ABSTRACT

MITCHELL, JENNIFER CHRISTINA. Nonnative Plant Invasion in Urban Forests Affects Understory Structure and Arthropod Communities. (Under the direction of Dr. Steven D. Frank).

Urban areas cover less than 3% of the earth's surface but contain more than half the global population. Human population growth and urban development threaten urban forests with increased degradation and fragmentation. Forests, even those surrounded by roads and buildings, provide ecosystem services including carbon sequestration and atmospheric cooling. These services will become increasingly necessary for the health of urban human populations as the earth's climate continues to warm. Additionally, forests in urban areas provide habitat for native plant and animal species that evolved to depend on forest ecosystems and would otherwise be forced into rural areas to survive. I investigated plant and arthropod communities in urban forests to determine how variability among 24 urban forests across two cities, Raleigh NC and Newark DE, affects community composition.

Temperate urban forests have similar traits and tend to be drier and warmer than rural forests, as impervious surfaces increase air and soil temperatures and reduce available moisture. Urban forests are commonly invaded by nonnative plants, often a result of unique human-mediated disturbances, which alters forest plant communities and changes forest structure. I used carabid beetle (Coleoptera: Carabidae) species as a model community to determine how understory vegetation and nonnative plant invasion affect ground-dwelling arthropod community composition. I found canopy openness correlated with increased nonnative plant invasion and understory density, and that nonnative plant invasion in turn reduced forest specialist species and increased open area specialist species. I then compared effects of understory vegetation to effects of forest size and surrounding impervious surface on urban forest carabid specialists. Across forests, carabid capture and diversity increased with greater forest size. Forest specialists

decreased and open area specialists increased with greater surrounding impervious surface. All carabids declined with increased understory vegetation density, ground cover vegetation, and leaf litter volume. These results support conserving forests with intact canopies to reduce long-term nonnative plant invasion, while managing forest understories short-term for removal of dense, nonnative vegetation, especially nonnative ground cover.

The recently termed 'Insect Apocalypse' often equates a reduction in arthropod abundance or biomass to a reduction in diversity, but without empirical evidence. I vacuum sampled urban forest understory arthropods to investigate relationships between abundance, biomass, richness, Shannon diversity index, and Simpson's diversity index. I found correlations between arthropod abundance and biomass, and between Shannon and Simpson's diversity indices, but found no correlations between abundance, biomass, richness, and either diversity index. It is therefore unlikely that arthropod biomass can be used to predict diversity across ecosystems, suggesting that quantifying arthropod biodiversity decline will continue to require specimen identification.

I then investigated effects of total, nonnative, and native structural complexity on arthropod abundance, biomass, richness, and diversity. Ecological theory and empirical evidence indicate greater structural complexity in plant communities will increase arthropod abundance and diversity, while nonnative plants are typically associated with low abundance and diversity. I documented arthropod abundance and biomass increased with greater total, nonnative, and native structural complexity, while richness and diversity declined with greater nonnative structural complexity. This suggests urban forests invaded by nonnative plants may provide adequate arthropod biomass as food for other taxa, like birds, but may fail to provide unique ecological services required in forests, as the number of species filling unique niches declines.

Urban forests are not negligible ecosystems and support diverse, native biotic communities. However, nonnative plants reduced urban forest arthropods and forest specialist species. Forest specialist arthropods are likely not the only organisms negatively affected by nonnative plant invasion in urban forests. These results outline the need to establish regional invasive management plans to strategically remove invasive species from urban forests and improve forest quality for native communities.

Nonnative Plant Invasion in Urban Forests Affects Understory Structure and Arthropod Communities

by
J. Christina Mitchell

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Entomology
Minor: Applied Ecology

Raleigh, North Carolina
2021

APPROVED BY:

Steven D. Frank Committee Chair	Christopher E. Moorman
Rebecca E. Irwin	Clyde E. Sorenson

DEDICATION

To R. David Mitchell

and

Eleanor J. Mitchell

BIOGRAPHY

"Weeds are flowers too, once you get to know them."

-Winnie the Pooh

There is so much to learn from our surroundings, if we only take the time to look and listen. As an ecologist, J. Christina Mitchell is continuously fascinated with how organisms interact with each other and their environment. She grew up in upstate New York wandering through the woods behind her house and getting to know the insects, herpetofauna, mammals, birds, fish, and plants that resided there. She went to high school at a small charter school in Pennsylvania where she honed her interest in ecology by taking fascinating biology classes and working as a gardener, while studying the local biota. She earned a Bachelor of Science in Wildlife Conservation at the University of Delaware, where she fell in love with field work and hands-on research. She moved to her fifth state, North Carolina, to earn a PhD in entomology, with a minor in applied ecology. Christina plans to perpetually explore her local ecology, while working towards native species conservation, throughout her life.

ACKNOWLEDGMENTS

Thank you to those who have participated in getting me on this path. R. David Mitchell, for being a true scientist and encouraging me to question everything. Sherri P. Mitchell, for showing me how to cook and fix things that are broken. Julia M. Korns, for loving me even though our passions could not be more different. Eleanor J. Mitchell, for teaching me how to fight for what I want and being amazed that I got paid to do it. Leloo and Charlie, for keeping me company no matter how early or late it was. And most of all, to Owen C. Cass, for being my partner in love and life. You explored our new state and created a home with me; you tended our home, yard, pets, and me when I was unable. I made it through because of you.

I especially want to thank the professionals for without whom, I would not be where I am today. To David Gardner, who first hired me as his field assistant and opened the door to being a paid scientist. To Debbie Delaney, Tara Trammell, and Vince D'Amico, for believing in my capabilities and giving me the chance to prove I had them. To Clyde Sorenson, Chris Moorman, and Becky Irwin, for joining me in this endeavor and providing lasting insight along the way. To the members of the Frank Lab, past and present, for answering my questions, sharing invaluable advice, and keeping me company through this journey. Finally, to Steve Frank, for hiring me and allowing me to earn this degree while staying true to my passions. I will be forever grateful for your advice and perspectives that apply not only to science, but also to life.

Thank you and I love you.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

Carabid specialists respond differently to nonnative plant invasion in urban forests

ABSTRACT

Forests within urban areas are important ecosystems for the survival of native plant and animal communities. Forests within the urban matrix are negatively affected by human-mediated disturbances, including those that lead to increased nonnative plant invasion. Nonnative plant species alter forest structure, and can contribute to dense understory vegetation, a more open canopy structure, and less leaf litter. This modified structure alters the function of urban forests for native forest specialist species. Carabid beetles (Coleoptera: Carabidae) are used globally to understand community-level responses to changes in ecosystem quality and structure. We sampled carabids in 24 urban forests in two cities, Raleigh, North Carolina and Newark, Delaware, to understand how carabid communities in different regions change in response to invasion by different nonnative plant communities. We predicted that forests invaded by nonnative plants would have a denser understory, carabid community composition would change to include less forest specialist species, and the carabid community would include more open area specialist species. We found greater native ground cover increased forest specialist diversity, greater canopy openness increased open area specialist capture and diversity, and understory vegetation density reduced open area specialist diversity. However, these relationships were dependent on regional plant and carabid community composition. This study suggests nonnative plant invasion and associated vegetation structure is a mechanism explaining differences found between rural and urban carabid communities and provides a unique example of how nonnative plants influence a guild of arthropods other than obligate herbivores. Our

results indicate that urban forests are not negligible ecosystems, but rather that they are a reservoir for native biota. We suggest that urban forest managers promote native species by managing nonnative species invasion in the understory of urban forests, to improve ecosystem quality for native forest specialist species.

INTRODUCTION

Nonnative plant species can alter forest ecosystems and reduce habitat quality for certain arthropod species (Ballard et al. 2013). Forests in urban and suburban areas (hereafter urban forests) are vulnerable to nonnative plant invasion as urban areas harbor more nonnative plants than rural areas (Aronson et al. 2015, Ariori et al. 2017, Malkinson et al. 2018). Urban forests are subject to unique human-mediated disturbances (Pickett et al. 2001) and forests with canopy gaps and forests surrounded by open area are positively correlated with increased nonnative plant invasion (Charbonneau & Fahrig 2004, Burton et al. 2014, Daniels & Larson 2020). Suggested mechanisms for invasion of nonnative plants in urban forests include the spread of ornamental plants from surrounding managed landscapes (Reichard & White 2001, McKinney 2008, Lehan et al. 2013), the legacy of historical land use (Pickett & Cadenasso 2009, Ziter et al. 2017, Trammell et al. 2020), and disturbances, including those that alter stand continuity and canopy formation (Ehrenfeld et al. 2001, Pickett & Cadenasso 2009, Mavimbela et al. 2018, Dyderski & Jagodziński 2019, Trammell et al. 2020). The presence of nonnative plants affects overall plant species diversity and community composition in forests. This shift in composition may alter ground cover, vertical vegetation structure, and leaf litter volume and composition (Ashton et al. 2005, Trammell et al. 2012, Dyderski & Jagodziński 2020). These changes in vegetation alter arthropod communities directly and indirectly by changing the availability and quality of food and cover resources (van Hengstum et al. 2014, De Smedt et al. 2021).

In temperate deciduous and mixed forests, nonnative plant species are most common and abundant in forest understories while overstories are typically comprised primarily of native species (Trammell & Carreiro 2011, Pregitzer et al. 2019, Beaury et al. 2020, Trammell et al. 2020). Common nonnative plant growth types and species in urban forests include vines, such as *Hedera helix* and *Lonicera japonica*, herbaceous annuals, such as *Microstegium vimineum*, and shrubs, such as *Elaeagnus* spp., *Ligustrum* spp., *Lonicera maackii*, and *Rosa multiflora*. Characteristic traits of invasive nonnative plant species include rapid propagation and spread, through the distribution of fruits and seeds by animals, and lateral spread by rooting vines and stems (Aronson et al. 2007, Vallet et al. 2010, Nunez-Mir et al. 2019). Often, nonnative plants in the forest understory contribute to dense ground cover, a dense shrub layer, or both. Many nonnative plant species in eastern forests are broadleaf evergreens or semi-evergreens (Miller 2003, Dirr 2009), causing invaded forests to retain dense understory and midstory vegetation throughout the year. The combined effects of nonnative plant growth, propagation habits, and leaf retention means that understory vegetation becomes denser as the number of nonnative plants increases (Trammell & Carreiro 2011, Templeton et al. 2019). Compared to uninvaded forests, dense nonnative understory vegetation can reduce forest regeneration and ultimately reduce future canopy density (Oswalt et al. 2007, Maynard-Bean & Kaye 2019). This may lead to permanent changes in forest structure and ecosystem quality (Collier et al. 2002, Trammell & Carreiro 2011) and alter urban plant and animal communities by limiting native species that rely on the characteristic structure and resources of temperate forests.

The forest floor and litter layers are critical for epigeal arthropods, and these layers may change as nonnative plants increase understory vegetation density and reduce leaf litter volume and quality. Leaf litter from evergreen plants is typically of lower nutritional quality and decomposes slower than deciduous leaf litter, but also does not accumulate as deeply since leaves drop throughout the year (Aerts 1996, Cornelissen et al. 2003). Leaf litter from deciduous nonnative species can decompose faster and be of lower nutritional quality than comparable native species (Trammell et al. 2012). Moreover, litter from both native and nonnative plants decomposes faster in urban forests, contributing to lower litter volume and reduced suitability for epigeal arthropods in urban landscapes (Pouyat & Carreiro 2003). Rapid decomposition of leaf litter in urban forests has been attributed to both abiotic factors like moisture, heat, and soil characteristics (Pouyat et al. 1997, Ehrenfeld et al. 2001, Pouyat & Carreiro 2003, Meyer et al. 2019) and biotic factors like plant species traits and invasive earthworms (Pouyat et al. 1997, Steinberg et al. 1997, Ehrenfeld et al. 2001, Szlavecz et al. 2006). Many forest-adapted arthropod species rely on leaf litter and woody debris for shelter from predators, food resources, and moisture to prevent desiccation. For example, characteristics of urban leaf litter change detritivore arthropod communities directly by altering moisture, which indirectly affects communities of predatory arthropods that rely on detritivores for food (Chen & Wise 1999, Meyer et al. 2019). The combination of less leaf litter deposition by nonnative plant species and rapid leaf litter decomposition suggests urban forests invaded by nonnative species would provide inferior litter resources for forest-adapted arthropods, such as forest specialist carabids.

Carabid beetles (Coleoptera: Carabidae) are abundant, taxonomically and ecologically diverse, and their community composition changes in response to abiotic and biotic conditions (Niemelä et al. 2000, Rainio & Niemelä 2003, Magura et al. 2004, Koivula 2011). Thus, carabids are studied globally to understand effects of ecosystem change on biodiversity and are used as indicator species of ecosystem quality and structure (Koivula 2011, Riley & Browne 2011). Carabid communities can change in response to nonnative plants because carabids are sensitive to alterations in light, temperature, vegetation structure and composition, and soil and litter moisture (Croci et al. 2008, Koivula 2011). Some carabid species are forest specialists that tend to be large, predaceous, and unable to fly. These species depend on moist, dense, litter, comprised of leaves, coarse woody debris, and other organic matter, to provide microclimatic conditions necessary for egg and larval survival, overwintering shelter, and prey items that include detritivores (Larochelle & Larivière 2003, Latty et al. 2006, Martinson & Raupp 2013, Meyer et al. 2019). For example, *Carabus vinctus* (Weber, 1801) is a relatively large (20-28 mm), flightless, and predatory forest specialist reliant on moist litter for larval and adult survival (Pilny & Morgan 1987, Larochelle & Larivière 2003, Bousquet 2010). *C. vinctus* is hygrophilous, so more light and the less dense, drier litter in forests invaded by nonnative plants would change the microclimate of this species' habitat and reduce reproductive or overwintering success (Pilny & Morgan 1987). *Sphaeroderus canadensis canadensis* (Chaudoir, 1861) is a smaller (10-13 mm) forest specialist with a thorax adapted for getting inside snail shells and mouthparts adapted with spoon-shaped palps to scoop snail tissue towards the mandibles (Larochelle & Larivière 2003, Bousquet 2010). Since snails also rely on moist microclimates and litter (Machin 1967), nonnative plant invasion can reduce the abundance or change the distribution of prey for *S. canadensis canadensis*. By limiting species like these, nonnative plant invasion may cause carabid communities in urban forests to be more similar to non-forest ecosystems and reduce ecological services provided by these forest specialist species.

In urban and invaded areas, forest specialist carabids can be replaced by open-area specialists or generalist species, which are typically smaller, omnivorous, capable of flight, and tolerate a wider range of environmental conditions (Larsen et al. 2003, Jennings & Tallamy 2006, Martinson & Raupp 2013). Dense understory vegetation impedes carabid surface locomotion (Lys & Nentwig 1992, Brose 2003, Croci et al. 2008) so communities in invaded forests may contain more individuals capable of flight, and therefore be less reliant on ground mobility for dispersal or finding food resources (Ewers & Didham 2006). Additionally, dense vegetation alters carabid communities by changing prey communities (Guillemain et al. 1997, Zou et al. 2015). For example, carnivorous carabids that rely on common prey like collembola and gastropods may be replaced by omnivorous species that can forage on seeds in addition to invertebrate prey. Dry microclimates in urban forests (Pouyat et al. 1997, Koivula et al. 1999, Magura et al. 2004) result in carabid communities shaped by drought-tolerant generalist species (Ribera et al. 2001). For example, *Poecilus lucublandus* (Say, 1823) is a smaller (9-14 mm), flight-capable species tolerant of variable environmental conditions and is associated with human activity including agriculture, lawns, and vacant lots (Larochelle & Larivière 2003, Bousquet 2010). The number of *P. lucublandus* collected in agricultural fields has been shown to increase in response to disturbance by tillage and by greater abundance of annual plants (Clark et al. 1997). Carabid communities are known to change in accordance with plant communities and soil and litter moisture (Butterfield & Coulson 1983, Gardner 1991, Ribera et al. 2001), and captures of open area specialist species increase with warmer ground temperatures and less coarse woody debris (Martinson & Raupp 2013). Specifically, Gagné and Fahrig (2011) found open area species replaced forest species in carabid communities with increasing housing density, a variable correlated with urbanization.

We studied plant and carabid communities in urban forests to determine if invaded forests alter urban forest carabid communities. We predicted that the composition of carabid communities in urban forests is driven, in part, by the density and diversity of nonnative plant species as they alter forest vegetation density and structure and the quantity and quality of the litter layer. Specifically, we predicted that nonnative plant density and diversity would be positively correlated with greater understory vegetation density, a more open canopy structure, and less leaf litter. These changes, in turn, would directly and indirectly reduce carabid abundance but increase species diversity, as forest specialist populations decrease, and open area and generalist species are added to the species pool. We predicted that as the proportion of nonnative plants increases in an urban forest, carabids would become less abundant and communities would become dominated by open-area specialists and generalist species because they tolerate dense vegetation, sparser canopy cover, and warmer temperatures (Spence & Spence 1988, Kotze & O'Hara 2003, Zou et al. 2015, Prass et al. 2017, Piano et al. 2017). Likewise, we predicted that forest-specialist carabids will exist in urban forests but will be more abundant in forests with fewer nonnative plants. To test our hypotheses, we quantified plant and carabid communities in 24 urban forests that varied in the amount of nonnative plant invasion. We conducted this study in Raleigh, North Carolina and Newark, Delaware to understand how carabid communities in different regions change in response to invasion by different nonnative plant communities. Understanding how nonnative plants affect carabid communities, and if these responses are consistent in different regions, can aid development of forest management practices to control nonnative plant species and maintain forest quality in expanding urban ecosystems. This research aimed to determine a theoretical tolerance level of native forest-specialized carabids to nonnative plant invasion, which can inform management practices to reduce nonnative plant invasion, maintain healthy forest communities, and conserve native biota in urban forests.

METHODS

Study area and research sites

We conducted this research in Raleigh, North Carolina (35.780˚N, 78.642˚W) and Newark, Delaware (39.683˚N, 75.753˚W), both cities in the eastern USA. Forest patches in these cities are part of the FRAME (FoRests Among Managed Ecosystems, https://sites.udel.edu/frame/) network of forests used to study urban forest ecology. To expand our scope of inference, we used the different regions and species communities of Raleigh and Newark to determine if relationships between nonnative plant invasion and arthropod communities were similar in urban forests with different species. We followed the FRAME protocol (Trammell et al. 2020) to sample 24 forests, 12 in each city (Figure 1.1).

We selected forest patches throughout each city, without prior knowledge of forest condition, to ensure forest patches were of various size and distributed across the city center. Each forest had at least one hard edge such a road, parking lot, or paved path. The forest patches were surrounded by a variety of landscape types including city infrastructure, residential areas and managed parks, agriculture, and other forest. We sampled throughout the entire area of smaller forest patches (0.8 – 16.2 ha, N = 11), and a portion of the total area in larger forest patches (5.8 – 211.0 ha, N = 13; Table 1.1). We established a grid using 25-m x 25-m spacing of alpha-numerically marked locations designated by marking flags (Presco Products Co., 53 cm tall) within the sampled forest area, hereafter referred to as points. Within this grid we randomly selected ten points for sampling, with the stipulation that sampling points could not be immediately next to each other, unless on a diagonal and at least 35.4 m apart. We monitored 239 sampling points in total, 120 in Newark and 119 in Raleigh (one small forest only accommodated nine sampling points) and collected all plant and carabid data at these sampling points (Figure 1.2).

Plant community sampling

We followed the FRAME protocol to quantify plant communities at each sampling point (Trammell et al. 2020). We collected vegetation data in 2015 for Newark and 2017 for Raleigh. We estimated the total percent of the area covered by ground vegetation and counted all plant stems within a 2.5-m radius of the sampling point. We defined ground vegetation as any plant species, including woody and herbaceous species, less than 0.5 m tall. We estimated percent of the 19.6-m^2 area covered by all ground vegetation, identified the dominant plant species, and estimated percent area covered by the dominant species. We also estimated percent of the area covered by nonnative ground vegetation, identified the dominant nonnative plant species, and estimated percent area covered by the dominant nonnative species. We defined shrub layer vegetation as any plant stem, including woody and herbaceous species, reaching 1.0 m or taller and less than or equal to 2.5-cm diameter at breast height (1.4 m; Nowak et al. 2008). Within 2.5-m radius of the sampling point, we counted and identified all plant stems meeting these criteria. To sample leaf litter, we stood at a sampling point and dropped a 0.5-m x 0.5-m PVC square from arm's length. We did this once per sampling point and rotated cardinal directions for each subsequent point. We measured leaf litter volume by gathering all leaf material from inside the PVC square and placing it into a five gallon bucket pre-labeled with 0.5-liter increments, up to 15 liters. We took densiometer readings (convex spherical crown densiometer, Model A, Forestry Suppliers) at 5 m from the sampling point in each cardinal direction and averaged them to get a value of canopy openness for each point. At 15 m from the sampling point in each cardinal direction, a single observer estimated understory vegetation density at four strata ranging from 0.0 – 2.0 m tall in 0.5 m increments with a Nudds board (Nudds 1977, Figure 1.3). We used these estimated values to calculate the average amount of vegetation obscuring the Nudds board at each sampling point. We identified all plant species with dichotomous keys specific to each city's biogeographic region (NC: Weakley 2015, DE: Gleason & Cronquist 1991).

Carabid community sampling

We collected carabid beetles using pitfall traps (Figure 1.4) of a design adapted from Koivula et al. (2003) and Spence & Niemelä (1994). At each sampling point, we dug a hole with an 8-cm diameter soil auger so the rim of an inserted 16-ounce plastic cup (Hefty® Everyday™ Cups) was flush with the soil surface. For the duration of each sampling season, we anchored one cup, with two 0.6-cm diameter holes punched in the bottom, in the soil cavity using an 8.5-cm long nail. We stacked a second cup with two opposing 0.6-cm diameter holes punched 3-cm below the cup lip inside the anchored cup to allow for easy removal and emptying of trap contents. During rain events, the holes punched into both cups allowed liquid to overflow and drain, while keeping trap contents below the cup lip. We ballasted the inside cup with ~30 g of landscape river rocks and during sampling periods added 150 ml of a preservative mixture, a 1:1 ratio of water and propylene glycol (Ocean Bio Chem Inc®, Starbrite Anti-freeze Antigel) (Koivula et al. 2003). We covered traps with a plywood 22-cm equilateral triangle propped up on the corners by 5-cm bolts to minimize debris falling into the trap while allowing space for carabids to walk beneath. To estimate localized carabid populations (Luff 1996), we collected carabids throughout the growing season during two-week periods in 2017 and 2018 by adding the preservative mixture to the inside cup and propping trap covers open. Between sampling periods, we made all traps inactive by filling cups with rocks only and pressing trap covers into the soil to seal the cup opening. We trapped carabids five times in 2017: May 28 to June 16, July 9 to July 26, August 23 to September 9, October 4 to October 21, and November 15 to December 2. We trapped carabids three times in 2018: March 28 to April 16, May 14 to June 1, and July 6 to July 23. We cleaned all trapped carabids with 95% ethanol, then pinned and identified each individual to species using dichotomous keys specific to each biogeographic region (NC: Ciegler 2000, DE: Bousquet 2010). We verified identifications by comparison to identified specimens housed in the North Carolina State University Insect Museum. We retained carabid voucher specimens, and all trap bycatch was preserved in 70% ethanol and stored for later analyses.

