was not explained by the presence of DSV (e.g. the diversity of species, nearby decaying wood), suggesting important factors relating to vegetation diversity and abundance regulating microarthropod communities were not considered. Other studies have attempted to use plant community composition as a predictor of microarthropod diversity with mixed results. Gormsen, Hedlund, and Huifu (2006) found that abandoned agricultural fields at different successional stages did not differ from each other in terms of richness or Shannon diversity, but community composition was different. Plants structure microarthropod communities through their contribution of fresh material to the litter layer (Gergocs, Rethati, & Hufnagel, 2015). Leaf litter composed of a greater diversity of plant material hosts a greater diversity of microarthropods, for example by supporting a larger variety of fungal decomposers (Hansen & Coleman, 1998). Diverse fungal and microbial communities in the litter are expected to support a more complex microarthropod community, as some of the most abundant litter microarthropod taxa (Oribatida and Collembola) show a dietary preference for

fungi (Anslan, Bahram, & Tedersoo, 2016; Behan-Pelletier, 1999). In support, Ilieva-Makulec, Olejniczak, and Szanser (2006) found the richness and abundance of fungivorous mites and Collembola increased with the age of experimental mesocosms as fungal colonization became more significant. Feeding habits vary within the Oribatid mites, with some taxa showing narrower feeding preferences than others (Schneider & Maraun, 2005). Despite this, the degree to which fungal and microbial biodiversity structure microarthropod communities is still poorly understood, with some suggesting environmental and spatiotemporal factors are more important than niche partitioning (Maaß, Maraun, Scheu, Rillig, & Caruso, 2015). Our study reinforces the idea that plant community only indirectly alters microarthropod communities, as we found fungivorous richness and abundance declined due to the interaction of urbanization and invasion more than other feeding guilds (Figure S1). The combination of lower plant diversity and mechanical disturbance to litter due to urbanization could reduce fungal diversity, thereby altering microarthropod communities; however, we did not find a significant effect of invasion on beta diversity, meaning the communities in invaded and non-invaded plots were no different. Ultimately, further research must be done to determine the mechanisms behind microarthropod diversity change due to plant invasion, and especially whether this is via DSV-driven chemical, physical or microbial changes in leaf litter and soils.

4.3 | Soil nutrients and microarthropod diversity in urban parks

Abundance and richness of microarthropods were positively correlated with soil ammonium and negatively correlated with soil nitrate concentration. Ammonium and nitrate concentrations in soil were negatively correlated (Figure S1). Nitrogen is a crucial nutrient limiting net primary production in many temperate ecosystems (Vitousek & Howarth, 1991) and has been observed to act as a regulator for Oribatid mite population size (Alatalo, Jägerbrand, Juhanson, Michelsen, & Luptáčík, 2017) and feeding guilds (Magilton, Maraun, Emmerson, & Caruso, 2019). Increased soil nitrate concentration is associated with less diverse floral communities, where the plants are not able to fully exploit the nitrate pool (Niklaus et al., 2001). Fungivorous microarthropods were more strongly negatively correlated to nitrate than were phytophagous or predatory mites as fungivorous species could be negatively affected by nitrate via negative effects on their food source.

5 | CONCLUSIONS

In this study, we found a decrease in litter microarthropod taxonomic richness and abundance with urbanization, but only in invaded plots, suggesting synergistic impacts may drive declines. It could be that urbanization might not be as severe a threat to these communities

as plant invasion. We show non-invaded plots were not affected by urbanization providing evidence that intact, non-invaded understorey habitat might buffer against the negative impacts of urban growth and are valuable to species involved in important ecosystem processes. Ecological trait diversity was highest at the most urban, non-invaded plots; moreover, there was significant turnover in microarthropod community composition with urbanization. Microarthropod communities were more diverse in invaded plots overall, a pattern driven by fungivorous taxa. As well this feeding guild was positively correlated with available nitrate, but there was no relationship between soil nutrients and urbanization or invasion. More work is needed to understand the impacts of urbanization on small-scale habitat criteria including soil nutrients which are known to drive patterns in these hyperdiverse biological communities. Knowledge of the interaction between soil nutrients, fauna, flora and fungi will ensure these communities and its diversity can be integrated into urban planning practices that support critical ecosystem functioning such as litter decomposition and nutrient cycling (Handa et al., 2014). Microarthropods are individually small and remain out-of-sight to many people yet play a critical component in the stability of broader ecosystems. They deserve more attention and consideration in management than they receive as we prepare for inevitable global urban expansion in the future.

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AUTHORS' CONTRIBUTIONS

J.S.M., S.S. and M.W.C. conceived the idea of the study; B.M., J.S.M. and S.S. collected the data and B.M. completed the microarthropod identifications; B.M. led the literature review of ecological traits; S.T. led the statistical analysis; B.M. and J.S.M. led the writing of the manuscript, and all other authors contributed; J.S.M. led the revisions. All authors have read and commented on the final version of the manuscript.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4xgxd256s> (Malloch et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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