Statistical analyses

All analyses were conducted in R version 4.0.5 (R Core Team, 2021). To compare carabid community compositions among forest sites, we created a similarity matrix of carabid species captured at each site, summed across all sampling periods. To visualize relationships between each site's carabid community, we conducted nonmetric multidimensional scaling (NMDS) using the metaMDS function in the package vegan with the Bray-Curtis distance measure and random starting configuration (Oksanen et al. 2020). All species were included in this matrix because singletons can drive differences in the diversity of community compositions (Pos et al. 2014). We overlaid a secondary matrix with ecological variables using the envfit function in the vegan package to determine which variables correlated with explaining variation in the dataset (Oksanen et al. 2020). The ecological variables were summed (species richness, stem density, total carabids captured) or averaged (percent nonnative ground cover, understory vegetation density, leaf litter volume) for all points in each forest.

To test relationships between carabid communities and ecological variables, we used a priori hypotheses and knowledge of the system to construct structural equation models (SEMs). We created SEMs using the psem function in the package piecewiseSEM (Lefcheck 2016). This method is similar to path analyses and can include direct and indirect relationships between variables. Indirect relationships can occur between three or more variables, as the influence of the predictor variable on intermediate variables is reflected in the influence of intermediate variables on the response variable. The total indirect effect on the response variable can be calculated from the product of intermediate relationships, positive, negative, or both, between variables along an indirect path (Stenegren et al. 2017). Piecewise SEMs validate hypotheses of assumed causality and work well with smaller sample sizes (Lefcheck 2015, Lefcheck 2019). The NMDS results indicated different carabid and plant communities in Raleigh and Newark and supported our choice to analyze each city separately. SEMs allowed us to test correlational relationships between independent (vegetation type and strata, canopy openness, and leaf litter) and dependent (total, forest specialist, and open area specialist carabid log+1-transformed capture and diversity) variables for each city. We analyzed SEMs at the level of sampling point, with site as a random effect, to determine the effect of nonnative plant invasion on carabid communities regardless of the amount of variation of these variables within a single forest (Schank & Koehnle 2009, Davies & Gray 2015). For each city, we constructed 12 SEMs to test our hypotheses regarding causal relationships between plant and carabid communities and determine whether these relationships are affected by plant origin (native, nonnative), vegetation type (ground cover, shrub layer), or carabid type (total, forest specialist, open area specialist). We constructed each SEM from 5 component models using the lme function in the package nlme (Pinheiro et al. 2021). Canopy openness separately predicted native and nonnative vegetation, native and nonnative vegetation both predicted 2 environmental variables, and vegetation and environmental variables in turn predicted carabid response (Figure 1.5). We tested component models for multicollinearity using variance inflation factors (VIF) (Neter et al 1983, Zuur et al. 2010) and since all VIF values were < 3, we assumed the collinearity among these variables was low and retained all variables in the models (James et al. 2013, Zuur et al. 2010). We evaluated final SEMs with a directed-separation test, to identify significant paths between variables that are supported by the data, and included a suggested link in each city's models where an $\alpha \leq 0.05$ indicated further model refinement was required. We added a link between understory vegetation density ~ canopy openness to Raleigh stem layer SEMs, a link between native ground cover ~ nonnative ground cover to Newark ground cover SEMs, and a link between leaf litter ~ understory vegetation density to Newark stem layer SEMs.

We created these SEMs to explicitly test each carabid response metric, either capture or diversity for each type of carabid, to understand how urban forest carabid communities vary with nonnative plant invasion and whether carabid communities respond differently to ground cover layer or shrub layer invasion. We determined whether each species was a forest specialist or an open-area specialist using species-specific life history traits (Noonan 1996, Larochelle & Larivière 2003, Bousquet & Webster 2004, Bousquet 2010). A species was determined to be a forest specialist if described as requiring forest canopy cover, leaf litter, coarse woody debris, or moist shaded woods to survive and reproduce. A species was determined to be an open-area specialist if it was described as requiring open areas like grasslands, shrublands, crop fields, meadows, gardens, vacant lots, forest edges and clearings, or open ground to survive and reproduce.

RESULTS

Plant and carabid communities

Across the 24 forest sites, we identified 114 unique plant species in the ground cover and shrub layers combined, of which 31 species were nonnative (Table 1.2). Across all sites we identified 48 species and 14 nonnative species in the ground cover, and 97 species and 26 nonnative species in the shrub layer (Table 1.3). Across sampling points, leaf litter volume ranged from 0.5 – 20.0 L (6.7 ± 4.4 L) in Raleigh and 0.5 – 11.5 L (5.4 ± 2.6 L) in Newark. The average estimate of understory vegetation density as measured by percent of the Nudds board obscured ranged from 13.4 – 98.4% (56.6 ± 21.6%) in Raleigh and 1.6 – 93.8% (44.4 ± 23.6%) in Newark. The average estimate of canopy openness as measured by percent of the densiometer not obscured ranged from 2.6 – 61.9% (11.4 ± 8.9%) in Raleigh and 3.1 – 35.4% (12.3 ± 7.3%) in Newark. Across the 24 sites, 1864 individual carabids of 57 species were caught over 14 months (Table 1.4). We captured 477 individuals of 29 species in Raleigh and 1387 individuals of 48 species in Newark. In Raleigh, we captured 29 individuals of 6 forest specialist species and 319 individuals of 14 open area specialist species. In Newark, we captured 356 individuals of 14 forest specialist species and 171 individuals of 15 open area specialist species.

Raleigh and Newark forests had similar amounts of total ground cover vegetation (39.3% and 32.4% respectively), however, Raleigh ground cover was composed of 54.8% nonnative species, whereas Newark ground cover was composed of 39.0% nonnative species. Averaged across all sampling points, nonnative ground layer covered 21.5% (± 26.5) of the 19.6 m^2 area sampled in Raleigh and 12.6% (± 17.5) in Newark. Raleigh had a greater density of nonnative stems (mean 12.2 ± 27.4 stems per 19.6 m^2) and 56.9% of all counted stems in the shrub layer were nonnative, whereas 47.0% of all counted stems in Newark were nonnative. Compared to

Raleigh, Newark had more native ground cover per sampling point (19.8% ± 17.9) and a greater density of native stems (mean 13.1 ± 23.5 stems per 19.6 m^2). In Raleigh, six of the seven most common species in the ground cover and shrub layer were vining or low-growing herbaceous species, and five of these common species were nonnative (Table 1.5). In Newark, four of the seven most common species in the ground cover and shrub layer were shrub species, and five of these common species were native (Table 1.5).

Nonmetric multidimensional scaling

The NMDS ordination of carabid communities are presented in two dimensions (Figure 1.6) with a final stress value of 0.15. The 24 urban forest sites separated in ordination space along Dimension 1 into two groups, each group containing all the sites of each city. The separation of these groups indicated large differences between each city's carabid community, and the denser cluster of points in the Newark group indicates more similar within-city carabid community composition compared to Raleigh. Dimension 1 positively correlated with carabid richness, capture, and Shannon's diversity, indicating these correlated with the greater similarity of the Newark forests. There was no distinct separation among forests along Dimension 2 indicating that this dimension represents the differences in carabid community composition among both cities. Dimension 2 positively correlated with understory vegetation density and negatively correlated with ground cover diversity, indicating understory vegetation and ground cover were important variables in carabid communities across regions. NMDS results supported our hypothesis that understory vegetation structure, an ecological component affected by nonnative plants, is important for carabid community composition and for inclusion of related variables in further analyses.

Structural equation modeling

SEM results differed for each city (Figure 1.7 and Figure 1.8). In Raleigh, canopy openness positively influenced nonnative ground cover and understory vegetation density. Nonnative ground cover positively influenced understory vegetation density and negatively influenced leaf litter. Nonnative and native stem density positively influenced understory vegetation density. Native ground cover had direct positive influence on total carabid diversity, a response driven by forest specialist diversity. Canopy openness had a direct positive influence on total carabid capture and diversity, a response driven by open area specialists. Leaf litter had a direct negative influence on open area specialist carabid diverstiy, so that nonnative ground cover indirectly increased open area specialist diversity through a reduction in leaf litter. These results indicate that native ground cover supports more forest specialists, while open canopies increase nonnative ground cover and support more open area specialists.

In Newark, canopy openness positively influenced native ground cover, nonnative ground cover, and nonnative stem density. Native and nonnative ground cover and native and nonnative stem density positively influenced understory vegetation density. Native ground cover, nonnative ground cover, and understory vegetation density negatively influenced leaf litter volume. Nonnative ground cover negatively influenced native ground cover, which may suggest competition. Leaf litter volume positively influenced open area specialist diversity. Nonnative ground cover positively influenced open area specialist diversity, while native ground cover negatively influenced forest specialist capture. Indirectly, canopy openness decreased native ground cover, increased understory vegetation density, and decreased leaf litter volume. These results indicate that open canopies increase native and nonnative understory density, which contribute to decreased forest specialist capture and increased open area specialist diversity.

Raleigh and Newark plant comunities differ in origin and structure, which results in different influences on forest and open area specialist carabids and varied community response.

DISCUSSION

Effects of plant origin and structure on carabid communities

In two cities, canopy openness exacerbates nonnative plant invasion, which increased understory vegetation density, reduced leaf litter volume, and altered carabid communities in urban forests. Total carabid richness and diversity are often greater in urban forests, but total carabids captured, forest specialists captured, and forest specialist diversity are often greater in rural forests (Niemelä et al. 2002, Magura et al. 2004, Magura et al. 2010, Jones & Leather 2012). Greater carabid richness and diversity in urban forests has been attributed to a decrease in forest specialists, an increase in generalists and species that prefer open areas, or both (Magura et al. 2004, Jones & Leather 2012). We argue that the mechanism for this structured change in urban carabid community composition is, in part, the greater occurrence of nonnative plants found in urban forests. In simple linear regressions, urban forest canopy openness correlated with increased nonnative plant invasion but did not affect forest or open area specialists, while greater understory nonnative plant richness reduced forest specialist capture, forest specialist diversity, and open area capture (J. C. Mitchell, *unpublished data*). Our results indicate that the open canopies, invaded and dense understories, and reduced leaf litter volume often found in urban forests correlated with a shift in the urban carabid community to contain more open area specialists. Additionally, our results support competition between nonnative ground cover and native ground cover and there is evidence that with time, heavily invaded forests may perpetuate open canopies (Oswalt et al. 2007, Maynard-Bean & Kaye 2019).

Plant species origin

Nonnative vegetation dominated the understory of Raleigh forests, where native ground cover was the only variable positively correlated with forest specialist diversity, whereas more than half of understory vegetation in Newark urban forests was native. Greater nonnative plant invasion in Raleigh forests may reflect greater plant invasion rates commonly seen in areas with a warmer climate (Beaury et al. 2020). Most studies that have examined changes in carabid communities along a rural to urban gradient did not include within-forest vegetation characteristics. Magura et al. (2004) included effects of herbaceous cover in their analyses of carabid communities but did not specify plant origin. Contrary to our results, Magura et al. (2004) found that herbaceous cover increased most carabid metrics with the notable exception of the number of open area species captured. The authors attribute this response to a 'habitat structure effect' and suggest carabid species depend on, and respond to, forest structure more than specific plant species, though plant species identifications are not reported in the paper. Other studies draw similar conclusions, stating that vegetation structure explains more variation in predatory ground beetle diversity than the taxonomic diversity of plants (Brose 2003, Lengyel et al. 2016). Our results support the influence of forest structure on carabid communities but go further to identify the role of nonnative plants in altering that structure. While we agree forest structure is important, we argue that unique plant species do play a role because of their effect on forest understory structure and resources. Additionally, studies that found carabid community differences along a rural to urban gradient may have detected an unmeasured effect of nonnative plant invasion separate from urbanization. Our results document a distinction between carabid responses to different vegetation, and specifically to native or nonnative vegetation.

Canopy openness

Our results indicate that the response of carabids to canopy openness is dependent on the species involved and the regional location of the city. In Raleigh, forests with more canopy openness had greater nonnative ground cover and greater open area specialist capture and diversity, which contributed to increased total carabid diversity. Newark forests, on average, had a more open canopy compared to Raleigh, yet increased canopy openness did not directly influence carabid specialists. However, canopy openness indirectly correlated with greater understory vegetation density by increasing nonnative stem density, which in turn indirectly correlated with reduced open area specialist diversity by reducing leaf litter volume. In other forests, increased forest structure correlated with increased relative abundance, richness, and diversity of beetles caught in flight-intercept traps (Mϋller & Brandl 2009), indicating small beetles capable of dispersal. Specifically, forest canopy openness increased beetles caught in flight-intercept traps and reduced beetles caught using pitfall traps (Mϋller & Brandl 2009), which is where forest specialist carabids would be captured. Alternatively, Davies & Asner (2014) concluded that beetles increased in richness and abundance in response to increasing canopy structural variability, including vertical heterogeneity, understory density, and topographic structure, but less so to canopy cover, which increased temperature and decreased moisture. We suggest urban forest canopy closure is crucial in maintaining forest communities, as our results show canopy openness can drastically alter carabid community compositions.

Vegetation density

We did not find a direct correlation between native and nonnative stem density and specialist carabids but we did find direct, though different, correlations between native and nonnative ground cover and specialists. We suggest the negative influence of native ground cover on forest specialist diversity in Newark, compared to the positive influence on Raleigh forest specialist diversity, may be related to the higher proportion of natives in Newark's understory and indicate a negative influence of vegetation density on forest specialists. Our results suggest ground layer vegetation exhibits more direct influence than stem density on urban carabid communities, which may reflect a change in available prey or a change in predator and prey dynamics caused by vegetation structure (McCary et al. 2016, De Smedt et al. 2021). Magura et al. (2004) found carabid richness and forest specialists increased with greater abundance of potential prey items. However, arthropod populations, including prey species, are reduced by nonnative plant invasions (van Hengstum et al. 2014). Increased forest specialist and open area specialist diversity contributed to increased total carabid diversity in Raleigh, but only open area specialist capture contributed to increased total carabid capture. This suggests that forest and open area specialist richness is comparable between invaded and uninvaded urban forests, but that carabid abundance is not. Open area specialist diversity increased with greater nonnative ground cover in Raleigh but decreased with greater understory vegetation density in Newark. Omnivorous insects, like open area specialists, use resources based on availability and preference (Frank et al. 2010) and they respond to changes in host plants more than prey density (Eubanks & Denno 1999), which may contribute to altered proportions of omnivorous carabids in forests invaded by nonnative plants.

Leaf litter volume

We expected our results to be similar to Guillemain et al. (1997) who reported total carabid abundance and richness decreased with greater litter depth, while the proportion of forest specialists increased. However, our results differed. Greater total ground cover and dense understory vegetation decreased leaf litter volume in Newark, while only nonnative ground cover reduced leaf litter in Raleigh. Canopy openness in both cities indirectly reduced leaf litter volume by increasing nonnative ground cover. These results indicate that tree leaves contribute more to urban forest litter volume than the leaves of shrubs and ground cover (Trammell et al. 2012) and suggest dense shrubs may intercept tree leaves before they reach the forest floor. Leaf litter volume had a direct negative influence on open area specialist diversity in Raleigh and a direct positive influence on open area specialist diversity in Newark. This suggests either differences in leaf litter quality or composition, some minimum threshold of leaf litter volume that was not met, or different habitat requirements for open area species in these different cities. There is potential that our results could be detecting a response from carabids to leaf litter characteristics not fully represented by nonnative plant invasion. A plant with evergreen leaves differs from a deciduous plant in the amount, timing, and characteristics of litter fall. Raleigh forests had greater average leaf litter volume per point compared to Newark and contained needles from loblolly pine (*Pinus taeda*), a species common to Raleigh but not found in Newark (J. C. Mitchell, *unpublished data*). Nonnative plant species are frequently evergreen; however, they are typically not conifers, and the differing effects of evergreen leaf litter on forest specialist and open area specialist dynamics could be a driving factor in effects of leaf litter found in our urban forests.

Conclusions and management recommendations

We found evidence that nonnative plant density and diversity positively correlated with increased understory vegetation density, canopy openness, and reduced leaf litter volume in urban forests. We found partial support for our prediction that nonnative plants would reduce carabid abundance and increase carabid diversity, as open area specialist diversity increased with greater nonnative ground cover. Finally, we found evidence that forests specialists exist in urban forests but are more diverse without nonnative plants. Our results indicate that promoting native plant species in urban forests, by managing nonnative species invasion in the understory, generally increases forest specialist carabid abundance and diversity by maintaining habitat for forest specialist species. Additionally, our results demonstrate that a region's pool of plant species and carabid species are important factors determining the relationship between plant and carabid communities in urban forests. We sampled carabids during a period of 14 months; effort should be taken to conduct repeat studies over time to determine if, once invaded, the presence of nonnative plants perpetuates urban forest canopy openness by inhibiting native species and tree regeneration, and to determine whether long-term nonnative invasion corresponds with a shift in arthropod communities.

This research supports the importance of parsing out effects of ecosystem disturbances by taxa with different life history traits, rather than focusing on total species abundance, richness, or diversity. Our results suggest there may be a threshold of nonnative plant invasion, particularly of evergreen species, after which carabid communities transition from forest to open area specialists. This may depend on geographic location but is important for designing restoration efforts. To ensure the quality of urban forests for native forest species, we recommend urban managers survey urban forests for native plant populations and prioritize those areas for nonnative species removal. Preventative measures against nonnative plant invasions in urban forests should be taken nationally and abroad, and we advocate for increased resources for urban managers to reduce nonnative plant populations. Urban forests are reservoirs for native biota in increasingly altered temperate deciduous and mixed forest ecosystems (Ordóñez & Duinker 2012, Johnson & Handel 2016, Ramírez-Cruz et al. 2018). In many regions, urban forests persist while surrounding land is developed, and therefore, remain the most accessible ecosystem for forest specialist species in that area (Ordóñez & Duinker 2012, Melliger et al. 2018, de Andrade et al. 2019). Since carabids are good indicators of ecosystem change and quality, we can use these results as support for managing nonnative plant species in urban forests to improve ecosystem quality for other organisms.

ACKNOWLEDGEMENTS

With sincere thanks, and fond remembrance, to David L. Stephan for select carabid identification confirmation.

Thank you to the City of Raleigh, Town of Cary, North Carolina State University, US Forest Service, City of Newark, and University of Delaware for providing access to research sites. Thank you to Annemarie Nagle from the Frank Lab for providing logistical support and research supplies. Thank you to Lawrence Long, Michael Just, Kristi Backe, Sarah Parsons, Elsa Youngsteadt, Samantha Larsen, and Nora Lahr from the Frank Lab for advice regarding research design, statistical analyses, and more. Thank you to Catherine Crofton, Doua Jim Lor, Logan Tyson, Kyle Sozanski, Hannah Frank, and Maggie Hamilton from NCSU for providing field help measuring vegetation (often thorny) and lab help processing trap samples (always smelly). Thank you to R. David Mitchell for assisting during Newark carabid collections. Thank you to FRAME researchers Vince D'Amico and Tara Trammell for collaboration and access to FRAME sites and protocols. Thank you to Covel McDermot, Eric Moore, Carl Rosier, Zach Ladin, Matt McDermitt, Nathaly Rodriguez, and Andrew Adams from University of Delaware for providing field help measuring vegetation (also often thorny). Thank you to Matt Bertone for additional carabid identification assistance, Alexander Krings for additional plant identification assistance, and Bob Blinn for full access to the NCSU Insect Museum's carabid collection and microscope use. Thank you to the US Department of Agriculture and US Geological Survey for funding.

REFERENCES

Aerts, R. (1996). Nutrient resorption from senescing leaves of perennials: are there general patterns? *Journal of Ecology*, 84, 597-608.

Ariori, C., Aiello-Lammens, M. E., & Silander, J. A. (2017). Plant invasion along an urban-to-rural gradient in northeast Connecticut. *Journal of Urban Ecology*. https://doi.org/10.1093/jue/jux008

Aronson, M. F. J., Handel, S. N., & Clemants, S. E. (2007). Fruit type, life form and origin determine the success of woody plant invaders in an urban landscape. *Biological Invasions*, *9*(4), 465–475. https://doi.org/10.1007/s10530-006-9053-1

Aronson, M. F. J., Handel, S. N., La Puma, I. P., & Clemants, S. E. (2015). Urbanization promotes non-native woody species and diverse plant assemblages in the New York metropolitan region. *Urban Ecosystems*, *18*(1), 31–45. https://doi.org/10.1007/s11252-014-0382-z

Ashton, I. W., Hyatt, L. A., Howe, K. M., Gurevitch, J., & Lerdau, M. T. (2005). Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecological Applications*, 15(4), 1263-1272. https://doi.org/10.1890/04-0741.

Ballard, M., Hough-Goldstein, J., & Tallamy, D. (2013). Arthropod Communities on Native and Nonnative Early Successional Plants. *Environmental Entomology*. https://doi.org/10.1603/EN12315

Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., & Bradley, B. A. (2020). Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecology Letters*, Vol. 23, pp. 476–482. https://doi.org/10.1111/ele.13446

Bousquet, Y. (2010). *Illustrated identification guide to adults of larvae of northeastern North American ground beetles (Coleoptera: Carabidae).* Pensoft.

Bousquet, Y., & Webster, R. (2004). Review of the Nearctic species of the Holarctic subgenus Argutor (Coleoptera: Carabidae). *Canadian Entomologist*, Vol. 136, pp. 645–660. https://doi.org/10.4039/n04-030

Brose, U. (2003). Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation structure or plant diversity? *Oecologia*, *135*(3), 407–413. https://doi.org/10.1007/s00442-003-1222-7

Burton, J. I., Mladenoff, D. J., Forrester, J. A., & Clayton, M. K. (2014). Experimentally linking disturbance, resources and productivity to diversity in forest ground-layer plant communities. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.12319

Butterfield, J., & Coulson, J. C. (1983). The Carabid Communities on Peat and Upland Grasslands in Northern England. *Holarctic Ecology*, 6(2), 163–174. http://www.jstor.org/stable/3682330

Charbonneau, N. C., & Fahrig L. (2004). Influence of canopy cover and amount of open habitat in the surrounding landscape on proportion of alien plant species in forest sites. *Ecoscience*, 11(3), 278-281. Doi: 10.1080/11956860.2004.11682833

Chen, B., & Wise, D. H. (1999). Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology*, 80(3), 761-772. https://doi.org/10.2307/177015

Ciegler, J. C. (2000). *Ground Beetles and Wrinkled Bark Beetles of South Carolina: (Coleoptera: Geadephaga : Carabidae and Rhysodidae).* Clemson University.

Clark, M. S., Gage, S. H., & Spence, J. R. (1997). *Habitats and Management Associated with Common Ground Beetles (Coleoptera: Carabidae) in a Michigan Agricultural Landscape*. https://academic.oup.com/ee/article/26/3/519/418182

Collier, M. H., Vankat, J. L., & Hughes, M. R. (2002). Diminished Plant Richness and Abundance Below Lonicera maackii, an Invasive Shrub. *Am. Midl. Nat*, 147(1): 60-71.

Cornelissen, J. H. C., Lavorel S., Garnier, E. B., Diaz S., Buchmann, N., et al. (2003). Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51(4). DOI:10.1071/BT02124

Croci, S., Butet, A., Georges, A., Aguejdad, R., & Clergeau, P. (2008). Small urban woodlands as biodiversity conservation hot-spot: A multi-taxon approach. *Landscape Ecology*, *23*(10), 1171–1186. https://doi.org/10.1007/s10980-008-9257-0

Daniels, M. K., & Larson, E. R. (2020). Effects of forest windstorm disturbance on invasive plants in protected areas of southern Illinois, USA. *Journal of Ecology*, *108*(1), 199–211. https://doi.org/10.1111/1365-2745.13254

Davies, A. B., & Asner, G. P. (2014). Advances in animal ecology from 3D-LiDAR ecosystem mapping. *Trends in Ecology and Evolution*, Vol. 29, pp. 681–691. https://doi.org/10.1016/j.tree.2014.10.005

Davies, G. M., & Gray, A. (2015). Don't let spurious accusations of pseudoreplication limit our ability to learn from natural experiments (and other messy kinds of ecological monitoring). *Ecology and Evolution*, *5*(22), 5295–5304. https://doi.org/10.1002/ece3.1782

de Andrade, A. C., Dellefrate Franzini, L., & Mesquita, D. O. (2019). Assessing the effect of urbanization on tropical forest dwelling teiid lizards. *Ecological Indicators*. https://doi.org/10.1016/j.ecolind.2018.12.037

De Smedt, P., Boeraeve, P., & Baeten, L. (2021). Intra-annual activity patterns of terrestrial isopods are tempered in forest compared to open habitat. *Soil Biology and Biochemistry*, 108342. https://doi.org/10.1016/j.soilbio.2021.108342

Dirr, M. A. (2009). *Manual of Woody Landscape Plants: Their Identification, Ornamental Characteristics, Culture, Propogation and Uses*. Stipes Pub LLC, Revised edition.

Dyderski, M., & Jagodziński, A. (2019). Context-Dependence of Urban Forest Vegetation Invasion Level and Alien Species' Ecological Success. *Forests*. https://doi.org/10.3390/f10010026

Dyderski, M. K., & Jagodziński, A. M. (2020). Impact of invasive tree species on natural regeneration species composition, diversity, and density. *Forests*, *11*(4). https://doi.org/10.3390/F11040456

Ehrenfeld, J. G., Kourtev, P., & Huang, W. (2001). Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecological Application*, 11(5), 1287-1300. https://doi.org/10.1890/1051-0761(2001)011[1287:CISFFI]2.0.CO;2

Eubanks, M. D., & Denno, R. F. (1999). The ecological consequences of variation in plants and prey for an omnivorous insect. *Ecology*, 80(4), 1253-1266.

Ewers, R. M., & Didham, R. K. (2006). Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews of the Cambridge Philosophical Society*. https://doi.org/10.1017/S1464793105006949

Frank, S. D., Shrewsbury, P. M., & Denno, R. F. (2010). Effects of alternative food on cannibalism and herbivore suppression by carabid larvae. *Ecological Entomology*, *35*(1), 61–68. https://doi.org/10.1111/j.1365-2311.2009.01156.x

Gagné, S. A., & Fahrig, L. (2011). Do birds and beetles show similar responses to urbanization? *Ecological Applications*, 21(6), 2297-2312. doi: 10.1890/09-1905.1.

Gardner, S. M. (1991). Ground Beetle (Coleoptera: Carabidae) Communities on Upland Heath and Their Association with Heathland Flora. *Journal of Biogeography*, 18(3), 281-289.

Gleason H. A. & Cronquist A. (1991). *Manual of Vascular Plants of Northeastern United States and Adjacent Canada.* New York Botanical Garden Pr Dept.

Guillemain, M., Loreau, M., & Daufresne, T. (1997). Relationships beetween the regional distribution of carabid beetles (Coleoptera, Carabidae) and the abundance of their potential prey. *Acta Æcologica*, 18(4), 465-483.

James, G., Witten, D., Hastie, T., & Tibshirani, R. (2013). *An Introduction to Statistical Learning: with applications in R.* Springer.

Jennings, V. H., & Tallamy, D. W. (2006). Composition and Abundance of Ground-Dwelling Coleoptera in a Fragmented and Continuous Forest. *Environ. Entomology*, 35. https://academic.oup.com/ee/article/35/6/1550/390022

Johnson, L. R. & Handel, S. N. (2016). Restoration treatments in urban park forests drive long-termchanges in vegetation trajectories. Ecological Applications, 26(3), 940–956.

Jones, E. L., & Leather, S. R. (2012). Invertebrates in urban areas: A review. *European Journal of Entomology*, Vol. 109, pp. 463–478. https://doi.org/10.14411/eje.2012.060

Koivula, M. J. (2011). Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys*. https://doi.org/10.3897/zookeys.100.1533

Koivula, M., Kotze, D. J., Hiisivuori, L., & Rita, H. (2003). Pitfall trap efficiency: Do trap size, collecting fluid and vegetation structure matter? *Entomologica Fennica*, *14*(1), 1–14. https://doi.org/10.33338/ef.84167

Koivula, M., Punttila, P., Haila, Y., & Nicnielii Koivula Punltila P-, J. M. (1999). Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography*, 22(4), 424-435.

Kotze, D. J., & O'Hara, R. B. (2003). Species decline - But why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*. https://doi.org/10.1007/s00442-002-1174-3

Larochelle, A. & Larivière, M.-C. (2003). *A Natural History of the Ground-Beetles (Coleoptera: Carabidae) of American north of Mexico*. Pensoft.

Larsen, K. J., Work, T. T., & Purrington, F. F. (2003). Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa. *Pedobiologia*, 47. http://www.urbanfischer.de/journals/pedo

Latty, E. F., Werner, S. M., Mladenoff, D. J., Raffa, K. F., & Sickley, T. A. (2006). Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood-hemlock forests. *Forest Ecology and Management*. https://doi.org/10.1016/j.foreco.2005.10.028

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Lefcheck, J. S., & Duffy, J. E. (2015). Multitrophic functional diversity predicts ecosystem functioning in experimental assemblages of estuarine consumers. *Ecology*, 96. https://github.com/jslefche/rsquared.glmer

Lefcheck, J. S., Hughes, B. B., Johnson, A. J., Pfirrmann, B. W., Rasher, D. B., et al. (2019). Are coastal habitats inportant nuseries? A meta-analysis. *Conservation Letters*, 12(4).

Lehan, N. E., Murphy, J. R., Thorburn, L. P., & Bradley, B. A. (2013). Accidental introductions are an important source of invasive plants in the continental United States. *American Journal of Botany*, *100*(7), 1287–1293. https://doi.org/10.3732/ajb.1300061

Lengyel, S., Déri, E., & Magura, T. (2016). Species richness responses to structural or compositional habitat diversity between and within grassland patches: A multi-taxon approach. *PLoS ONE*, *11*(2). https://doi.org/10.1371/journal.pone.0149662

Luff, M. L. (1996). Use of carabids as environmental indicators in grasslands and cereals. *Ann. Zool. Fennici*, 33:185–195.

Lys, J.-A., & Nentwig, W. (1992). Augmentation of beneficial arthropods by strip-management. *Oecologia*, 92, 373-382.

Machin, H. N. (1967). Structural adaptation for reducing water-loss in three species of terrestrial snail. *J. Zool., Lond*, 152, 55-65.

Magura, T., Tóthmérész, B., & Molnár, T. (2004). Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology*. https://doi.org/10.1007/s10980-005-1128-4

Magura, Tibor, Lövei, G. L., & Tóthmérész, B. (2010). Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? *Global Ecology and Biogeography*, *19*(1), 16–26. https://doi.org/10.1111/j.1466-8238.2009.00499.x

Malkinson, D., Kopel, D., & Wittenberg, L. (2018). From rural-urban gradients to patch – matrix frameworks: Plant diversity patterns in urban landscapes. *Landscape and Urban Planning*, *169*, 260–268. https://doi.org/10.1016/j.landurbplan.2017.09.021

Martinson, H. M., & Raupp, M. J. (2013). A meta-analysis of the effects of urbanization on ground beetle communities. *Ecosphere*. https://doi.org/10.1890/ES12-00262.1

Mavimbela, L. Z., Sieben, E. J. J., & Procheş, Ş. (2018). Invasive alien plant species, fragmentation and scale effects on urban forest community composition in Durban, South Africa. *New Zealand Journal of Forestry Science*, 48(19). https://doi.org/10.1186/s40490-018-0124-8

Maynard-Bean, E., & Kaye, M. (2019). Invasive shrub removal benefits native plants in an eastern deciduous forest of North America. *Invasive Plant Science and Management*, *12*(1), 3–10. https://doi.org/10.1017/inp.2018.35

McCary, M. A., Mores, R., Farfan, M. A., & Wise, D. H. (2016). Invasive plants have different effects on trophic structure of green and brown food webs in terrestrial ecosystems: A meta-analysis. *Ecology Letters*, *19*(3), 328–335. https://doi.org/10.1111/ele.12562

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*(2), 161–176. https://doi.org/10.1007/s11252-007-0045-4

Melliger, R. L., Braschler, B., Rusterholz, H. P., & Baur, B. (2018). Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. *PLoS ONE*, *13*(6). https://doi.org/10.1371/journal.pone.0199245

Meyer, S., Rusterholz, H.-P., Salamon, J.-A., & Baur, B. (2019). Leaf litter decomposition and litter fauna in urban forests: Effect of the degree of urbanisation and forest size. *Pedobiologia*. https://doi.org/10.1016/j.pedobi.2019.150609

Miller, J. H. (2003). *Nonnative Invasive Plants of Southern Forests: a field guide for identification and control.* Forest Service Southern Research Station, General Technical Report SRS-62.

Müller, J., & Brandl, R. (2009). Assessing biodiversity by remote sensing in mountainous terrain: The potential of LiDAR to predict forest beetle assemblages. *Journal of Applied Ecology*, *46*(4), 897–905. https://doi.org/10.1111/j.1365-2664.2009.01677.x

Neter, J., Wasserman, W., & Kutner, M. H. (1983). *Applied Linear Regression Models.* Richard D. Irwin, INC.

Niemelä, J., Kotze, J., Ashworth, A., Brandmayr, P., Desender, K., … Spence, J. (2000). The search for common anthropogenic impacts on biodiversity: a global network. *Journal of Insect Conservation*, 4, 3-9.

Niemelä, J, Kotze, D. J., Venn, S., Penev, L., Stoyanov, I., Spence, J., … Montes De Oca, E. (2002). Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecology*, 17, 387-401.

Noonan, G. R. (1996). Classification, cladistics, and natural history of species of the subgenus Anisodactylus Dejean (Insecta: Coleoptera: Carabidae: Harpalini: Anisodactylus). 89,1-210.

Nowak, D. J., Crane, D. E., Stevens, J. C., Hoehn, R. E., Walton, J. T. et al. (2008). A Ground-Based Method of Assessing Urban Forest Structure and Ecosystem Services. *Arboriculture & Urban Forestry*, 34(6), 347-358.

Nudds, T. D. (1977). Quantifying the Vegetative Structure of Wildlife Cover. *Bulletin*, 5.

Nunez-Mir, G. C., Guo, Q., Rejmánek, M., Iannone, B. V., & Fei, S. (2019). Predicting invasiveness of exotic woody species using a traits-based framework. *Ecology*, *100*(10). https://doi.org/10.1002/ecy.2797

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., … Maintainer, H. W. (2020). *'vegan' Community Ecology Package Version 2.5-7.*

Ordóñez, C., & Duinker, P. N. (2012). Ecological integrity in urban forests. *Urban Ecosystems*, *15*(4), 863–877. https://doi.org/10.1007/s11252-012-0235-6

Oswalt, C. M., Oswalt, S. N., & Clatterbuck, W. K. (2007). Effects of Microstegium Vimineum (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *Forest Ecology and Management*, *242*(2–3), 727–732. https://doi.org/10.1016/j.foreco.2007.02.008

Piano, E., De Wolf, K., Bona, F., Bonte, D., Bowler, D. E., Isaia, M., … Hendrickx, F. (2017). Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Global Change Biology*, *23*(7), 2554–2564. https://doi.org/10.1111/gcb.13606

Pickett, S. T. A., & Cadenasso, M. L. (2009). Altered resources, disturbance, and heterogeneity: A framework for comparing urban and non-urban soils. *Urban Ecosystems*, *12*(1), 23–44. https://doi.org/10.1007/s11252-008-0047-x

Pickett, S. T. A., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V, Zipperer, W. C., & Costanza, R. (2001). Urban Ecological Systems: Linking Terrestrial Ecological, Physical, and Socioeconomic Components of Metropolitan Areas. *Annu. Rev. Ecol. Syst*., 16, 127-157.

Pilny, J. J., & Morgan, A. V. (1987). Paleoclimatic implications of a Late Wisconsinan insect assemblage from Rostock, southwestern Ontario. *Can. J. Earth Sci.* 24, 617-630.

Pinheiro, J., Bates, D., DebRoy, S., & Sarkar, D. R Core Team (2021). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-152, https://CRAN.R-project.org/package=nlme.

Pos, E. T., Guevara Andino, J. E., Sabatier, D., Molino, J. F., Pitman, N., Mogollón, H., … ter Steege, H. (2014). Are all species necessary to reveal ecologically important patterns? *Ecology and Evolution*, *4*(24), 4626–4636. https://doi.org/10.1002/ece3.1246

Pouyat, R. V., & Carreiro, M. M. (2003). Controls on mass loss and nitrogen dynamics of oak leaf litter along an urban-rural land-use gradient. *Oecologia*, *135*(2), 288–298. https://doi.org/10.1007/s00442-003-1190-y

Pouyat, R. V, Mcdonnell, M. J., & Pickett, S. T. A. (1997). Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land use gradient. *Urban Ecosystems*, 1, 117-131.

Prass, M., Vrezec, A., Setälä, H., & Kotze, D. J. (2017). The matrix affects carabid beetle assemblages in linear urban ruderal habitats. *Urban Ecosystems*, 20(5). https://doi.org/10.1007/s11252-017-0650-9

Pregitzer, C. C., Charlop-Powers, S., Bibbo, S., Forgione, H. M., Gunther, B., Hallett, R. A., & Bradford, M. A. (2019). A city-scale assessment reveals that native forest types and overstory species dominate New York City forests. *Ecological Applications*, *29*(1). https://doi.org/10.1002/eap.1819

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rainio, J., & Niemela, J. (2003). Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, 12, 487-506.

Ramírez-Cruz, G. A., Mendoza-Hernández, P. E., Solano-Zavaleta, I., & Zúñiga-Vega, J. J. (2018). How Widespread are Nonnative Species? Estimating Habitat Occupancy in an Ecological Reserve within a Megacity. *Natural Areas Journal*. https://doi.org/10.3375/043.038.0108

Reichard, S. H., & White, P. (2001). Articles Horticulture as a Pathway of Invasive Plant Introductions in the United States. *BioScience*, 51. https://academic.oup.com/bioscience/article/51/2/103/390610

Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, 82(4), 1112-1129.

Riley, K. N., & Browne, R. A. (2011). Changes in ground beetle diversity and community composition in age structured forests (Coleoptera, Carabidae). *ZooKeys*. https://doi.org/10.3897/zookeys.147.2102

Schank, J. C., & Koehnle, T. J. (2009). Pseudoreplication is a Pseudoproblem. *Journal of Comparative Psychology*, *123*(4), 421–433. https://doi.org/10.1037/a0013579

Spence, J. R., & Niemelä, J. (1994). Sampling carabid assemblages with pitfall traps: The madness and the method. *The Canadian Entomologist*, 126(3).

Spence, J. R., & Spence, D. H. (1988). Of ground-beetles and men: introduced species and the synanthropic fauna of western Canada. *Memoirs of the Entomological Society of Canada*. https://doi.org/10.4039/entm120144151-1

Steinberg, D. A., Pouyat, R. V., Parmelee, R. W., & Groffman, P. M. (1997). Earthworm abundance and nitrogen mineralization rates along an urban-rural land use gradient. *Soil Biology and Biochemistry*. https://doi.org/10.1016/S0038-0717(96)00043-0

Stenegren, M., Berg, C., Padilla, C. C., David, S. S., Montoya, J. P., Yager, P. L., & Foster, R. A. (2017). Piecewise Structural Equation Model (SEM) disentangles the environmental conditions favoring Diatom Diazotroph Associations (DDAs) in the Western Tropical North Atlantic (WTNA). *Frontiers in Microbiology*, 8. https://doi.org/10.3389/fmicb.2017.00810

Szlavecz, K., Placella, S. A., Pouyat, R. V., Groffman, P. M., Csuzdi, C., & Yesilonis, I. (2006). Invasive earthworm species and nitrogen cycling in remnant forest patches. *Applied Soil Ecology*. https://doi.org/10.1016/j.apsoil.2005.01.006

Templeton, L. K., Neel, M. C., Groffman, P. M., Cadenasso, M. L., & Sullivan, J. H. (2019). Changes in vegetation structure and composition of urban and rural forest patches in Baltimore from 1998 to 2015. *Forest Ecology and Management*, *454*. https://doi.org/10.1016/j.foreco.2019.117665

Trammell, T. L. E., & Carreiro, M. M. (2011). Vegetation composition and structure of woody plant communities along urban interstate corridors in Louisville, KY, U.S.A. *Urban Ecosystems*. https://doi.org/10.1007/s11252-011-0193-4

Trammell, T. L. E., Ralston, H. A., Scroggins, S. A., & Carreiro, M. M. (2012). Foliar production and decomposition rates in urban forests invaded by the exotic invasive shrub, Lonicera maackii. *Biological Invasions*. https://doi.org/10.1007/s10530-011-0093-9

Trammell, T. L. E., D'Amico, V., Avolio, M. L., Mitchell, J. C., & Moore, E. (2020). Temperate deciduous forests embedded across developed landscapes: younger forests harbor invasive plants and urban forests maintain native species. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.13400

Vallet, J., Daniel, H., Beaujouan, V., Rozé, F., & Pavoine, S. (2010). Using biological traits to assess how urbanization filters plant species of small woodlands. *Applied Vegetation Science*. https://doi.org/10.1111/j.1654-109X.2010.01087.x

van Hengstum, T., Hooftman, D. A. P., Oostermeijer, J. G. B., & van Tienderen, P. H. (2014). Impact of plant invasions on local arthropod communities: A meta-analysis. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.12176

Weakley, A. S. (2015). *Flora of the Southern and Mid-Atlantic States.* University of North Carolina Herbarium, UNC at Chapel Hill.

Ziter, C., Graves, R. A., & Turner, M. G. (2017). How do land-use legacies affect ecosystem services in United States cultural landscapes? *Landscape Ecology*. https://doi.org/10.1007/s10980-017-0545-4

Zou, Y., Sang, W., Wang, S., Warren-Thomas, E., Liu, Y., Yu, Z., … Axmacher, J. C. (2015). Diversity patterns of ground beetles and understory vegetation in mature, secondary, and plantation forest regions of temperate northern China. *Ecology and Evolution*, *5*(3), 531–542. https://doi.org/10.1002/ece3.1367

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. https://doi.org/10.1111/j.2041- 210x.2009.00001.x

TABLES AND FIGURES

Table 1.1. *Summary of urban forests and research site sizes. Sampled forests were flagged with a 25-m x 25-m grid, and a number of those points were chosen for sampling.*

City and Site	Forest size (ha)	Sampled forest size (ha)	Number of points	Number of sampling points
Raleigh, NC				
Achievement	2.7	2.7	41	10
Capability	1.3	1.3	24	10
Hymettus Woods	0.9	0.9	23	10
Kyle Drive	6.3	5.2	102	10
Lake Raleigh	40.0	8.2	152	10
Leesville	12.0	8.1	169	10
Marla Dorrel	8.7	1.6	31	10
Parnell	2.3	2.3	45	10
Rocky Branch	1.2	1.2	22	10
Schenck	77.0	10.1	152	10
University	5.8	2.0	34	10
Varsity	0.8	0.8	18	9
Newark, DE				
Christina Creek 2	12.0	8.3	120	10
Chrysler Woods	4.9	4.5	73	10
Dorothy Miller	51.0	4.2	69	10
Ecology Woods	16.2	16.2	156	10
Iron Hill 2	131.0	5.1	72	10
Motor Pool	5.1	5.1	87	10
Phillips	3.6	3.6	56	10
Reservoir	24.0	5.0	72	10
Rittenhouse	13.0	11.0	149	10
Sunset Lake 1	30.0	4.5	65	10
Webb Farm	10.0	8.7	129	10
White Clay 1	211.0	5.2	72	10

Table 1.2. *Summary of urban forest understory vegetation sampling.*

City	Ground Cover			Shrub Layer		
	Native	Nonnative	Total	Native	Nonnative	Total
Raleigh, NC summary (12 sites)						
Number of species	16	10	26	54	17	71
Number of counted stems				1101	1451	2552
Newark, DE summary (12 sites)						
Number of species	24	8	32	42	14	56
Number of counted stems				1574	1394	2968
Total summary (24 sites)						
Number of unique species	34	15	49	71	26	97
Number of counted stems				2675	2845	5520
Number of species shared between cities			9			30

Table 1.3. *Summary of all 24 sites; ground cover and shrub layer species and plant origin.*

Ground cover plant species	Plant origin	Shrub layer plant species	Plant origin
Acer rubrum	native	*Acer floridanum*	native
Albizia julibrissin	nonnative	*Acer negundo*	native
Alliaria petiolata	nonnative	*Acer platanoides*	nonnative
Arctium lappa	nonnative	*Acer rubrum*	native
Arundinaria sp.	native	*Aesculus parviflora*	native
Bignonia capreolata	native	*Alliaria petiolata*	nonnative
Boehmeria sp.	native	*Ampelopsis brevipedunculata*	nonnative
Carya ovata	native	*Amphicarpaea bracteata*	native
Celastrus orbiculatus	nonnative	*Apocynum cannabinum*	native
Clethra alnifolia	native	*Aralia spinosa*	native
Cornus florida	native	*Arundinaria gigantea*	native
Elaeagnus umbellata	nonnative	*Arundinaria tecta*	native
Eremochloa sp.	nonnative	*Aster sp.*	native
Eurybia divaricata	native	*Bignonia capreolata*	native
Glechoma hederacea	nonnative	*Boehmeria sp.*	native
Hedera helix	nonnative	*Campsis radicans*	native
Kalmia latifolia	native	*Carpinus caroliniana*	native
Ligustrum sinense	nonnative	*Carya glabra*	native
Lindera benzoin	native	*Carya tomentosa*	native
Liquidambar styraciflua	native	*Celastrus orbiculatus*	nonnative
Lonicera japonica	nonnative	*Celtis occidentalis*	native

Table 1.3 *(continued).*

Malus sp.	native	*Clematis terniflora*	nonnative
Microstegium vimineum	nonnative	*Clethra alnifolia*	native
Nyssa sylvatica	native	*Cornus florida*	native
Onoclea sensibilis	native	*Crataegus sp.*	native
Parthenocissus quinquefolia	native	*Diospyros virginiana*	native
Pinus taeda	native	*Elaeagnus pungens*	nonnative
Podophyllum peltatum	native	*Elaeagnus umbellata*	nonnative
Polystichum acrostichoides	native	*Euonymus alatus*	nonnative
Prunus serotina	native	*Euonymus americanus*	native
Quercus alba	native	*Eupatorium leptophyllum*	native
Quercus falcata	native	*Fagus grandifolia*	native
Quercus montana	native	*Fallopia japonica*	nonnative
Quercus phellos	native	*Fraxinus americana*	native
Rosa multiflora	nonnative	*Fraxinus pennsylvanica*	native
Rubus sp.	native	*Hamamelis vernalis*	native
Sanguinaria canadensis	native	*Hedera helix*	nonnative
Smilacina racemosa	native	*Hibiscus syriacus*	nonnative
Smilax rotundifolia	native	*Ilex glabra*	native
Symplocarpus foetidus	native	*Ilex opaca*	native
Thelypteris noveboracensis	native	*Ilex verticillata*	native
Toxicodendron radicans	native	*Impatiens capensis*	native
Viburnum acerifolium	native	*Juglans nigra*	native
Viburnum dentatum	native	*Juniperus virginiana*	native
Vinca sp.	nonnative	*Kalmia latifolia*	native
Vitis rotundifolia	native	*Lespedeza cuneata*	nonnative
Vitis sp.	native	*Ligustrum japonicum*	nonnative
Wisteria sinensis	nonnative	*Ligustrum sinense*	nonnative
		Ligustrum vulgare	nonnative
		Lindera benzoin	native
		Liquidambar styraciflua	native
		Liriodendron tulipifera	native
		Lonicera japonica	nonnative
		Lonicera maackii	nonnative
		Magnolia grandiflora	native
		Mahonia sp.	nonnative
		Malus sp.	native
		Microstegium vimineum	nonnative
		Morella cerifera	native
		Morus alba	nonnative
		Nyssa sylvatica	native

Table 1.3 *(continued).*

Ostrya virginiana	native
Oxydendrum arboreum	native
Parthenocissus quinquefolia	native
Phytolacca americana	native
Pinus taeda	native
Pinus virginiana	native
Pistacia chinensis	nonnative
Prunus caroliniana	native
Prunus serotina	native
Prunus sp.	native
Pueraria montana	nonnative
Pyrus calleryana	nonnative
Quercus alba	native
Quercus bicolor	native
Quercus falcata	native
Quercus nigra	native
Quercus phellos	native
Quercus rubra	native
Quercus stellata	native
Rosa multiflora	nonnative
Rubus occidentalis	native
Rubus phoenicolasius	nonnative
Rubus sp.	native
Sassafras albidum	native
Smilax rotundifolia	native
Solidago caesia	native
Toxicodendron radicans	native
Ulmus alata	native
Vaccinium arboreum	native
Vaccinium corymbosum	native
Viburnum acerifolium	native
Viburnum dentatum	native
Viburnum prunifolium	native
Vitis rotundifolia	native
Vitis sp.	native
Wisteria sinensis	nonnative

Table 1.4. *Summary of urban forest carabid beetle sampling.*

City	**Carabids**			
	Species	Individuals	% of total caught	Singletons
Raleigh, NC summary (12 sites)	29	477		4
Top three species captured:			74.4	
1. *Cyclotrachelus unicolor*		263	55.1	
2. *Pterostichus sculptus*		52	10.9	
3. *Galerita bicolor*		40	8.4	
Forest specialists	6	29	6.1	1
Open area specialists	14	319	66.9	3
Generalists	7	110	23.1	0
Newark, DE summary (12 sites)	48	1387		7
Top three species captured:			62.9	
1. *Chlaenius aestivus*		521	37.6	
2. *Pterostichus stygicus*		179	12.9	
3. *Carabus goryi*		172	12.4	
Forest specialists	14	356	25.7	2
Open area specialists	15	171	12.3	4
Generalists	11	307	22.1	1
Total summary (24 sites)	57	1864		11
Number of species shared between cities	19			
Forest specialists	16	385	20.7	3
Open area specialists	22	490	26.3	7
Generalists	12	417	22.4	1

Table 1.5. *Summary of common understory plant species and characteristics in each city.*

City	Ground Cover			Shrub Layer			
	Species	Plant origin	Growth habit	Species	Plant origin	Total % of stems	Growth habit
Raleigh, NC: most common species							
1	*Microstegium vimineum*	nonnative	low-growing grass	*Ligustrum sinense*	nonnative	14.9	shrub
2	*Hedera helix*	nonnative	vining	*Lonicera japonica*	nonnative	14.6	vining
3	*Vitis rotundifolia*	native	vining	*Vitis rotundifolia*	native	12.2	vining
4	*Vinca sp.*	nonnative	vining	*Smilax rotundifolia*	native	10.5	vining
Newark, DE: most common species							
1	*Rosa multiflora*	nonnative	shrub	*Rosa multiflora*	nonnative	20.6	shrub
2	*Thelypteris noveboracensis*	native	low-growing fern	*Lonicera japonica*	nonnative	15.6	vining
3	*Toxicodendron radicans*	native	vining	*Lindera benzoin*	native	12.9	shrub
4	*Clethra alnifolia*	native	shrub	*Viburnum dentatum*	native	9.6	shrub

Figure 1.1. *Maps of (a) the east coast showing the location of Raleigh and Newark, (b) a close up of Raleigh showing roads, in white, and location of sampled forests, in red, and (c) a close up of Newark showing roads, in white, and location of sampled forests, in red.*

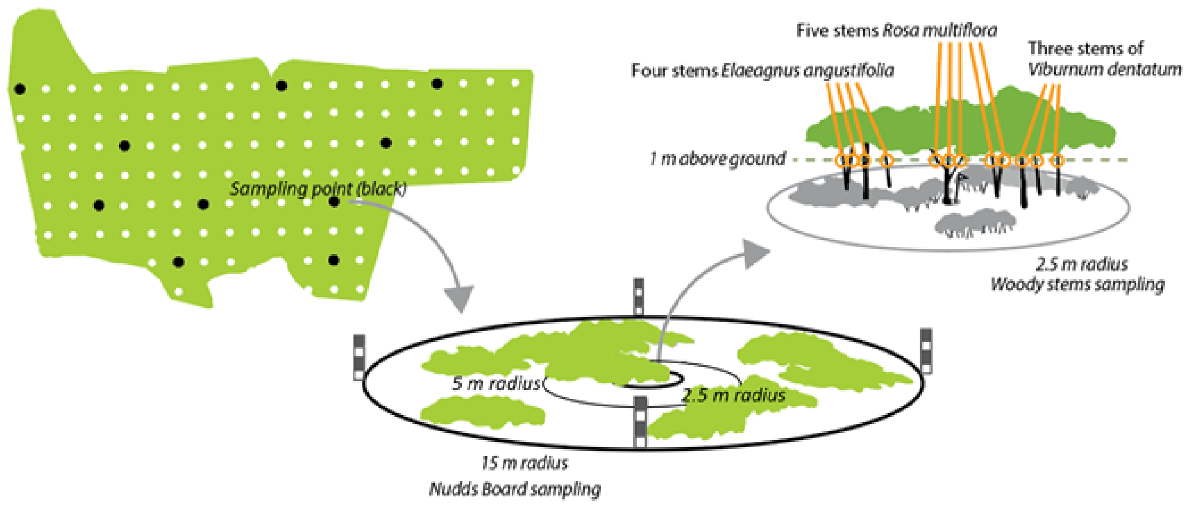


Figure 1.2. *Diagram of forest site set up and vegetation sampling protocol. White points within the sampled forest represent the 25-m x 25-m grid and black points represent sampling points. At each sampling point, vegetation is measured at varying radii: understory density at 15 m, canopy openness at 5 m, and ground cover and stem density at 2.5 m. Image adapted from V. D'Amico.*

Figure 1.3. *The size and placement of the Nudds board is the same within each extreme example of (a) low-density and (b) high-density understory vegetation in two urban forests in Raleigh, NC and (c) low-density and (d) high-density understory vegetation in two urban forests in Newark, DE. Photo credits: J. Christina Mitchell.*

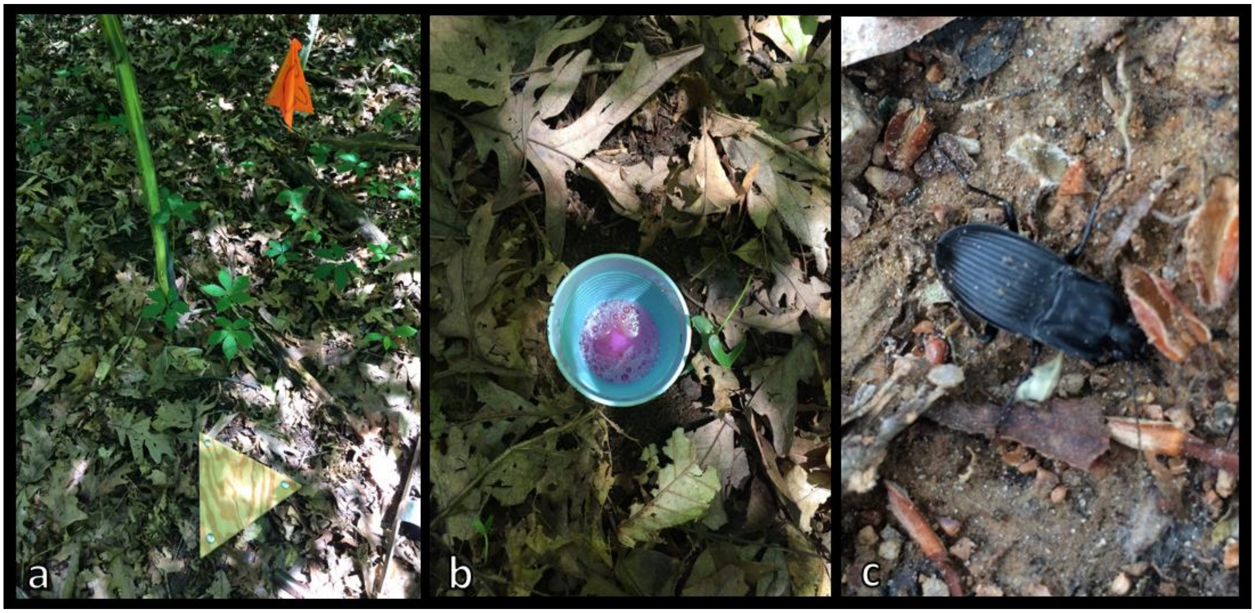


Figure 1.4. A *(a) pitfall trap covered with a plywood triangle and set up next to a sampling point with a (b) plastic cup containing pitfall sampling preservative, and (c) a carabid, Dicaelus sp., moving along the forest floor. Photo credits: J. Christina Mitchell.*

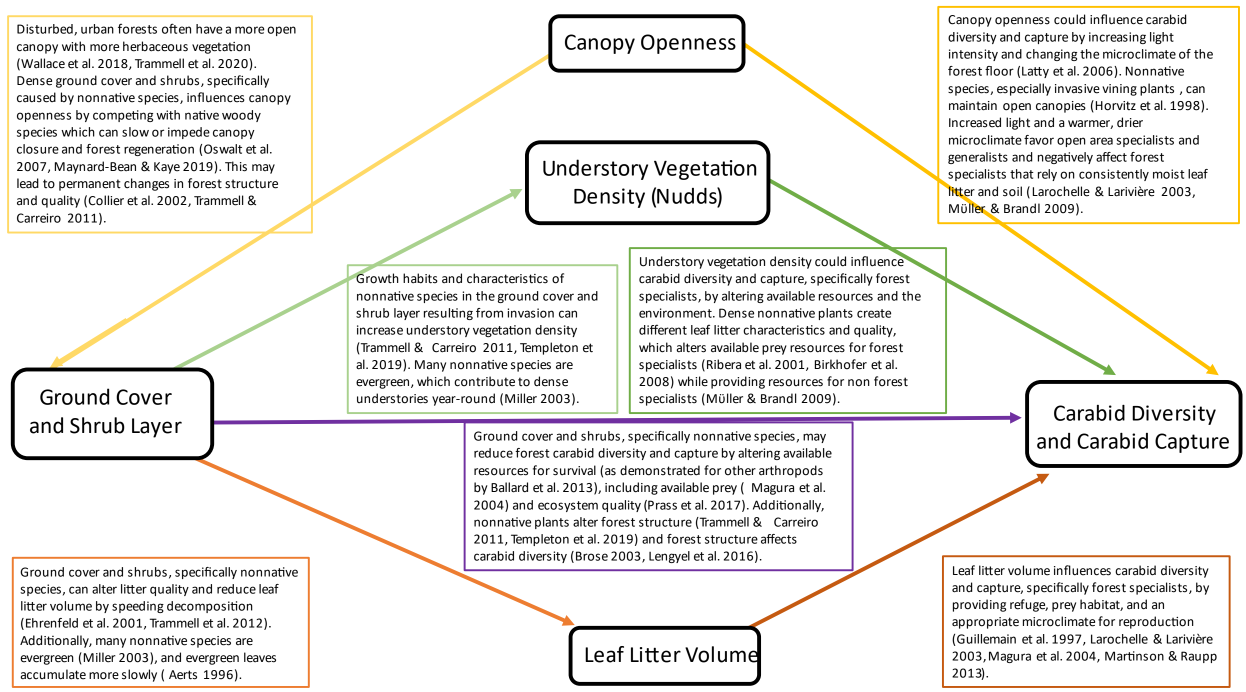


Figure 1.5. *Logic model outlining a-priori hypotheses for structural equation models. Boxes are color-coded and detail hypothesized relationships between variables and describe possible direct and indirect effects on vegetation and carabids.*

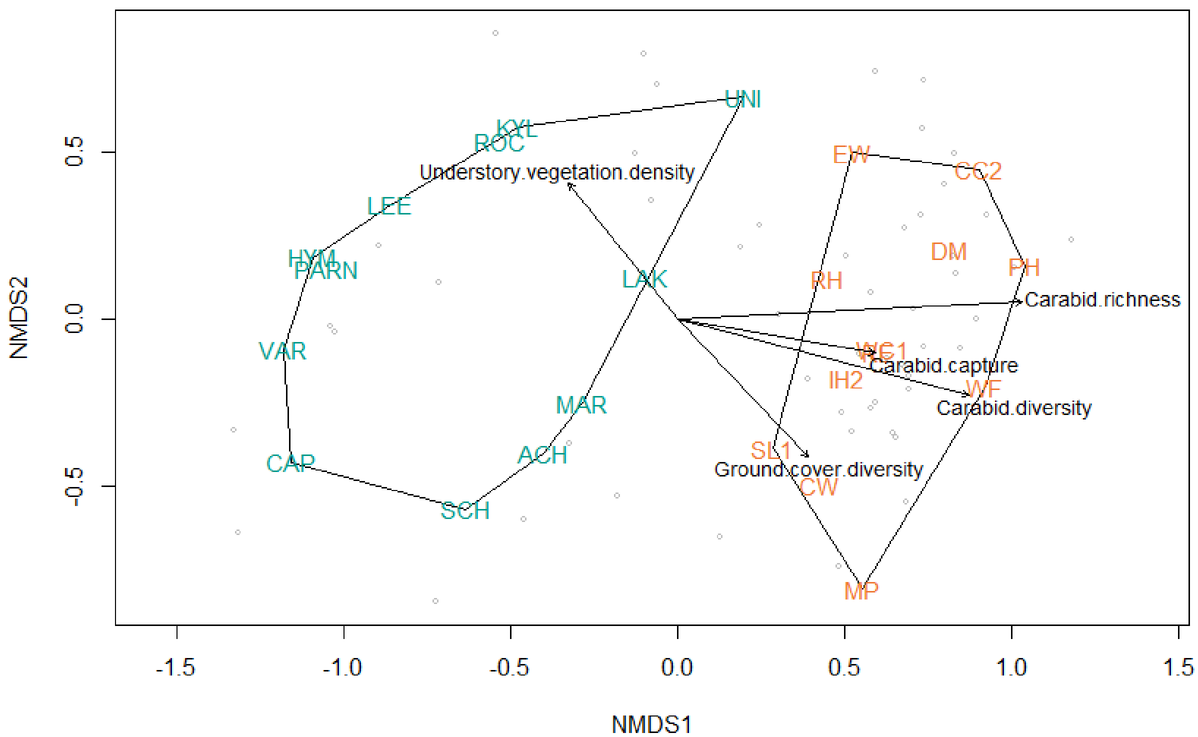


Figure 1.6. *Nonmetric multidimensional scaling ordination showing the similarity of carabid communities in different urban forests, with a final stress value of 0.15. Gray circles represent the position of each carabid species in ordination space. Raleigh, NC sites are labeled in teal and Newark, DE sites are labeled in orange. Black arrows indicate vectors associated with included variables, at α = 0.15 to suggest possible trends, and represent the strength, indicated by length, and direction of maximum change of variables through the ordination field.*

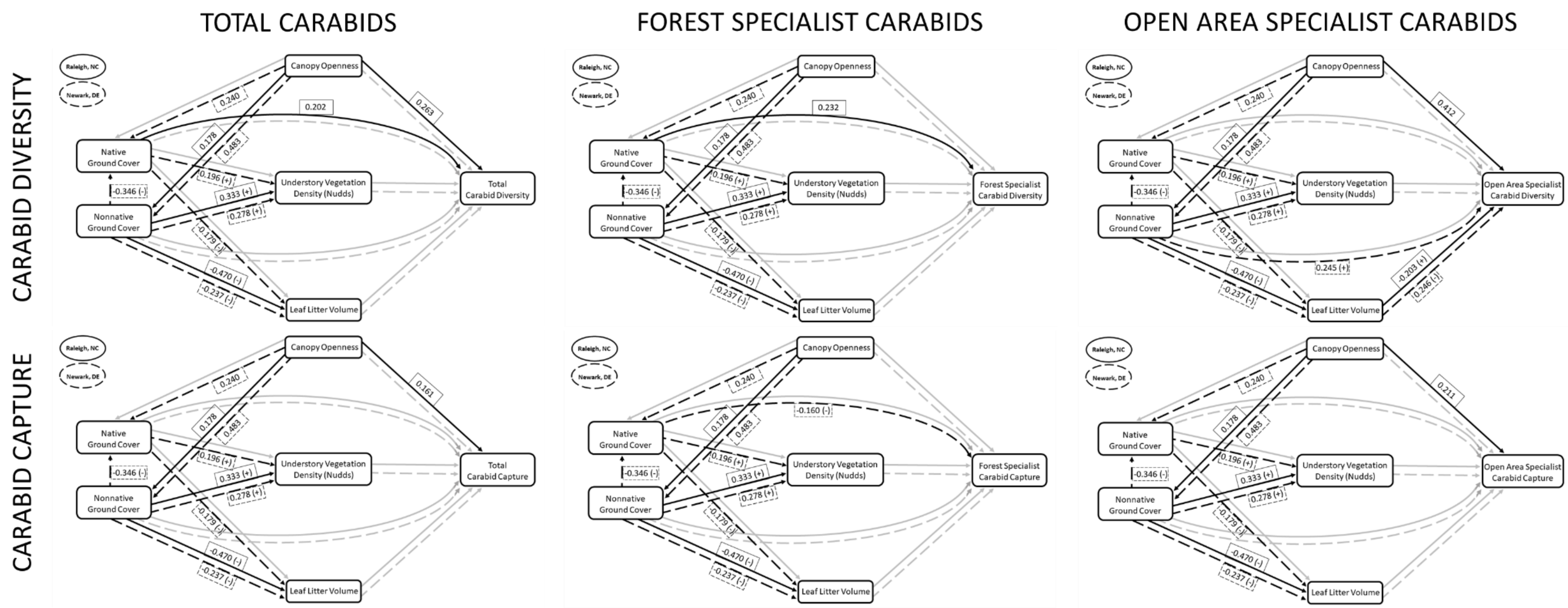


Figure 1.7. *Results of ground cover SEM models. Raleigh results are represented by solid lines and Newark results are represented by dashed lines. Significant results are shown in black and nonsignificant results are in gray. Significant numerical values correspond to each line. For clarity, numbers associated with non-significant relationships are not included. For interpretation of indirect effects, signs (+/-) are included in parentheses.*

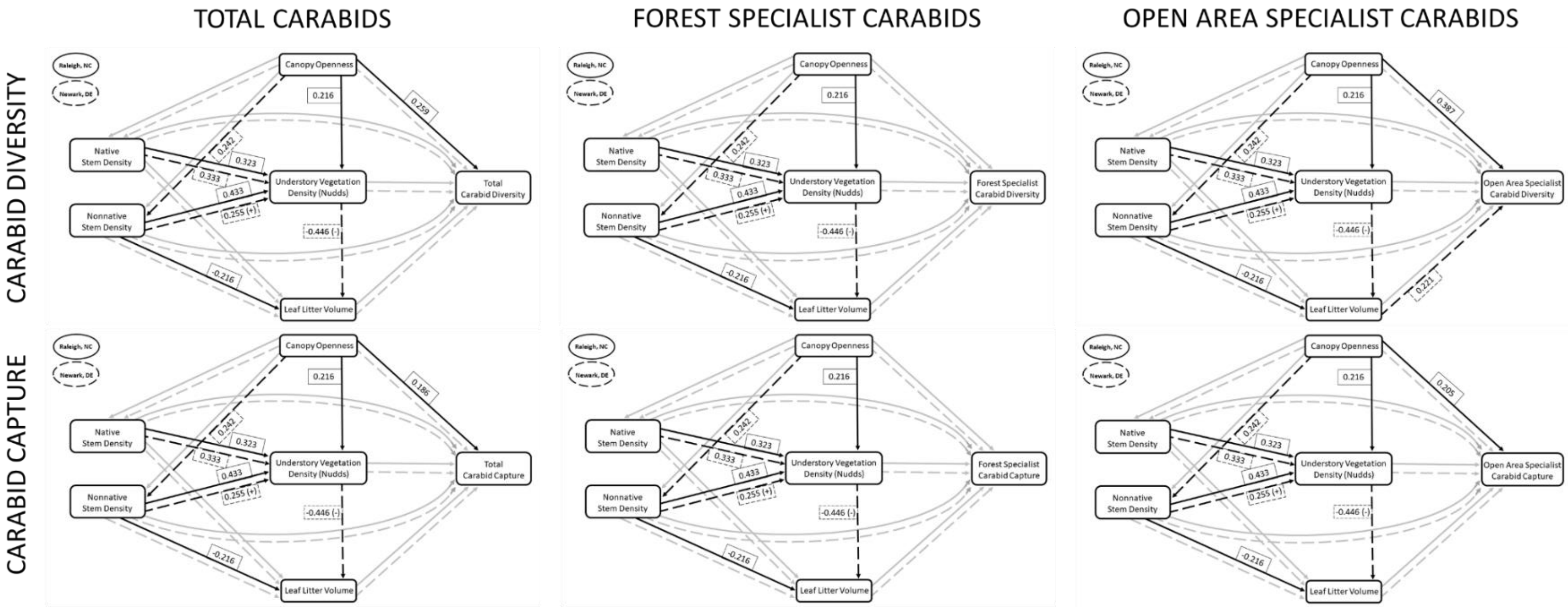


Figure 1.8. *Results of stem density SEM models. Raleigh results are represented by solid lines and Newark results are represented by dashed lines. Significant results are shown in black and nonsignificant results are in gray. Significant numerical values correspond to each line. For clarity, numbers associated with non-significant relationships are not included. For interpretation of indirect effects, signs (+/-) are included in parentheses.*

CHAPTER 2

Forest characteristics have more influence than urbanization on urban forest carabid communities

ABSTRACT

Urban forests are important native species' habitat and face degradation by urban development, urban heat island effects, and nonnative species invasions. These external and internal factors affect the quality of urban forests for native forest-associated species and alter biotic community compositions. Disturbance and other urban conditions typically favor open area specialist species and generalist species, frequent urban adaptors, over forest-associated and forest specialized species that require more forest-specific conditions. We investigated the effects of external factors, forest size and surrounding impervious surface, and internal factors, canopy openness, understory vegetation density, ground cover vegetation, and leaf litter, on urban forest carabid community composition. Carabid beetle (Coleoptera: Carabidae) communities change in response to altered abiotic and biotic conditions, including the warmer, drier microclimates and increased nonnative plant invasions commonly found in urban forests. We sampled carabid communities in 24 urban forests located in two cities, Raleigh, NC and Newark, DE, to understand how external and internal forest factors affect two types of carabids, forest specialist species and open area specialist species, and whether these relationships are consistent in different regions. We predicted urban forest carabid communities would be primarily influenced by forest size, and that internal forest characteristics would be more important drivers of community composition than surrounding impervious surface. We found carabid capture and diversity increased with forest size, and Raleigh carabids were more affected by internal forest

characteristics, while Newark carabids were more affected by external impervious surface. Our results show that while carabid capture and diversity increase with forest size, small urban forests had comparable forest specialist capture and diversity to large urban forests. We recommend the conservation of any urban forest with sufficient canopy cover and region-specific management of understory vegetation to promote native canopy regeneration.

INTRODUCTION

Forests in and around cities provide crucial habitat for native species (Fujita et al. 2008, Ordóñez & Duinker 2012, Ramírez-Cruz et al. 2018, Melliger et al. 2018, de Andrade et al. 2019, Fidino et al. 2020). Urban forests are subjected to fragmentation, regeneration, urban heat island effects, invasive species, and other disturbances (Deichsel 2006, Beninde et al. 2015, Concepción et al. 2016, Borges et al. 2020). Urban forests also tend to be smaller than rural forests and shrink further as cities expand (United Nations 2018, Huang et al. 2019, V. D'Amico, S. Frank, T.L.E. Trammell, & J. Henning, *unpublished data*). These external and internal factors affect the ability of urban forests to provide habitat for forest-associated wildlife species, including arthropods, by changing urban forest resources, structure, and microclimate (Deichsel 2006, Aronson et al. 2014, van Hengstum et al. 2014, Aronson et al. 2016, Dale & Frank 2018, Long et al. 2018, Melliger et al. 2018, Landsman et al. 2019, Amburgey et al. 2020, Long & Frank 2020). Disturbance and environmental changes associated with urbanization typically favor open area specialist species and generalist species, frequent urban adaptors, over forest-associated and forest specialized species that require more forest-specific conditions (Ribera et al. 2001, McKinney 2002, Deichsel 2006, Fujita et al. 2008, Jones & Leather 2012, Concepción et al. 2016, Fournier et al. 2020, Adams et al. 2020). However, urban forests still have conservation value. Understanding the influence of external urban characteristics, such as impervious surface, and internal forest characteristics, such as invasive plants and leaf litter, on forest biodiversity will help managers predict forest quality for different taxa and guide restoration.

Carabid beetles (Coleoptera: Carabidae) are abundant, taxonomically and ecologically diverse, and their community composition changes in response to abiotic and biotic conditions (Niemelä et al. 2002, Rainio & Niemelä 2003, Magura et al. 2004, Koivula 2011). Differences between carabid communities have been studied in rural and urban forests, but in many cases the specific drivers of community change are not well characterized. Forest specialists require moist, dense, litter comprised of leaves, coarse woody debris, and other organic matter for egg and larval survival, overwintering shelter, and prey (Larochelle & Larivière 2003, Latty et al. 2006, Martinson & Raupp 2013). Forest specialists tend to be less abundant and diverse in forests that are small, disturbed, or both (Alaruikka et al. 2002, Niemelä et al. 2002, Venn et al. 2003). Small forests have greater edge to interior ratios which enables heat (Ren et al. 2013) and invasive plants (Cadenasso & Pickett 2001, Yates et al. 2004, Vallet et al. 2010) to permeate farther in the forest interior and reduces forest quality for forest specialists (Venn et al. 2003, Magura et al. 2004, Sadler et al. 2006, McCary et al. 2018). Forest specialists also tend to be less abundant and diverse in forests surrounded by a large amount of impervious surface (Sadler et al. 2006, Croci et al. 2008), which can increase forest temperature due to the urban heat island effect (McDonnell et al. 2008) and reduce forest specialist dispersal and recruitment (Sadler et al. 2006, Croci et al. 2008).

Carabids and other arthropods can also be less abundant and diverse in areas with dense vegetation (Larsen et al. 2003, Croci et al. 2008), particularly that caused by nonnative plant invasion (van Hengstum et al. 2014, Mitchell Chapter 1), as it impedes locomotion (Lys & Nentwig 1992, Larsen et al. 2003, Croci et al. 2008), changes litter accumulation dynamics (Ashton et al. 2005, Trammell et al. 2012, Wallace et al. 2018) and can inhibit canopy regeneration and alter forest structure (Meiners 2007, Oswalt et al. 2007, Langmaier & Lapin 2020). Urban forests can have warmer and drier litter and soil layers (Pouyat et al. 1997) and urban and nonnative forest litter can have less nutrients for soil communities (Pouyat & Carreiro 2003, McCary et al. 2015) and decompose faster than rural forest litter (Pouyat et al. 1997, Pouyat & Carreiro 2003, Meyer et al. 2019), altering forest conditions and providing less habitat for forest specialists (Koivula et al. 1999, Venn et al. 2003). These changes in urban forest litter and soil conditions affect arthropod prey communities (McCary et al. 2018, De Smedt et al. 2021), which in turn alters the proportion of predators, a frequent trait of forest specialists, in carabid communities (Birkhofer et al. 2008, Vele et al. 2011, Jones & Leather 2012).

Open area specialists and generalists tolerate a wider range of light and temperature conditions (Larsen et al. 2003, Jennings & Tallamy 2006, Martinson & Raupp 2013) than forest specialists. Open area specialists require at least partial absence of canopy cover and their presence in urban forests may indicate a shift in forest structure, while generalists are found in forests and non-forests. These two categories of carabids are common in agriculture fields, forest edges, managed yards, and vacant lots (Larochelle & Larivière 2003, Bousquet 2010). Open area specialists are adapted to the warmer, drier microclimate (Halme & Niemelä 1993, Ribera et al. 2001, Magura et al. 2004) found in urban forests that are small (Halme & Niemelä 1993, Ren et al. 2013), surrounded by imperious surface (McDonnell et al. 2008), and have disturbed canopies (Perry & Herms 2019). Urban forests are typically more disturbed than rural forests, and often have a more open canopy and more herbaceous vegetation (Wallace et al. 2018, Trammell et al.

2020), which provide microclimates and food resources needed by open area specialists (Halme & Niemelä 1993, Magura et al. 2004, Martinson & Raupp 2013). We predict that the internal forest changes to vegetation and litter characteristics caused by urbanization and nonnative plant invasion alter forest structure and promote greater abundance and diversity of open area specialist species, thereby providing one mechanism for carabid community change in urban forests.

Large forests within cities can support biodiversity (Miller & Hobbs 2002, Puppim de Oliveira et al. 2011) and ecosystem functions that are diminished in small, disturbed, and fragmented forests (McKinney 2002, Alberti 2005). We predict that urban carabid communities will be influenced primarily by forest size because forest specialist species require forest habitat, but open area specialist species benefit from canopy disturbance and edge effects. Second, we predict that internal forest characteristics will influence carabid communities more than external impervious surface because vegetation communities and litter characteristics directly influence carabid activity and survival by providing the appropriate microclimate and organic material necessary for food and reproduction (Thiele 1977, Halme & Niemelä 1993, Brose 2003, Rainio & Niemelä 2003), while impervious surface indirectly influences carabids (Sadler et al. 2006, Croci et al. 2008). Specifically, we predict that different compositions of urban carabid communities will be driven by the exchange of forest and open area specialist species, as forest specialists are replaced by open area specialists in disturbed urban forests. Additionally, we predict that relationships between large-scale external factors, small-scale internal factors, and carabid community composition will be similar in urban forests in different cities. To test our hypotheses we quantified forest size, percent surrounding impervious surface within 100m and 1000m buffers, vegetation characteristics, and carabid communities in 24 urban forests that varied in size and amount of urbanization. We conducted this experiment in Raleigh, North Carolina and Newark, Delaware to determine whether urban carabid communities in different regions respond similarly to large-scale external and small-scale internal factors. If we understand how urban carabid communities are affected by forest size, surrounding impervious surfaces, and plant community characteristics, we can develop management methods that preserve and improve forest ecosystems for urban arthropod communities.

METHODS

Site selection and site characteristics

We sampled urban forests in two eastern USA cities to determine if relationships between external forest characteristics, internal forest characteristics, and carabid communities were similar in different regions. This research was conducted in Raleigh, North Carolina (35.780˚N, 78.642˚W) and Newark, Delaware (39.683˚N, 75.753˚W). These cities are part of the FRAME (FoRests Among Managed Ecosystems, https://sites.udel.edu/frame/) network of forests used to study urban forest ecology. In 2019, Raleigh, NC was 370.1 km^2 with a population of 474,069 and Newark, DE was 23.8 km^2 with a population of 33,515 (https://www.census.gov/quickfacts/fact/table/raleighcitynorthcarolina,newarkcitydelaware/PST045219).

Sampling of external characteristics

To measure forest patch size and amount of circumjacent impervious surface, we used ArcMap 10.6.1 (ESRI, Redlands, CA, USA). We created 24 forest polygons to represent each forest patch containing the sampled area and calculated total area in hectares. We then created a 100 m buffer and 1000 m buffer extending out from each forest polygon (Figure 2.1). We clipped the National Land Cover Dataset (NLCD) 2016 Percent Developed Imperviousness (CONUS) raster file to the extent of each buffer (N = 48; Wickham et al. 2021). We used attribute table data for each buffer to calculate the total percentage of impervious surface within each buffer. For each buffer we multiplied value, the percent of impervious cover in each 30m x 30m pixel, by count, the number of pixels for each percentage of impervious cover, and summed these values. We divided this value by total count, the total number of pixels in a buffer, which gave the total percent of impervious surface for each buffer.

Sampling of internal characteristics

Details of forest vegetation and carabid sampling are described elsewhere (Mitchell Chapter 1). We followed the FRAME protocol (Trammell et al. 2020) to sample 24 forest patches, 12 in each city. Each forest contained 10 sampling locations, except for one Raleigh forest that only accommodated nine, for a total of 239 sampling locations. Vegetation communities were quantified for each forest by sampling leaf litter volume, percent cover of ground vegetation, density of understory vegetation, and amount of canopy openness at each sampling location. Vegetation communities were sampled in Raleigh in 2017 and in Newark in 2015. Carabids were captured at each sampling location using pitfall traps activated for two weeks at a time and eight sampling events occurred between 2017 to 2018. To understand carabid community change based on species' habitat specialization, we determined whether each species was a forest specialist or an open area specialist using species-specific life history trait literature (Noonan 1996, Larochelle & Larivière 2003, Bousquet & Webster 2004, Bousquet 2010).

Statistical analyses

All subsequent analyses were conducted in R version 4.0.5 (R Core Team, 2021). We calculated external forest factors and carabid diversity for each site, and summarized site totals for carabid capture and site averages for canopy openness, understory density, ground cover, and leaf litter. We used the glm function from the ‘stats’ package to create models appropriate for our small sample size count data and used carabid capture and carabid diversity (Shannon index) as the response variables. For carabid capture models, we first log (x + 1) transformed the response variable to improve the distribution of residuals and correct for effects of zeros (Zuur et al. 2009, Zuur et al. 2010, Ives 2015). We did not transform models with carabid diversity as the response variable. To address the question of whether carabid specialists drive community change in urban forests, we created models with total carabid capture and diversity, forest specialist carabid capture and diversity, and open area specialist carabid capture and diversity as the response variables. To address the question of whether urban carabid communities respond similarly in different cities, we created models for all forests combined, Raleigh forests only, and Newark forests only. We then created full models (N=18) for each response variable and our seven predictor variables: forest area, impervious surface within 100 m buffer, impervious surface within 1000 m buffer, leaf litter, ground cover, understory vegetation density, and canopy openness. We used the stepAIC function in the package MASS (Venables & Ripley 2002) to iteratively remove the variable with the highest AIC, calculated in either direction, and retest the model until left with the best model with lowest AIC. We confirmed the appropriateness of each final model using summary statistics and residual plots. To adjust for our small sample size (N = 24; Burnham & Anderson 2002), we calculated AICcs for each model using the AICc function in the package MuMIn (Barton 2020).

RESULTS

All forests combined

In all forests combined, forest size and internal forest conditions contributed to more parsimonious models of influence on carabid community metrics, compared to surrounding impervious surface (Table 2.1). Generally, total carabid capture and diversity increased as forest size increased. Total carabid capture and diversity decreased as leaf litter, ground cover, and understory vegetation density increased. Forest specialist capture and diversity increased as forest size increased and decreased as leaf litter increased. Additionally, forest specialist capture and diversity declined as understory vegetation density increased, a condition often associated with nonnative plant invasion (Templeton et al. 2019, Dyderski & Jagodziński 2020). Surrounding impervious surface had little significant effect on carabid communities, except at a large scale where it increased open area specialist diversity. Open area specialist capture decreased as ground cover increased, and open area specialist diversity decreased as leaf litter increased. Though not significant, open area specialist capture had a positive response to increased canopy openness. Overall, these results indicate that carabid capture and diversity are greater in large forests whereas carabid capture and diversity are lower in forests with dense understory and ground vegetation.

Raleigh forests

In Raleigh forests, forest specialist diversity increased as forest size increased. Total carabid and forest specialist capture decreased as percent impervious surface within 100m increased. Total carabid capture, forest specialist capture, and open area specialist capture declined as total ground cover increased. Total carabid capture and diversity, forest specialist capture and diversity, and open area specialist diversity declined as leaf litter increased. Open area specialist diversity increased as canopy openness increased. Though not significant, total carabid capture and diversity and forest specialist capture had a positive response to increased percent impervious surface within 1000m.

Newark forests

In Newark forests, open area specialist capture increased as forest size increased. Total carabid diversity decreased and open area specialist capture increased as percent impervious surface within 100m increased. Total carabid and open area specialist diversity increased and forest specialist capture decreased as percent impervious surface within 1000m increased. Total carabid diversity increased as total ground cover increased. Total carabid diversity and forest specialist capture increased as leaf litter increased. Though not significant, forest specialist capture had a negative response, while open area specialist capture had a positive response to increased canopy openness. Additionally, forest specialist diversity had a negative response to increased understory density.

DISCUSSION

Our results indicate that forest size is critical for maintaining carabid abundance and diversity in urban forests across cities, especially for forest specialists, which are indicators of forest ecosystem health and quality (Koivula 2011, Riley & Browne 2011). Each city had different relationships between external and internal forest characteristics, and carabid metrics. In Raleigh, forest specialists were negatively correlated with surrounding impervious surface and open area specialists were positively correlated with canopy openness. Internal forest characteristics, including understory density, total ground cover, and leaf litter, had greater influence on carabid communities than external forest characteristics. In Newark, forest specialists were negatively correlated with surrounding impervious surface and open area specialists were positively correlated with surrounding impervious surface. External impervious surface had greater influence on carabid communities than internal forest characteristics, including total ground cover and leaf litter. So, while large forests can preserve carabid communities across cities, the effects of impervious surface and internal urban forest characteristics on carabid communities depends on city region.

Influence of size and external forest characteristics on urban carabids

Carabid communities in both cities, especially forest specialists, benefited from large forests. We are not the first to suggest that large forests are important for carabid conservation, as late-successional forest structure can provide cool, moist microclimates for forest-associated carabids (Halme & Niemelä 1993, Niemelä 2001, Lövei et al. 2006, Croci et al. 2008). In Newark, open area specialist capture also increased with greater forest size, potentially indicating that edge margins and canopy gaps are sufficient in large forests to retain open area specialists. Halme & Niemelä (1993) found some open area specialist carabid species in large to medium (21.5 – 4.2 ha) forest patches, and found similarities between small forest patches and edges of large forest patches. Forest specialists were reduced by greater surrounding impervious surface in forests in both cities and, in Newark forests, open area specialists also increased with greater surrounding impervious surface. Others have found less forest specialists and more open area specialists in urban, compared to rural, forests (Halme & Niemelä 1993, Magura et al. 2004, Elek & Lövei 2007, Gaublomme et al. 2008), but only Gaublomme et al. tested and found significant effects of surrounding impervious surface. Our results support the idea that increased impervious surface across the urban landscape may affect carabid community structure, in part, through carabid dispersal, carabid recruitment, and the urban heat island effect (Weller & Ganzhorn 2004, Sadler et al. 2006, Croci et al. 2008, Pickett et al. 2008).

Influence of internal forest characteristics on urban carabids

Our prediction that internal forest characteristics would influence carabid communities more than external impervious surface was supported when all forests were considered together and in Raleigh, but not in Newark. Raleigh carabid communities were most affected by internal leaf litter, while Newark carabid communities were most affected by external impervious surface. A review by Nielsen et al. (2014) found negative effects of the urban matrix on invertebrate species richness but found structural heterogeneity, including vegetation, within urban parks was an overall better predictor of richness and community composition. We expected carabids in Raleigh and Newark to respond similarly to urban forest vegetation structure; to have a positive correlation with greater leaf litter volume and a negative correlation with greater understory vegetation, as these affect the forest floor microclimate and carabid mobility (Thiele 1977, Lys & Nentwig 1992, Koivula et al. 1999, Brose 2003, Croci et al. 2008). However, carabids in Raleigh were negatively correlated with total ground cover and leaf litter volume, whereas carabids in Newark were positively correlated with total ground cover and leaf litter volume. This suggests either a difference in ground cover and litter composition, or a difference in carabid communities and the resource requirements of individual species. Croci et al. (2008) found carabid diversity declined with dense shrub cover and with declines in richness and diversity of the herbaceous layer, regardless of whether the community was in a rural or urban forest. We found understory density reduced total carabids and forest specialists in Raleigh and Newark forests combined, but had no significant effect on carabids in either city alone. This may indicate that dense understory vegetation in general reduced carabids, but that vegetation communities in each city differed enough to decouple this effect when analyzed separately.

From previous work in these forests (Mitchell Chapter 1) we know nonnative species comprised more of the understory vegetation in Raleigh, while native species comprised more of the understory vegetation in Newark. This difference between vegetation communities may indicate that forest specialists responded negatively to nonnative ground cover in Raleigh, and negatively to dense, mostly native ground cover in Newark. Additionally, differences in forest vegetation communities can persist as differences in forest litter, which affects carabid communities. Raleigh forests had more leaf litter on average than Newark forests (Mitchell Chapter 1), and Raleigh leaf litter was composed of more pine needles than Newark (J. C. Mitchell, *unpublished data*). Leaf litter affects carabid distribution patterns and in boreal forests, especially degraded forests, deciduous tree leaves were an important component of litter for increased carabid capture (Koivula et al. 1999). Our results could suggest that though Raleigh had more leaf litter, Newark leaf litter was more beneficial for urban forest carabids. We expected canopy openness to have greater influence in increasing open area specialist capture and diversity (Thiele 1977), but only open area specialist diversity in Raleigh increased with greater canopy openness. We showed the responses of urban carabid communities to urban forest characteristics in two different cities are driven by changes in specialist species, as forest specialists declined and open area specialists increased in disturbed urban forests.

Conclusions and management implications

Even though carabid capture and diversity increased with forest size, three smaller urban forests (2.7-4.9 ha), one in Raleigh and two in Newark, had comparable or greater forest specialist capture and diversity as three larger urban forests (39.8-77.2 ha), also one in Raleigh and two in Newark. Conservation efforts should focus on maintaining forests of any size with sufficient canopy cover, as we found forest specialists in all forests 2.7 ha and larger, and one forest specialist in a 1.2 ha Raleigh forest. Carabids responded to external and internal forest conditions differently, indicating urban forest management should be tailored by region and perhaps more specifically by city. Our results from Raleigh, a larger, warmer, and more urbanized city differed from Newark, a smaller, temperate, and less urbanized city. This could suggest that as cities expand and climate warms, preserved forests may become lower quality, especially if allowed to be invaded by nonnative plants. Additionally, if urban forests are unable to maintain canopy regeneration, as caused by nonnative invasion (Meiners 2007, Oswalt et al. 2007, Burton & Samuelson 2008, Langmaier & Lapin 2020), future urban carabid communities may shift to include greater proportions of open area tolerant species. While increasing forest size and decreasing impervious surface around urban forests is unlikely, our results highlight the potential to manage forest interiors to maintain viable habitat for forest specialist species and support that urban forest management methods should be tailored to regional urban communities. However, all regions should conserve forests of any size with intact canopies and manage understory vegetation to reduce invasion by nonnative plants and promote the regeneration of the forest canopy by native woody species.

ACKNOWLEDGEMENTS

Thank you to the City of Raleigh, Town of Cary, North Carolina State University, US Forest Service, City of Newark, and University of Delaware for providing access to research sites. Thank you to Annemarie Nagle, Lawrence Long, Michael Just, Kristi Backe, Sarah Parsons, Elsa Youngsteadt, Samantha Larsen, Nora Lahr, and Caleb Wilson from the Frank Lab for advice regarding research design, statistical analyses, and more. Thank you to Vince D'Amico and Tara Trammell for access to the FRAME network. Thank you to Catherine Crofton, Doua Jim Lor, Logan Tyson, Kyle Sozanski, Hannah Frank, and Maggie Hamilton, R. David Mitchell, Covel McDermot, Eric Moore, Carl Rosier, Zach Ladin, Matt McDermitt, Nathaly Rodriguez, and Andrew Adams for field and lab help. Thank you to the US Department of Agriculture and US Geological Survey for funding.

REFERENCES

Adams, B. J., Li, E., Bahlai, C. A., Meineke, E. K., McGlynn, T. P., & Brown, B. V. (2020). Local- and landscape-scale variables shape insect diversity in an urban biodiversity hot spot. *Ecological Applications*, *30*(4). https://doi.org/10.1002/eap.2089

Alaruikka, D., Kotze, D. J., Matveinen, K., & Niemelä, J. (2002). Carabid beetle and spider assemblages along a forested urban-rural gradient in southern Finland. *Journal of Insect Conservation*, *6*(4), 195–206. https://doi.org/10.1023/A:1024432830064

Alberti, M. (2005). The effects of urban patterns on ecosystem function. *International Regional Science Review*, 28, 168–192. https://doi.org/10.1177/0160017605275160

Amburgey, S. M., Miller, D. A. W., Rochester, C. J., Delaney, K. S., Riley, S. P. D., Brehme, C. S., … Fisher, R. N. (2020). The influence of species life history and distribution characteristics on species responses to habitat fragmentation in an urban landscape. *Journal of Animal Ecology*, 1365-2656.13403. https://doi.org/10.1111/1365-2656.13403

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2013.3330

Aronson, M. F. J., Nilon, C. H., Lepczyk, C. A., Parker, T. S., Warren, P. S., Cilliers, S. S., … Zipperer, W. (2016). Hierarchical filters determine community assembly of urban species pools. *Ecology*, 97(11), 2952-2963.

Ashton, I. W., Hyatt, L. A., Howe, K. M., Gurevitch, J., & Lerdau, M. T. (2005). Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecological Applications*, 15(4), 1263-1272. https://doi.org/10.1890/04-0741.

Barton, K. (2020). *Multi-model inference*. R package version 1.43. 17. 2020.

Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18, 581–592. https://doi.org/10.1111/ele.12427

Birkhofer, K., Wise, D. H., Scheu, S., Birkhofer, K., & Scheu, S. (2008). Subsidy from the detrital food web, but not microhabitat complexity, affects the role of generalist predators in an aboveground herbivore food web. *Oikos*, 117, 494-500. https://doi.org/10.1111/j.2007.0030-1299.16361.x

Borges, E. R., Dexter, K. G., Bueno, M. L., Pontara, V., & Carvalho, F. A. (2020). The evolutionary diversity of urban forests depends on their land-use history. *Urban Ecosystems*. https://doi.org/10.1007/s11252-020-00938-y

Bousquet, Y. (2010). *Illustrated identification guide to adults of larvae of northeastern North American ground beetles (Coleoptera: Carabidae).* Pensoft.

Bousquet, Y., & Webster, R. (2004). Review of the Nearctic species of the Holarctic subgenus Argutor (Coleoptera: Carabidae). *Canadian Entomologist*, 136, 645–660.

https://doi.org/10.4039/n04-030

Brose, U. (2003). Bottom-up control of carabid beetle communities in early successional wetlands: Mediated by vegetation structure or plant diversity? *Oecologia*, 135(3), 407–413. https://doi.org/10.1007/s00442-003-1222-7

Burnham, K. P. & Anderson D. R. (2002). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer.

Burton, M. L., & Samuelson, L. J. (2008). Influence of urbanization on riparian forest diversity and structure in the Georgia Piedmont, US. *Plant Ecology*, 195(1), 99–115. https://doi.org/10.1007/s11258-007-9305-x

Cadenasso, M. L., & Pickett, S. T. A. (2001). Effect of Edge Structure on the Flux of Species into Forest Interiors. *Conservation Biology*, 15.

Concepción, E. D., Obrist, M. K., Moretti, M., Altermatt, F., Baur, B., & Nobis, M. P. (2016). Impacts of urban sprawl on species richness of plants, butterflies, gastropods and birds: not only built-up area matters. *Urban Ecosystems*, 19(1), 225–242. https://doi.org/10.1007/s11252-015-0474-4

Croci, S., Butet, A., Georges, A., Aguejdad, R., & Clergeau, P. (2008). Small urban woodlands as biodiversity conservation hot-spot: A multi-taxon approach. *Landscape Ecology*, *23*(10), 1171–1186. https://doi.org/10.1007/s10980-008-9257-0

Dale, A. G., & Frank, S. D. (2018). Urban plants and climate drive unique arthropod interactions with unpredictable consequences. *Current Opinion in Insect Science*, 29, 27–33. https://doi.org/10.1016/j.cois.2018.06.001

de Andrade, A. C., Dellefrate Franzini, L., & Mesquita, D. O. (2019). Assessing the effect of urbanization on tropical forest dwelling teiid lizards. *Ecological Indicators*. https://doi.org/10.1016/j.ecolind.2018.12.037

De Smedt, P., Boeraeve, P., & Baeten, L. (2021). Intra-annual activity patterns of terrestrial isopods are tempered in forest compared to open habitat. *Soil Biology and Biochemistry*, 108342. https://doi.org/10.1016/j.soilbio.2021.108342

Deichsel, R. (2006). Species change in an urban setting-ground and rove beetles (Coleoptera: Carabidae and Staphylinidae) in Berlin. *Urban Ecosystems*. https://doi.org/10.1007/s11252-006-8588-3

Dyderski, M. K., & Jagodziński, A. M. (2020). Impact of invasive tree species on natural regeneration species composition, diversity, and density. *Forests*, *11*(4). https://doi.org/10.3390/F11040456

Elek, Z., & Lövei, G. L. (2007). Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. *Acta Oecologica*. https://doi.org/10.1016/j.actao.2007.03.008

Fidino, M., Gallo, T., Lehrer, E. W., Murray, M. H., Kay, C., Sander, H. A., … Magle, S. B. (2020). Landscape-scale differences among cities alter common species' responses to urbanization. *Ecological Applications*. https://doi.org/10.1002/eap.2253

Fournier, B., Frey, D., & Moretti, M. (2020). *The origin of urban communities: From the regional species pool to community assemblages in city*. McKinney.

Fujita, A., Maeto, K., Kagawa, Y., & Ito, N. (2008). Effects of forest fragmentation on species richness and composition of ground beetles (Coleoptera: Carabidae and Brachinidae) in urban landscapes. *Entomological Science*. https://doi.org/10.1111/j.1479-8298.2007.00243.x

Gaublomme, E., Hendrickx, F., Dhuyvetter, H., & Desender, K. (2008). The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. *Biological Conservation*. https://doi.org/10.1016/j.biocon.2008.07.022

Halme, E., & Niemelä, J. (1993). Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici*, 30.

Huang, K., Li, X., Liu, X., & Seto, K. C. (2019). Projecting global urban land expansion and heat island intensification through 2050. *Environmental Research Letters*, *14*(11). https://doi.org/10.1088/1748-9326/ab4b71

Ives, A. R. (2015). For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution*, *6*(7), 828–835. https://doi.org/10.1111/2041-210X.12386

Jennings, V. H., & Tallamy, D. W. (2006). Composition and Abundance of Ground-Dwelling Coleoptera in a Fragmented and Continuous Forest. *Environ. Entomology*, 35. https://academic.oup.com/ee/article/35/6/1550/390022

Jones, E. L., & Leather, S. R. (2012). Invertebrates in urban areas: A review. *European Journal of Entomology*, Vol. 109, pp. 463–478. https://doi.org/10.14411/eje.2012.060

Koivula, M. J. (2011). Useful model organisms, indicators, or both? Ground beetles (Coleoptera, Carabidae) reflecting environmental conditions. *ZooKeys*. https://doi.org/10.3897/zookeys.100.1533

Koivula, M., Punttila, P., Haila, Y., & Nicnielii Koivula Punltila P-, J. M. (1999). Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography*, 22(4), 424-435.

Landsman, A. P., Ladin, Z. S., Gardner, D., Bowman, J. L., Shriver, G., D'Amico, V., & Delaney, D. A. (2019). Local landscapes and microhabitat characteristics are important determinants of urban–suburban forest bee communities. *Ecosphere*, *10*(10). https://doi.org/10.1002/ecs2.2908

Langmaier, M., & Lapin, K. (2020). A Systematic Review of the Impact of Invasive Alien Plants on Forest Regeneration in European Temperate Forests. *Frontiers in Plant Science*, 11. https://doi.org/10.3389/fpls.2020.524969

Larochelle, A. & Larivière, M.-C. (2003). *A Natural History of the Ground-Beetles (Coleoptera:*

Carabidae) of American north of Mexico. Pensoft.

Larsen, K. J., Work, T. T., & Purrington, F. F. (2003). Habitat use patterns by ground beetles (Coleoptera: Carabidae) of northeastern Iowa. *Pedobiologia*, 47. http://www.urbanfischer.de/journals/pedo

Latty, E. F., Werner, S. M., Mladenoff, D. J., Raffa, K. F., & Sickley, T. A. (2006). Response of ground beetle (Carabidae) assemblages to logging history in northern hardwood-hemlock forests. *Forest Ecology and Management*. https://doi.org/10.1016/j.foreco.2005.10.028

Long, L. C., D'Amico, V., & Frank, S. D. (2018). Urban forest fragments buffer trees from warming and pests. *Science of The Total Environment*. https://doi.org/10.1016/j.scitotenv.2018.12.293

Long, L. C., & Frank, S. D. (2020). Risk of bird predation and defoliating insect abundance are greater in urban forest fragments than street trees. *Urban Ecosystems*. https://doi.org/10.1007/s11252-020-00939-x

Lövei, G. L., Magura, T., Tóthmérész, B., & Ködöböcz, V. (2006). The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera: Carabidae) in habitat islands. *Global Ecology and Biogeography*. https://doi.org/10.1111/j.1466-822X.2005.00221.x

Lys, J.-A., & Nentwig, W. (1992). Augmentation of beneficial arthropods by strip-management. *Oecologia*, 92, 373-382.

Magura, T., Tóthmérész, B., & Molnár, T. (2004). Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology*. https://doi.org/10.1007/s10980-005-1128-4

Martinson, H. M., & Raupp, M. J. (2013). A meta-analysis of the effects of urbanization on ground beetle communities. *Ecosphere*. https://doi.org/10.1890/ES12-00262.1

McCary, M. A., Martínez, J. C., Umek, L., Heneghan, L., & Wise, D. H. (2015). Effects of woodland restoration and management on the community of surface-active arthropods in the metropolitan Chicago region. *Biological Conservation*, *190*, 154–166. https://doi.org/10.1016/j.biocon.2015.06.005

McCary, M. A., Minor, E., & Wise, D. H. (2018). Covariation between local and landscape factors influences the structure of ground-active arthropod communities in fragmented metropolitan woodlands. *Landscape Ecology*, *33*(2), 225–239. https://doi.org/10.1007/s10980-017-0593-9

McDonnell, M. J., & Hahs, A. K. (2008). The use of gradient analysis studies in advancing our understanding of the ecology of urbanizing landscapes: Current status and future directions. *Landscape Ecology*, 23, 1143–1155. https://doi.org/10.1007/s10980-008-9253-4

McKinney. (2002). *Urbanization, Biodiversity, and Conservation*.

Meiners, S. J. (2007). Apparent competition: An impact of exotic shrub invasion on tree regeneration. *Biological Invasions*, *9*(7), 849–855. https://doi.org/10.1007/s10530-006-9086-5

Melliger, R. L., Braschler, B., Rusterholz, H. P., & Baur, B. (2018). Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. *PLoS ONE*, *13*(6). https://doi.org/10.1371/journal.pone.0199245

Meyer, S., Rusterholz, H.-P., Salamon, J.-A., & Baur, B. (2019). Leaf litter decomposition and litter fauna in urban forests: Effect of the degree of urbanisation and forest size. *Pedobiologia*. https://doi.org/10.1016/j.pedobi.2019.150609

Miller, J. R., & Hobbs, R. J. (2002). Conservation Where People Live and Work. *Conservation Biology*, 16.

Nielsen, A. B., van den Bosch, M., Maruthaveeran, S., & van den Bosch, C. K. (2014). Species richness in urban parks and its drivers: A review of empirical evidence. *Urban Ecosystems*. https://doi.org/10.1007/s11252-013-0316-1

Niemelä, J. (2001). Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: A review. *European Journal of Entomology*, *98*(2), 127–132. https://doi.org/10.14411/eje.2001.023

Niemelä, J, Kotze, D. J., Venn, S., Penev, L., Stoyanov, I., Spence, J., … Montes De Oca, E. (2002). Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecology*, 17, 387-401.

Noonan, G. R. (1996). Classification, cladistics, and natural history of species of the subgenus Anisodactylus Dejean (Insecta: Coleoptera: Carabidae: Harpalini: Anisodactylus). 89,1-210.

Ordóñez, C., & Duinker, P. N. (2012). Ecological integrity in urban forests. *Urban Ecosystems*, *15*(4), 863–877. https://doi.org/10.1007/s11252-012-0235-6

Oswalt, C. M., Oswalt, S. N., & Clatterbuck, W. K. (2007). Effects of Microstegium Vimineum (Trin.) A. Camus on native woody species density and diversity in a productive mixed-hardwood forest in Tennessee. *Forest Ecology and Management*, *242*(2–3), 727–732. https://doi.org/10.1016/j.foreco.2007.02.008

Perry, K., & Herms, D. (2019). Dynamic Responses of Ground-Dwelling Invertebrate Communities to Disturbance in Forest Ecosystems. *Insects*. https://doi.org/10.3390/insects10030061

Pickett, S. T. A, Cadenasso, M. L., Grove, J.M., Nilon, C.H., Pouyat, R.V., et al. (2008). Urban Ecological Systems: Linking Terrestrial Ecological, Physical, and Socioeconomic Components of Metropolitan Areas. *In Urban Ecology: an International Perspective on the Interaction between Humans and Nature.* Springer.

Pouyat, R. V., & Carreiro, M. M. (2003). Controls on mass loss and nitrogen dynamics of oak leaf litter along an urban-rural land-use gradient. *Oecologia*, *135*(2), 288–298. https://doi.org/10.1007/s00442-003-1190-y

Pouyat, R. V, Mcdonnell, M. J., & Pickett, S. T. A. (1997). Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land use gradient. *Urban Ecosystems*, 1, 117-131.

Puppim de Oliveira, J. A., Balaban, O., Doll, C. N. H., Moreno-Peñaranda, R., Gasparatos, A., Iossifova, D., & Suwa, A. (2011). Cities and biodiversity: Perspectives and governance challenges for implementing the convention on biological diversity (CBD) at the city level. *Biological Conservation*, 144, 1302–1313. https://doi.org/10.1016/j.biocon.2010.12.007

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rainio, J., & Niemela, J. (2003). Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation*, 12, 487-506.

Ramírez-Cruz, G. A., Mendoza-Hernández, P. E., Solano-Zavaleta, I., & Zúñiga-Vega, J. J. (2018). How Widespread are Nonnative Species? Estimating Habitat Occupancy in an Ecological Reserve within a Megacity. *Natural Areas Journal*. https://doi.org/10.3375/043.038.0108

Ren, Z., He, X., Zheng, H., Zhang, D., Yu, X., Shen, G., & Guo, R. (2013). Estimation of the relationship between urban park characteristics and park cool island intensity by remote sensing data and field measurement. *Forests*, *4*(4), 868–886. https://doi.org/10.3390/f4040868

Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, 82(4), 1112-1129.

Riley, K. N., & Browne, R. A. (2011). Changes in ground beetle diversity and community composition in age structured forests (Coleoptera, Carabidae). *ZooKeys*. https://doi.org/10.3897/zookeys.147.2102

Sadler, J. P., Small, E. C., Fiszpan, H., Telfer, M. G., & Niemelä, J. (2006). Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. *Journal of Biogeography*. https://doi.org/10.1111/j.1365-2699.2006.01476.x

Templeton, L. K., Neel, M. C., Groffman, P. M., Cadenasso, M. L., & Sullivan, J. H. (2019). Changes in vegetation structure and composition of urban and rural forest patches in Baltimore from 1998 to 2015. *Forest Ecology and Management, 454.* https://doi.org/10.1016/j.foreco.2019.117665

Thiele, H.-U. (1977). *Carabid Beetles in their Environments: a study on habitat selection by adaptations in physiology and behaviour*. Springer-Verlag.

Trammell, T. L. E., Ralston, H. A., Scroggins, S. A., & Carreiro, M. M. (2012). Foliar production and decomposition rates in urban forests invaded by the exotic invasive shrub, Lonicera maackii. *Biological Invasions*. https://doi.org/10.1007/s10530-011-0093-9

Trammell, T. L. E., D'Amico, V., Avolio, M. L., Mitchell, J. C., & Moore, E. (2020). Temperate deciduous forests embedded across developed landscapes: younger forests harbor invasive plants and urban forests maintain native species. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.13400

United Nations, Department of Economic and Social Affairs, Population Division (2018). *The World's Cities in 2018—Data Booklet* (ST/ESA/ SER.A/417).

Vallet, J., Daniel, H., Beaujouan, V., Rozé, F., & Pavoine, S. (2010). Using biological traits to assess how urbanization filters plant species of small woodlands. *Applied Vegetation Science*. https://doi.org/10.1111/j.1654-109X.2010.01087.x

van Hengstum, T., Hooftman, D. A. P., Oostermeijer, J. G. B., & van Tienderen, P. H. (2014). Impact of plant invasions on local arthropod communities: A meta-analysis. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.12176

Vele, A., Holusa, J., Frouz, J., & Konvicka, O. (2011). Local and landscape drivers of ant and carabid beetle communities during spruce forest succession. *European Journal of Soil Biology*. https://doi.org/10.1016/j.ejsobi.2011.09.003

Venables, W. N., & Ripley, B. D. (2002). *Modern applied statistics with S (fourth).* New York: Springer. Available at: http://www.stats.ox.ac.uk/pub/MASS4.

Venn, S. J., Kotze, D. J., & Niemelä, J. (2003). Urbanization effects on carabid diversity in boreal forests. *European Journal of Entomology*, *100*(1), 73–80. https://doi.org/10.14411/eje.2003.015

Wallace, K. J., Laughlin, D. C., Clarkson, B. D., & Schipper, L. A. (2018). Forest canopy restoration has indirect effects on litter decomposition and no effect on denitrification. *Ecosphere*, *9*(12). https://doi.org/10.1002/ecs2.2534

Weller, B., & Ganzhorn, J. U. (2004). Carabid beetle community composition, body size, and fluctuating asymmetry along an urban-rural gradient. *Basic and Applied Ecology*. https://doi.org/10.1078/1439-1791-00220

Wickham, J., Stehman, S. V., Sorenson, D. G., Gass, L., & Dewitz, J. A. (2021). Thematic accuracy assessment of the NLCD 2016 land cover for the conterminous United States. *Remote Sensing of Environment*, 257. https://doi.org/10.1016/j.rse.2021.112357

Yates, E. D., Levia, D. F., & Williams, C. L. (2004). Recruitment of three non-native invasive plants into a fragmented forest in southern Illinois. *Forest Ecology and Management*, *190*(2–3), 119–130. https://doi.org/10.1016/j.foreco.2003.11.008

Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R.* Springer.

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. https://doi.org/10.1111/j.2041- 210x.2009.00001.x

TABLES AND FIGURES

Table 2.1. *Final models representing the most relevant external and internal factors for each carabid response variable. AICc is included for each model and estimate, standard error, t value, and p value are included for each parameter within each model. Variables in bold indicate significance α < 0.05 and p values in italics indicate α < 0.1.*

Response variable	AICc	Parameters	Estimate	SE	t value	p value
All sites, both cities						
Total carabid capture	68.606	**Forest size**	**0.007896**	**0.003761**	**2.099**	**0.04867**
		Total ground cover	**-0.057218**	**0.015392**	**-3.717**	**0.00136**
		Leaf litter	-0.184105	0.097026	-1.897	*0.07230*
Total carabid diversity	45.989	Forest size	0.004919	0.002676	1.839	*0.08166*
		Impervious: 1000 m	0.023108	0.011104	2.081	*0.05120*
		Understory density	**-0.017915**	**0.008042**	**-2.228**	**0.03819**
		Leaf litter	**-0.172858**	**0.057233**	**-3.020**	**0.00704**
Forest specialist carabid capture	72.872	**Forest size**	**0.009252**	**0.004411**	**2.097**	**0.048862**
		Understory density	**-0.061680**	**0.014795**	**-4.169**	**0.000474**
		Leaf litter	**-0.284933**	**0.102822**	**-2.771**	**0.011785**
Forest specialist carabid diversity	32.164	**Forest size**	**0.004839**	**0.001889**	**2.562**	**0.01860**
		Understory density	**-0.021218**	**0.006336**	**-3.349**	**0.00320**
		Leaf litter	**-0.163388**	**0.044033**	**-3.711**	**0.00138**
Open area specialist carabid capture	69.316	Canopy openness	0.08654	0.05086	1.701	0.10362
		Total ground cover	**-0.05270**	**0.01446**	**-3.607**	**0.00151**
Open area specialist carabid diversity	37.438	Forest size	0.002974	0.002119	1.404	0.17660
		Impervious: 1000m	**0.033904**	**0.009292**	**3.649**	**0.00171**
		Total ground cover	-0.011006	0.007652	-1.438	0.16661
		Leaf litter	**-0.130936**	**0.049346**	**-2.653**	**0.01569**

Table 2.1 *(continued).*

Raleigh, NC						
Total carabid capture	78.911	Forest size	0.01320	0.01332	0.991	0.3674
		Impervious: 1000m	0.17469	0.07162	2.439	*0.0587*
		Impervious: 100m	**-0.15427**	**0.05092**	**-3.029**	**0.0291**
		Understory density	0.04613	0.03398	1.357	0.2327
		Total ground cover	**-0.11150**	**0.03415**	**-3.265**	**0.0223**
		Leaf litter	**-0.40267**	**0.15328**	**-2.627**	**0.0467**
Total carabid diversity	42.129	Impervious: 1000m	0.04664	0.02600	1.794	0.1230
		Impervious: 100m	-0.04347	0.02223	-1.955	*0.0984*
		Canopy openness	0.06877	0.03939	1.746	0.1315
		Total ground cover	-0.02450	0.01048	-2.338	*0.0580*
		Leaf litter	**-0.28964**	**0.07193**	**-4.027**	**0.0069**
Forest specialist carabid capture	74.585	Forest size	0.01212	0.01113	1.089	0.3258
		Impervious: 1000m	0.11813	0.05981	1.975	0.1052
		Impervious: 100m	**-0.12535**	**0.04252**	**-2.948**	**0.0320**
		Understory density	0.03307	0.02838	1.165	0.2965
		Total ground cover	**-0.07460**	**0.02852**	**-2.616**	**0.0473**
		Leaf litter	**-0.50358**	**0.12800**	**-3.934**	**0.0110**
Forest specialist carabid diversity	15.700	**Forest size**	**0.007943**	**0.003186**	**2.493**	**0.0414**
		Impervious: 100m	-0.011619	0.006803	-1.708	0.1314
		Total ground cover	-0.006292	0.004741	-1.327	0.2261
		Leaf litter	**-0.090047**	**0.033030**	**-2.726**	**0.0295**
Open area specialist carabid capture	38.899	**Total ground cover**	**-0.07458**	**0.01811**	**-4.117**	**0.00209**
Open area specialist carabid diversity	16.339	**Canopy openness**	**0.08052**	**0.02708**	**2.974**	**0.0156**
		Leaf litter	**-0.11928**	**0.04221**	**-2.826**	**0.0199**

Table 2.1 *(continued).*

Newark, DE

Total carabid capture	58.205	Forest size	0.005782	0.004892	1.182	0.28189
		Impervious: 1000m	-0.041627	0.027710	-1.502	0.18372
		Impervious: 100m	0.044343	0.022768	1.948	*0.09939*
		Total ground cover	-0.097354	0.043736	-2.226	*0.06764*
		Leaf litter	-0.275760	0.214328	-1.287	0.24564
Total carabid diversity	26.741	**Impervious: 1000m**	**0.035403**	**0.011258**	**3.145**	**0.01627**
		Impervious: 100m	**-0.035486**	**0.009598**	**-3.697**	**0.00768**
		Total ground cover	**0.054704**	**0.017932**	**3.051**	**0.01857**
		Leaf litter	**0.287905**	**0.082125**	**3.506**	**0.00992**
Forest specialist carabid capture	34.876	**Impervious: 1000m**	**-0.03909**	**0.01296**	**-3.017**	**0.0166**
		Canopy openness	-0.08384	0.04481	-1.871	*0.0982*
		Leaf litter	**0.33694**	**0.10612**	**3.175**	**0.0131**
Forest specialist carabid diversity	34.522	Forest size	0.005887	0.002976	1.978	*0.0884*
		Impervious: 1000m	0.017509	0.015502	1.129	0.2959
		Understory density	-0.028586	0.013735	-2.081	*0.0759*
		Leaf litter	-0.267620	0.125192	-2.138	*0.0699*
Open area specialist carabid capture	52.663	**Forest size**	**0.010099**	**0.003734**	**2.704**	**0.0354**
		Impervious: 100m	**0.038510**	**0.014187**	**2.715**	**0.0349**
		Canopy openness	0.084343	0.049181	1.715	0.1372
		Total ground cover	-0.085294	0.035949	-2.373	*0.0553*
		Leaf litter	-0.398626	0.164665	-2.421	*0.0518*
Open area specialist carabid diversity	21.756	**Impervious: 1000m**	**0.02276**	**0.01006**	**2.263**	**0.0472**

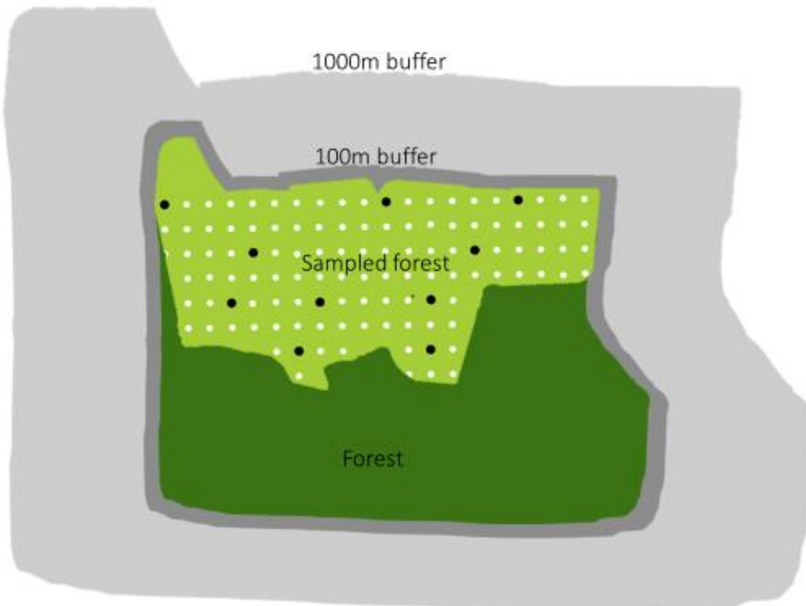


Figure 2.1. *Diagram of example urban forest FRAME site. Total forest size includes unsampled forest (dark green). Surrounding impervious surface was calculated within a 100m buffer (dark gray) and 1000m buffer (light gray) area extending out from forest edge.*

CHAPTER 3

Arthropod biomass not a surrogate for arthropod diversity in urban forests

ABSTRACT

Recent promotion of an 'Insect Apocalypse' has fueled a need to better understand relationships between arthropod abundance, biomass, richness, and diversity across different regions. A correlation between arthropod abundance or biomass and diversity has been suggested, but there is little evidence to support such a relationship. There is evidence to support correlations between arthropod abundance and biomass, and arthropod richness and diversity. However, these relationships depend on additional factors that may vary between regions and species pools. We tested relationships between arthropod abundance, biomass, richness, and diversity using extensive collections of urban forest arthropods from two latitudes. We vacuum sampled arthropods from understory forest vegetation in 24 urban forests, 12 forests in Raleigh, NC and 12 forests in Newark, DE, to test the validity of substituting biomass for diversity to quantify change in arthropod biodiversity. We found different arthropod communities in Raleigh and Newark, and no correlation between arthropod abundance or biomass and diversity in either city. Our results suggest quantifying arthropod decline will continue to require specimen identification in urban, and likely other, ecosystems, and support the use of multiple metrics to describe community structure. Here, we established a reference point of urban arthropod communities and recommend future sampling to quantify change over time, as knowledge of urban ecosystems may be invaluable in predicting trends of future global ecological conditions.

INTRODUCTION

Recent popular and peer-reviewed publications suggest a global decline in arthropod abundance, biomass, and diversity (e.g., Carrington 2017, Hallmann et al. 2017, Lister & Garcia 2018, Sánchez-Bayo & Wyckhuys 2019). Direct measurements of diversity are difficult and require extensive processing time and expertise (Cardoso & Leather 2019, Ärje et al. 2020). As a result, studies frequently focus on a limited group of taxa (summarized in Sánchez-Bayo & Wyckhuys 2019, Kinsella et al. 2020, Hallmann et al. 2021), broadly generalize taxa (Lister & Garcia 2018, Nagy et al. 2018), or use biomass (Saint-Germain et al. 2007, Shortall et al. 2009, Hallmann et al. 2017) to quantify arthropod communities. Biomass, in particular, has been used as an indicator of arthropod decline both for its ease of measurement and consequences for higher trophic levels (Saint-Germain et al. 2007, Simons et al. 2014, Hallmann et al. 2017, Montgomery et al. 2020). Biomass results have been extrapolated to infer trends in diversity (Hallmann et al. 2017, Hallmann et al. 2021), though there is theory against such a relationship (Gough et al. 1996), and empirical evidence to support a relationship is limited and mixed (Southwood et al. 1982, Shortall et al. 2009, Simons et al. 2014, Seibold et al. 2019, Rosenheim & Ward 2020). We tested relationships between arthropod abundance, biomass, richness, and diversity using extensive collections from urban forests at two latitudes. Our goal was to test the validity of substituting biomass for diversity and to establish a reference point for how arthropod communities change in urban ecosystems with time.

Arthropod biomass, abundance, and diversity are frequently used, often in combination, to describe spatial or temporal changes in arthropod populations and ecosystem functions. Unfortunately, few studies report relationships between these variables and therefore correlations between them remain unclear. Biomass and abundance can be positively correlated with diversity as species accumulate in an ecosystem (Simberloff & Wilson 1969, Hallmann et al. 2021). However, biomass and abundance can also increase due to ecological disturbances, such as invasion (Hillebrand et al. 2008) or the urban heat island effect (Meineke et al. 2013, Meineke et al. 2019, Frank et al. 2019), and thus be negatively correlated with diversity (Southwood et al. 1982). In Germany, Hallmann et al. (2017) found arthropod biomass declined in protected natural areas over time and inferred a change in arthropod abundance, however, they did not report arthropod abundance or identification. Lister & Garcia (2018) found that arthropod abundance and biomass declined in response to climate change over time but did not correlate abundance with biomass. One metanalysis summarized effects on arthropod abundance, biomass, and diversity but did not investigate correlations, and may have presented an inflated view of arthropod decline by only including literature found with the search criteria '[insect*] AND [declin*]' (Sánchez-Bayo & Wyckhuys 2019). In one example, a theoretical model related changes in hoverfly (Syrphidae) abundance and diversity (Hallmann et al. 2021) to long-term flying arthropod biomass decline (Hallmann et al. 2017), however, concurrent data collection and direct within-taxon correlations are necessary to understand the true relationships between arthropod abundance, biomass, and diversity. Despite the relative ease of measurement, there is little evidence that biomass or abundance alone can adequately describe arthropod diversity, arthropod decline, or ecosystem condition.

Urbanization, agriculture, ecosystem fragmentation, pollution, artificial lights, and climate change are frequently cited as potential mechanisms for arthropod decline (Sánchez-Bayo & Wyckhuys 2019, Boyes et al. 2021, Raven & Wagner 2021). Our goal was to document arthropod abundance, biomass, richness, and diversity in urban forests and determine which of these metrics are correlated in this ecosystem. We expect arthropod abundance and biomass to correlate, and arthropod richness and diversity to correlate, but we do not expect a correlation between arthropod abundance or biomass and diversity. If there is a correlation, arthropod abundance or biomass, which is easier to measure and does not require taxonomic expertise, could be used to infer changes in richness or diversity. However, arthropod biomass and diversity respond differently to changes in arthropod abundance, arthropod size, and community composition. Additionally, arthropod biomass can be unrelated to abundance as morphological variations within and between species change with season, region, and latitude (Niemelä & Kotze 2009, McCall & Pennings 2012, Horne et al. 2017). If, as we predict, arthropod biomass and diversity are not correlated, it suggests that determining trends and mechanisms of arthropod decline will continue to require specimen identification in urban, and likely other, ecosystems. To test our hypothesis, we sampled arthropods from understory vegetation in 24 urban forests located in Raleigh, North Carolina, USA and Newark, Delaware, USA, two regions with different species pools and climates. Additionally, these data provide an initial reference point to track urban arthropod community change in the future. This is relevant because urban ecosystems may provide insight to how species, communities, and ecosystems respond to large scale changes in climate and land use (Lahr et al. 2018). Understanding how arthropod biomass and diversity relate to each other, and whether this relationship is similar in different regions, will provide support for or against inferring trends of diversity from biomass data.

METHODS

Site selection and arthropod collecting

This research was conducted in Raleigh, North Carolina (35.780˚N, 78.642˚W) and Newark, Delaware (39.683˚N, 75.753˚W) USA as part of the FRAME (FoRests Among

Managed Ecosystems, https://sites.udel.edu/frame/) network of forests used to study urban forest ecology. We sampled 12 urban forests in each city for a total of 24 forests. Within each forest, we collected arthropods at established sampling points (N = 239, Mitchell Chapter 1) using a vacuum method. Arthropods were vacuumed twice in 2019, in Raleigh between June 14-19 and July 17-19 and in Newark between June 22-24 and July 22-25.

Prior to arthropod collecting, all sampling points were outfitted with 4 equally spaced marking flags (Presco Products Co., 21 in tall) to designate a 5-m radius circle (78.5-m^2) centered around the sampling point, hereafter referred to as the sampling circle. We used an adapted leaf blower (HUSQVARNA 125BVX) on the vacuum function to collect arthropods from forest understory vegetation within each sampling circle. We adapted the vacuum for arthropod collection by inserting a hardware cloth (1/2 in squares, 19-gauge galvanized steel, ACORN International) funnel into the vacuum tube. This ensured the mesh bags used for sample collection would not get sucked into machine components near the motor. We sewed mesh bags from organza fabric (6400 holes per in^2) to fit the diameter of the vacuum tube (18-in x 10-12-in) and when placed inside the vacuum tube for sampling, the excess material was inverted around the edge of the tube and secured in place with two rubber bands.

During arthropod collecting, we started the bug vacuum outside of the sampling circle then vacuumed all forest vegetation, including ground cover, shrubs, and low tree branches, within reach inside the circle (about 2.3 m from the ground) for three minutes. After collecting, we tied each mesh bag together quickly with a rubber band before turning off the vacuum. In the field, we kept mesh bags containing arthropods in a sealable 5-gallon bucket with ethyl acetate-soaked cotton, then stored them in a freezer until processing.

Arthropod processing

Vacuumed contents from each mesh bag were emptied into a tray and hand-sorted to removed large debris, like leaves and sticks, from arthropods and small debris. The remaining material was transferred to 70% ethanol until it was sorted under a dissecting scope to remove all arthropods from remaining debris. To quantify diversity, each arthropod was identified and counted, then placed in a pre-weighed 10 ml vial (VWR® Micro Centrifuge Tubes, Cat. No. 10025-724) with 95% ethanol. Non-spider arthropods were identified to order and placed in one vial, caterpillars, if present, were counted and placed in a second vial, and spiders were identified to family and placed in and a third vial. To quantify biomass, all vials were opened and placed under a hood for 24 hours to allow excess ethanol to evaporate, then placed in a drying oven set at 50˚ C for 48 hours (McCluney et al. 2017). Once dry, all vials were closed and weighed in milligrams (Sartorius Cubis® Micro Lab Balance, Item#: MSA6.6S0TRDM). For each vial, arthropod biomass was determined by subtracting the empty vial weight from the full vial weight.

Statistical Analyses

All analyses were conducted in R version 4.0.5 (R Core Team, 2021). We pooled arthropod data by forest site and calculated total abundance, total biomass, total richness, Shannon diversity index (H), and Simpson's diversity index (D) for non-spider arthropods and spiders. To compare arthropod communities between forests and cities, we created a similarity matrix of non-spider arthropods and spiders, using the metaMDS function in the package vegan, with the Bray-Curtis distance measure and random starting configuration (Oksanen et al. 2020). Each similarity matrix was inputted to a nonmetric multidimensional scaling (NMDS) model to visualize relationships between each site's arthropod communities. The NMDS results indicated different arthropod communities in Raleigh and Newark and supported our choice to analyze each city separately. We used linear regressions to elucidate relationships between arthropod abundance, biomass, richness, and diversity in urban forests. We log (x + 1) transformed arthropod abundance and biomass data but did not transform arthropod richness or diversity (Zuur et al. 2010, Ives 2015), and used the glm function from the 'stats' package to create regression models.

RESULTS

Nonmetric multidimensional scaling

The NMDS ordination of non-spider arthropod communities (Figure 3.1) and spider communities (Figure 3.2) are presented in two dimensions, with final acceptable stress values of 0.16 and 0.20 respectively (Kruskal 1964, Clarke 1993, McCune & Grace 2002). In the non-spider arthropod NMDS, the 24 urban forests separated in ordination space along Dimension 1 into two groups, indicating large differences between each city's communities. There was no distinct separation among forests along Dimension 2, indicating that this axis represents the differences in non-spider arthropod community composition among both cities. In the spider NMDS, there was no distinct separation among forests along Dimension 1 or 2, indicating greater similarity among the spider communities, compared to the non-spider arthropod communities, in Raleigh and Newark urban forests.

Arthropod communities

In both cities, the arthropod orders Araneae, Diptera, Hemiptera, and Hymenoptera were the most abundant and accounted for 88.9% of all arthropods in Raleigh and 76.3% in Newark (Figures 3.3 & 3.4). We collected 26 orders and 74,864 individual arthropods in Raleigh, and collected 25 orders and 81,427 individual arthropods in Newark. We collected 56,981 non-spider arthropods and 17,883 spiders in Raleigh and 67,715 non-spider arthropods and 13,712 spiders in Newark. Total biomass of collected arthropods in Raleigh was 27,508.3 mg; non-spider arthropods weighed 22,306.7 mg and spiders weighed 5,201.6 mg. Total biomass of collected arthropods in Newark was 28,060.3 mg; non-spider arthropods weighed 23,165.6 mg and spiders weighed 4,894.6 mg. The arthropod community in Raleigh was overall more diverse than Newark. Calculated Shannon and Simpson's diversity indices were 2.01 and 0.82 for Raleigh, and 1.75 and 0.77 for Newark, respectively.

Linear regressions

The only significant relationships between variables that were consistent between cities and between arthropod groups was a positive correlation between abundance and biomass, and a positive correlation between Shannon and Simpson's diversity indices (Figures 3.5 & 3.6). In Raleigh, non-spider arthropod richness was positively correlated with non-spider arthropod abundance and biomass. There were no other significant relationships between variables, however, arthropod abundance, biomass, and richness had generally positive trends while diversity generally declined in response to other variables.

DISCUSSION

We found little evidence to support a correlation between arthropod biomass and arthropod diversity in urban forests. We only tested two diversity indices out of many (Chao et al. 2005, Gotelli & Chao 2013, Hsieh et al. 2016, Roswell et al. 2021) but we chose the traditionally most reported diversity indices, which differ in sensitivity towards common and rare species and offer two representations of each community (Daly et al. 2018). Additionally, we found non-spider arthropod and spider communities vary by region, and trends between arthropod abundance, biomass, richness, and diversity should not be generalized across large spatial scales.

Arthropod communities differ among cities

Urban forests in Raleigh and Newark had different arthropod communities. NMDS results indicated that the non-spider arthropod communities were distinct in each city, while spider communities, at the family level, had overlap in community composition. We found similarities between regions; Raleigh and Newark arthropod communities were dominated by the same four orders, though in different rank order. Surveys of complete urban arthropod communities are limited, so we cannot compare our results to other reports of dominant urban arthropod orders, but commonly sampled taxa include Araneae (Alaruikka et al. 2002, Meineke et al. 2017, Melliger et al. 2018), Coleoptera (Alaruikka et al. 2002, Croci et l. 2008, Niemelä & Kotze 2009, Mitchell Chapter 1), Diptera (Adams et al. 2020), Hymenoptera (Hamblin et al. 2018, Melliger et al. 2018, Landsman et al. 2019, Adams et al. 2020), and Lepidoptera (Agra Iserhard et al. 2018, de Andrade et al. 2019, Adams et al. 2020, Orlandin & Carneiro 2021). However, whether these reports represent more urban-abundant taxon or a research-bias towards certain groups remains unclear. We also found differences between regions; Raleigh had a larger proportion of total arthropods that were spiders and had a more diverse arthropod community, compared to Newark. Factors other than being derived from different species pools can also affect relationships between abundance, biomass, richness, and diversity in urban arthropod communities of different regions. Regional comparisons, like those across latitude, demonstrate single species can exhibit different morphological traits, including body size, that may complicate expected trends between arthropod abundance and biomass (Niemelä & Kotze 2009, McCall & Pennings 2012, Horne et al. 2017). Other regional comparisons have found evidence for (Pennings et al. 2009, Heino et al. 2019) and against (Andrew & Hughes 2005, Schuch et al. 2011, Youngsteadt et al. 2017) latitudinal differences in arthropod diversity. Increasingly, there may be an underlying effect of climate on urban arthropod community change, as species' distributions and abundance can shift with climate change and increased warming (Butterfield 1996, Heino et al. 2015), which can be further exacerbated by the urban heat island effect (Meineke et al. 2013, Meineke et al. 2017, Youngsteadt et al. 2017, Hamblin et al. 2018, Lahr et al. 2018).

Correlations between arthropod abundance, biomass, richness, and diversity

As predicted, we found no correlation between arthropod abundance or biomass and diversity in urban forests in Raleigh or Newark (Gough et al. 1996, McArt et al. 2012, Youngsteadt et al. 2017). Likewise, we were unable to find published evidence of arthropod biomass correlating with diversity, though others have inferred a correlation (Hallmann et al. 2017, Hallmann et al. 2021). We expected to find correlations between arthropod abundance and biomass, as adding an individual of any size to a group will increase biomass. We did not quantify arthropod age or instar, but it may be expected that individual insects will increase in size as growing seasons progress, which may influence the positive relationship between abundance and biomass. Additionally, we did not sample sedentary, immobile arthropods like scale insects, which can become abundant in urban areas but have low biomass. We did not weigh arthropods separately by order, but we predict different relationships may exist between orders and feeding guilds, which could provide more detail regarding community change. We expected to find some correlation between arthropod richness and abundance or biomass, as supported by some (Southwood et al. 1982, McArt et al. 2012, Robertson et al. 2012, Ballard et al. 2013, Adams et al. 2020), though others found no correlation (Schuch et al. 2012, Hamblin et al. 2018). We also expected Shannon and Simpson's diversity indices to be positively correlated, since we included both to represent different aspects of the same diversity.

Conclusions and recommendations for research, interpretation, and management

Our results confirm our prediction that urban forest arthropod abundance and biomass are not correlated with diversity, and suggest quantifying the trends and mechanisms of arthropod decline will continue to require specimen identification in urban, and likely other, ecosystems. Our results support the use of multiple predictors of community structure in ecological studies, as varied metrics provide a more complete description of communities. Our results caution against generalizing or interpreting trends between arthropod abundance, biomass, richness and diversity across a range of regions or taxon. Additionally, we acknowledge these data were collected over six weeks and therefore cannot speak to changes in arthropod metrics over time. We recommend future sampling to quantify community metrics over time, as knowledge of urban ecosystems and communities may be invaluable in predicting trends of future global ecological conditions.

ACKNOWLEDGEMENTS

Thank you to the City of Raleigh, Town of Cary, North Carolina State University, US Forest Service, City of Newark, and University of Delaware for providing access to research sites. Thank you to Annemarie Nagle from the Frank Lab for providing logistical support and research supplies. Thank you to Michael Just, Caleb Wilson, Jane Petzoldt, and Sophia Copeman from the Frank Lab for advice regarding research design, statistical analyses, and more. Thank you to Alyanna Wilson, R. Kevin Aiken, Laney Kimble, R. David Mitchell, Owen Cass, Molly

Carlson, Chandler Purser, and Shawn Janairo for providing field help measuring vegetation and lab help processing vacuum samples and sorting arthropods. An additional thank you to Sophia Copeman for help identify arthropods to order. Thank you to FRAME researchers Vince D'Amico and Tara Trammell for collaboration and access to FRAME sites and protocols. Thank you to the US Department of Agriculture, US Geological Survey, NC Forest Service, and NC Invasive Plant Council for funding.

REFERENCES

Adams, B. J., Li, E., Bahlai, C. A., Meineke, E. K., McGlynn, T. P., & Brown, B. V. (2020). Local- and landscape-scale variables shape insect diversity in an urban biodiversity hot spot. *Ecological Applications*, *30*(4). https://doi.org/10.1002/eap.2089

Agra Iserhard, C., Duarte, L., Seraphim, Noemy, V. A., & Freitas, L. (2018). How urbanization affects multiple dimensions of biodiversity in tropical butterfly assemblages. *Biodiversity and Conservation*. https://doi.org/10.1007/s10531-018-1678-8

Alaruikka, D., Kotze, D. J., Matveinen, K., & Niemelä, J. (2002). Carabid beetle and spider assemblages along a forested urban-rural gradient in southern Finland. *Journal of Insect Conservation*, 6(4), 195–206. https://doi.org/10.1023/A:1024432830064

Andrew, N. R., & Hughes, L. (2005). Arthropod community structure along a latitudinal gradient: Implications for future impacts of climate change. In *Austral Ecology* (Vol. 30).

Ärje, J., Melvad, C., Jeppesen, M. R., Madsen, S. A., Raitoharju, J., Rasmussen, M. S., … Høye, T. T. (2020). Automatic image-based identification and biomass estimation of invertebrates. *Methods in Ecology and Evolution*, *11*(8), 922–931. https://doi.org/10.1111/2041-210X.13428

Ballard, M., Hough-Goldstein, J., & Tallamy, D. (2013). Arthropod Communities on Native and Nonnative Early Successional Plants. *Environmental Entomology*. https://doi.org/10.1603/EN12315

Boyes, D. H., Evans, D. M., Fox, R., Parsons, M. S., & Pocock, M. J. O. (2021). Is light pollution driving moth population declines? A review of causal mechanisms across the life cycle. *Insect Conservation and Diversity*, 14, 167–187. https://doi.org/10.1111/icad.12447

Butterfield, J. (1996). Carabid life-cycle strategies and climate change: A study on an altitude transect. *Ecological Entomology*. https://doi.org/10.1111/j.1365-2311.1996.tb00260.x

Cardoso, P., & Leather, S. R. (2019). Predicting a global insect apocalypse. *Insect Conservation and Diversity*, *12*(4), 263–267. https://doi.org/10.1111/icad.12367

Carrington, D. (2017). Warning of “ecological Armageddon” after dramatic plunge in insect numbers. *The Guardian*. www.theguardian.com/environment/2017/oct/18/warning-of-ecological-armageddon-after-dramatic-plunge-in-insect-number

Chao, A., Chazdon, R. L., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, *8*(2), 148–159. https://doi.org/10.1111/j.1461-0248.2004.00707.x

Clarke, K. R., & Ainsworth, M. (1993). A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*. https://doi.org/10.3354/meps092205

Croci, S., Butet, A., Georges, A., Aguejdad, R., & Clergeau, P. (2008). Small urban woodlands as biodiversity conservation hot-spot: A multi-taxon approach. *Landscape Ecology*, *23*(10), 1171–1186. https://doi.org/10.1007/s10980-008-9257-0

Daly, A. J., Baetens, J. M., & De Baets, B. (2018). Ecological diversity: Measuring the unmeasurable. *Mathematics*, 6. https://doi.org/10.3390/math6070119

de Andrade A. C., Dellefrate Franzini, L., & Mesquita, D. O. (2019). Assessing the effect of urbanization on tropical forest dwelling teiid lizards. *Ecological Indicators*. https://doi.org/10.1016/j.ecolind.2018.12.037

Frank, S. D., Backe, K. M., McDaniel, C., Green, M., Widney, S., & Dunn, R. R. (2019). Exotic urban trees conserve similar natural enemy communities to native congeners but have fewer pests. *Peer J*. https://doi.org/10.7717/peerj.6531

Gotelli, N. J., & Chao, A. (2013). Measuring and Estimating Species Richness, Species Diversity, and Biotic Similarity from Sampling Data. *Encyclopedia of Biodiversity: Second Edition*, 195–211. https://doi.org/10.1016/B978-0-12-384719-5.00424-X

Gough, G., Author, T., Marrs, R. H., Grace, J. B., & Gough, L. (1996). On the Relationship between Plant Species Diversity and Biomass: A Comment on a Paper by Gough, Grace and Taylor. *Oikos*, 75. https://www.jstor.org/stable/3546258?seq=1&cid=pdf-

Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., … De Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE*. https://doi.org/10.1371/journal.pone.0185809

Hallmann, C. A., Ssymank, A., Sorg, M., De Kroon, H., & Jongejans, E. (2021). *Insect biomass decline scaled to species diversity: General patterns derived from a hoverfly community*. https://doi.org/10.1073/pnas.2002554117/-/DCSupplemental.y

Hamblin, A. L., Youngsteadt, E., & Frank, S. D. (2018). Wild bee abundance declines with urban warming, regardless of floral density. *Urban Ecosystems*, *21*(3), 419–428. https://doi.org/10.1007/s11252-018-0731-4

Heino, J., Alahuhta, J., & Fattorini, S. (2015). Phylogenetic diversity of regional beetle faunas at high latitudes: patterns, drivers and chance along ecological gradients. *Biodiversity and Conservation*, *24*(11), 2751–2767. https://doi.org/10.1007/s10531-015-0963-z

Heino, J., Alahuhta, J., & Fattorini, S. (2019). Macroecology of ground beetles: Species richness, range size and body size show different geographical patterns across a climatically heterogeneous area. *Journal of Biogeography*, 46(11), 2548-2557. https://doi.org/10.1111/jbi.13693

Hillebrand, H., Bennett, D. M., & Cadotte, M. W. (2008). Consequences of Dominance: A Review of Evenness Effects on Local and Regional Ecosystem Processes. *Ecology*, 89(6), 1510-1520.

Horne, C. R., Hirst, A. G., & Atkinson, D. (2017). Seasonal body size reductions with warming covary with major body size gradients in arthropod species. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 1851. https://doi.org/10.1098/rspb.2017.0238

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, *7*(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Ives , A. R. (2015). For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution*, *6*(7), 828–835. https://doi.org/10.1111/2041-210X.12386

Kinsella, R. S., Thomas, C. D., Crawford, T. J., Hill, J. K., Mayhew, P. J., & Macgregor, C. J. (2020). Unlocking the potential of historical abundance datasets to study biomass change in flying insects. https://doi.org/10.1002/ece3.6546

Kruskal, J. B. (1964). Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika*, 29, 1–27.

Lahr, E. C., Dunn, R. R., & Frank, S. D. (2018). Getting ahead of the curve: cities as surrogates for global change. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2018.0643

Landsman, A. P., Ladin, Z. S., Gardner, D., Bowman, J. L., Shriver, G., D'Amico, V., & Delaney, D. A. (2019). Local landscapes and microhabitat characteristics are important determinants of urban–suburban forest bee communities. *Ecosphere*, *10*(10). https://doi.org/10.1002/ecs2.2908

Lister, B. C., & Garcia, A. (2018). Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proceedings of the National Academy of Sciences*. https://doi.org/10.1073/pnas.1722477115

McArt, S. H., Cook-Patton, S. C., & Thaler, J. S. (2012). Relationships between arthropod richness, evenness, and diversity are altered by complementarity among plant genotypes. *Oecologia*, *168*(4), 1013–1021. https://doi.org/10.1007/s00442-011-2150-6

McCall, B. D., & Pennings, S. C. (2012). Geographic variation in salt marsh structure and function. *Oecologia*, *170*(3), 777–787. https://doi.org/10.1007/s00442-012-2352-6

McCluney, K. E., Burdine, J. D., & Frank, S. D. (2017). Variation in arthropod hydration across US cities with distinct climate. *Journal of Urban Ecology*. https://doi.org/10.1093/jue/jux003

McCune, B. & Grace, J. B. (2002). *Analysis of Ecological Communities*. MJM Software Design.

Meineke, E. K., Dunn, R. R., Sexton, J. O., & Frank, S. D. (2013). Urban Warming Drives Insect Pest Abundance on Street Trees. *PLoS ONE*, *8*(3). https://doi.org/10.1371/journal.pone.0059687

Meineke, E. K., Holmquist, A. J., Wimp, G. M., & Frank, S. D. (2017). Changes in spider community composition are associated with urban temperature, not herbivore abundance. *Journal of Urban Ecology*. https://doi.org/10.1093/jue/juw010

Meineke, E. K., Classen, A. T., Sanders, N. J., & Jonathan Davies, T. (2019). Herbarium specimens reveal increasing herbivory over the past century. *Journal of Ecology*, *107*(1). https://doi.org/10.1111/1365-2745.13057

Melliger, R. L., Braschler, B., Rusterholz, H. P., & Baur, B. (2018). Diverse effects of degree of urbanisation and forest size on species richness and functional diversity of plants, and ground surface-active ants and spiders. *PLoS ONE*, *13*(6).

https://doi.org/10.1371/journal.pone.0199245

Montgomery, G. A., Dunn, R. R., Fox, R., Jongejans, E., Leather, S. R., Saunders, M. E., … Wagner, D. L. (2020). Is the insect apocalypse upon us? How to find out. *Biological Conservation*, 241. https://doi.org/10.1016/j.biocon.2019.108327

Nagy, D. D., Magura, T., Horváth, R., Debnár, Z., & Tóthmérész, B. (2018). Arthropod assemblages and functional responses along an urbanization gradient: A trait-based multi-taxa approach. *Urban Forestry and Urban Greening*, *30*, 157–168. https://doi.org/10.1016/j.ufug.2018.01.002

Niemelä, J., & Kotze, D. J. (2009). Carabid beetle assemblages along urban to rural gradients: A review. *Landscape and Urban Planning*. https://doi.org/10.1016/j.landurbplan.2009.05.016

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., … Maintainer, H. W. (2020). *'vegan' Community Ecology Package Version 2.5-7*.

Orlandin, E., & Carneiro, E. (2021). Classes of protection in urban forest fragments are effectiveless in structuring butterfly assemblages: landscape and forest structure are far better predictors. *Urban Ecosystems*. https://doi.org/10.1007/s11252-020-01086-z

Pennings, S. C., Salgado, C. S., Davé, N., Kunza, A. E., & Wason, E. L. (2009). Latitudinal variation in herbivore pressure in Atlantic Coast salt marshes. *Ecology*, 90.

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Raven, P. H., & Wagner, D. L. (2021). Agricultural intensification and climate change are rapidly decreasing insect biodiversity. *Proceedings of the National Academy of Sciences of the United States of America*, 118. https://doi.org/10.1073/PNAS.2002548117

Robertson, B. A., Porter, C., Landis, D. A., & Schemske, D. W. (2012). Agroenergy Crops Influence the Diversity, Biomass, and Guild Structure of Terrestrial Arthropod Communities. *Bioenergy Research*, *5*(1), 179–188. https://doi.org/10.1007/s12155-011-9161-3

Rosenheim, J. A., & Ward, P. S. (2020). Insect diversity over 36 years at a protected Sierra Nevada (California) site: towards an evaluation of the insect apocalypse hypothesis. *Ecological Entomology*, *45*(6), 1490–1494. https://doi.org/10.1111/een.12888

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. *Oikos*, *130*(3), 321–338. https://doi.org/10.1111/oik.07202

Saint-Germain, M., Buddle, C. M., Larrivée, M., Mercado, A., Motchula, T., Reichert, E., … Webb, A. (2007). Should biomass be considered more frequently as a currency in terrestrial arthropod community analyses? *Journal of Applied Ecology*, *44*(2), 330–339. https://doi.org/10.1111/j.1365-2664.2006.01269.x

Sánchez-Bayo, F., & Wyckhuys, K. A. G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*, 232, 8–27. https://doi.org/10.1016/j.biocon.2019.01.020

Schuch, S., Bock, J., Leuschner, C., Schaefer, M., & Wesche, K. (2011). Minor changes in orthopteran assemblages of Central European protected dry grasslands during the last 40 years. *Journal of Insect Conservation*, *15*(6), 811–822. https://doi.org/10.1007/s10841-011-9379-6

Schuch, S., Wesche, K., & Schaefer, M. (2012). Long-term decline in the abundance of leafhoppers and planthoppers (Auchenorrhyncha) in Central European protected dry grasslands. *Biological Conservation*, *149*(1), 75–83. https://doi.org/10.1016/j.biocon.2012.02.006

Seibold, S., Gossner, M. M., Simons, N. K., Blüthgen, N., Müller, J., Ambarlı, D., … Weisser, W. W. (2019). Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature*, *574*(7780), 671–674. https://doi.org/10.1038/s41586-019-1684-3

Shortall, R. C., Moore, A., Smith, E., Hall, J. M., Woiwod, P. I., & Harrington, R. (2009). Long-term changes in the abundance of flying insects. *Insect Conservation and Diversity*, *2*(4), 251–260. https://doi.org/10.1111/j.1752-4598.2009.00062.x

Simberloff, D. S., & Wilson, E. O. (1969). Experimental Zoogeography of Islands: The Colonization of Empty Islands. *Ecology*, 50(2), 278-296.

Simons, N. K., Gossner, M. M., Lewinsohn, T. M., Boch, S., Lange, M., Müller, J., … Weisser, W. W. (2014). Resource-mediated indirect effects of grassland management on arthropod diversity. *PLoS ONE*, *9*(9). https://doi.org/10.1371/journal.pone.0107033

Southwood, T. R. E., Moran, V. C., Kennedy, C. E. J., & Morant, V. C. (1982). The Richness, Abundance and Biomass of the Arthropod Communities on Trees. *Journal of Animal Ecology*, 51.

Youngsteadt, E., Ernst, A. F., Dunn, R. R., & Frank, S. D. (2017). Responses of arthropod populations to warming depend on latitude: evidence from urban heat islands. *Global Change Biology*. https://doi.org/10.1111/gcb.13550

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. https://doi.org/10.1111/j.2041- 210x.2009.00001.x

FIGURES

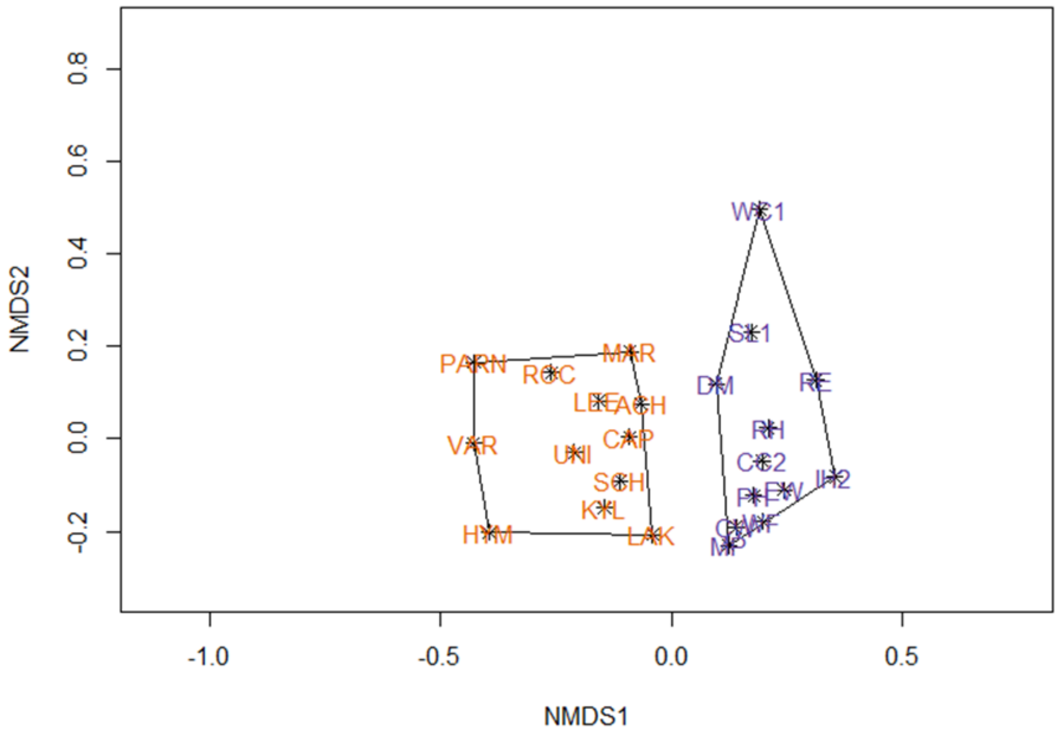


Figure 3.1. *NMDS of non-spider arthropod communities in Raleigh urban forests (orange labels) and Newark urban forests (purple labels). Final stress = 0. 156, nonmetric fit r2 = 0.976, linear fit r2 = 0.875.*

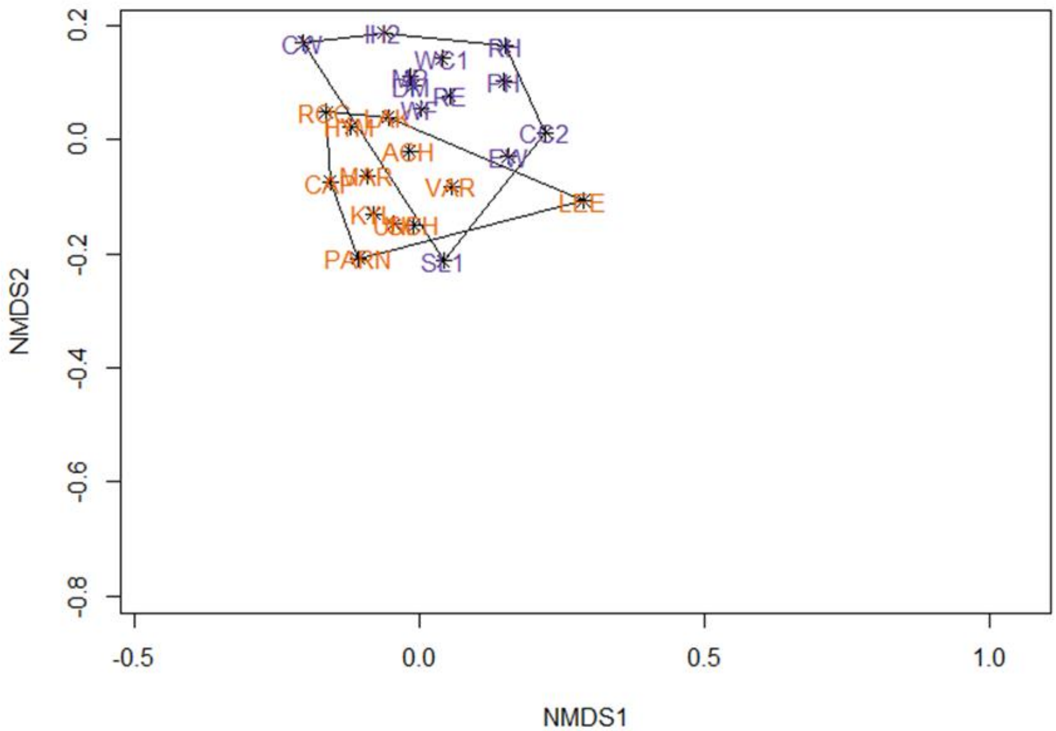


Figure 3.2. *NMDS of spider arthropod communities in Raleigh urban forests (orange labels) and Newark urban forests (purple labels). Final stress = 0.203, nonmetric fit r2 = 0.959, linear fit r2 = 0.767.*

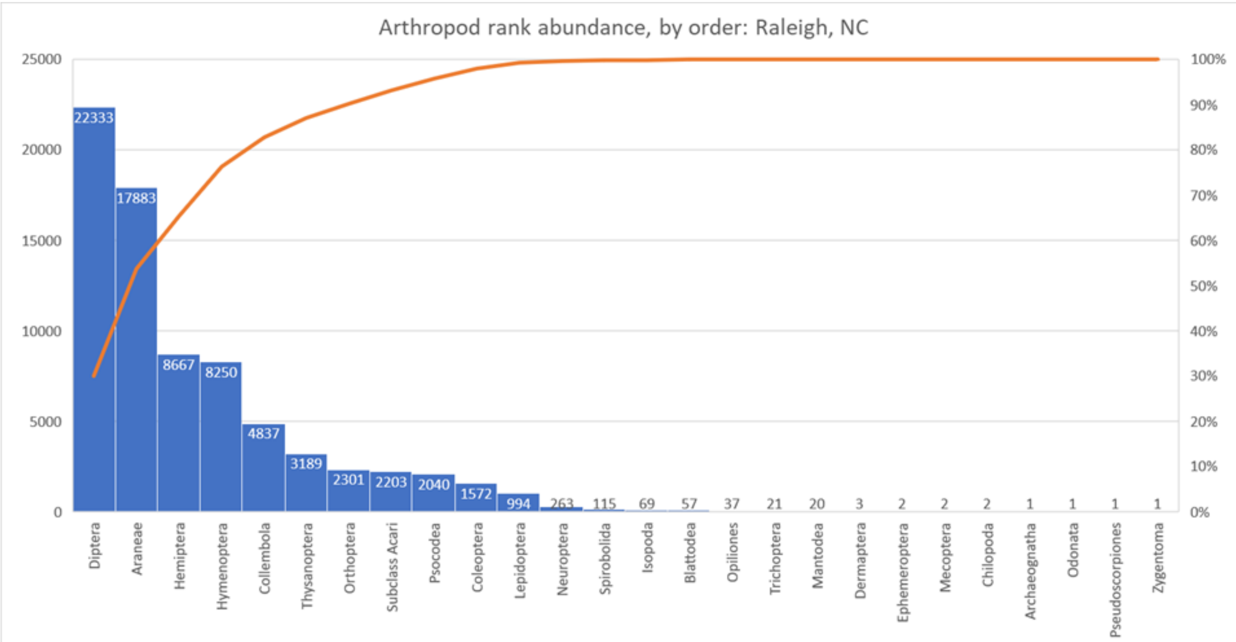


Figure 3.3. *Rank abundance of all captured arthropod orders in Raleigh urban forest understories. The blue bars quantify abundance of each arthropod order, labeled on the left y axis. The orange line quantifies the proportion of total arthropods captured, labeled on the right y axis, with each additional abundance-ranked order.*

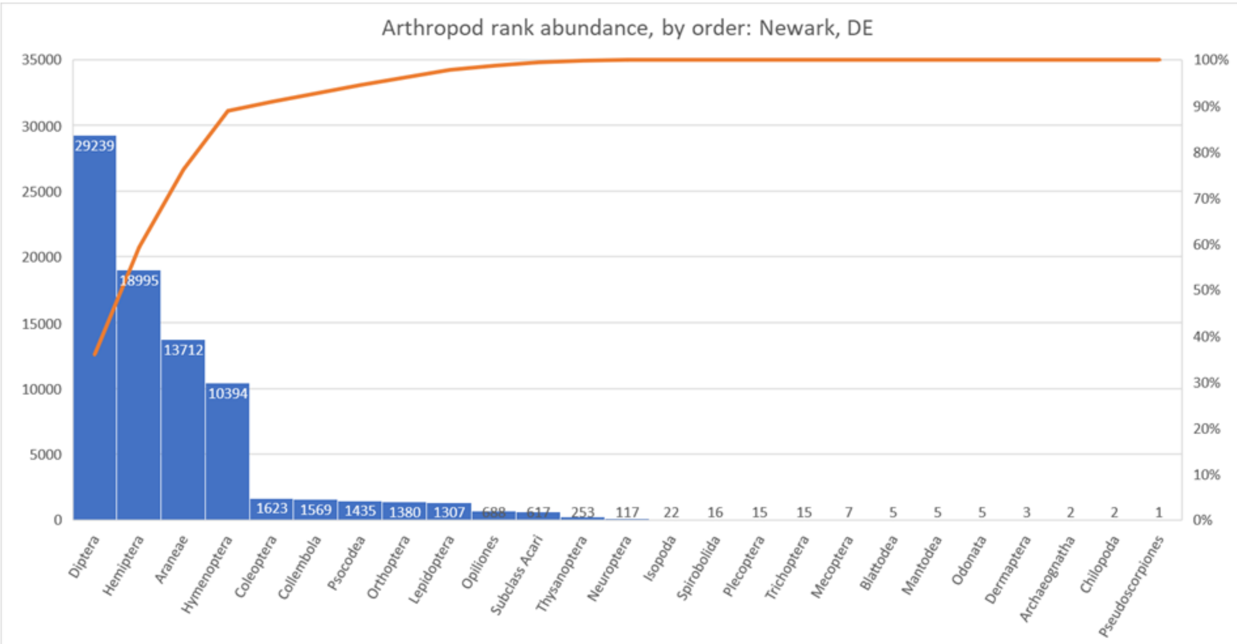


Figure 3.4. *Rank abundance of all captured arthropod orders in Newark urban forest understories. The blue bars quantify abundance of each arthropod order, labeled on the left y axis. The orange line quantifies the proportion of total arthropods captured, labeled on the right y axis, with each additional abundance-ranked order.*

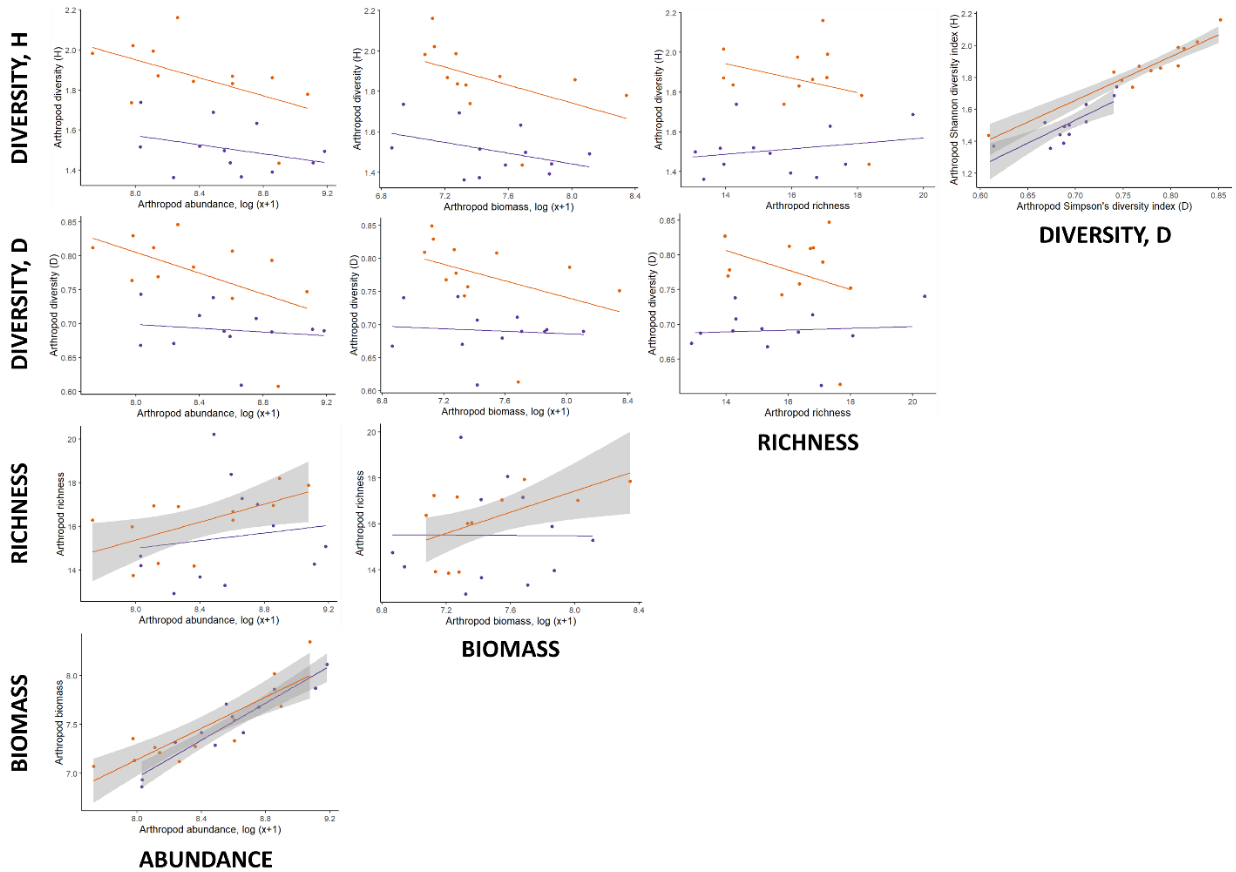


Figure 3.5. *Linear regressions between non-spider arthropod abundance, biomass, richness, Shannon diversity index (H), and Simpson's diversity index (D). Raleigh communities are shown in orange and Newark communities are shown in purple. Trend lines with 95% confidence intervals are significant.*

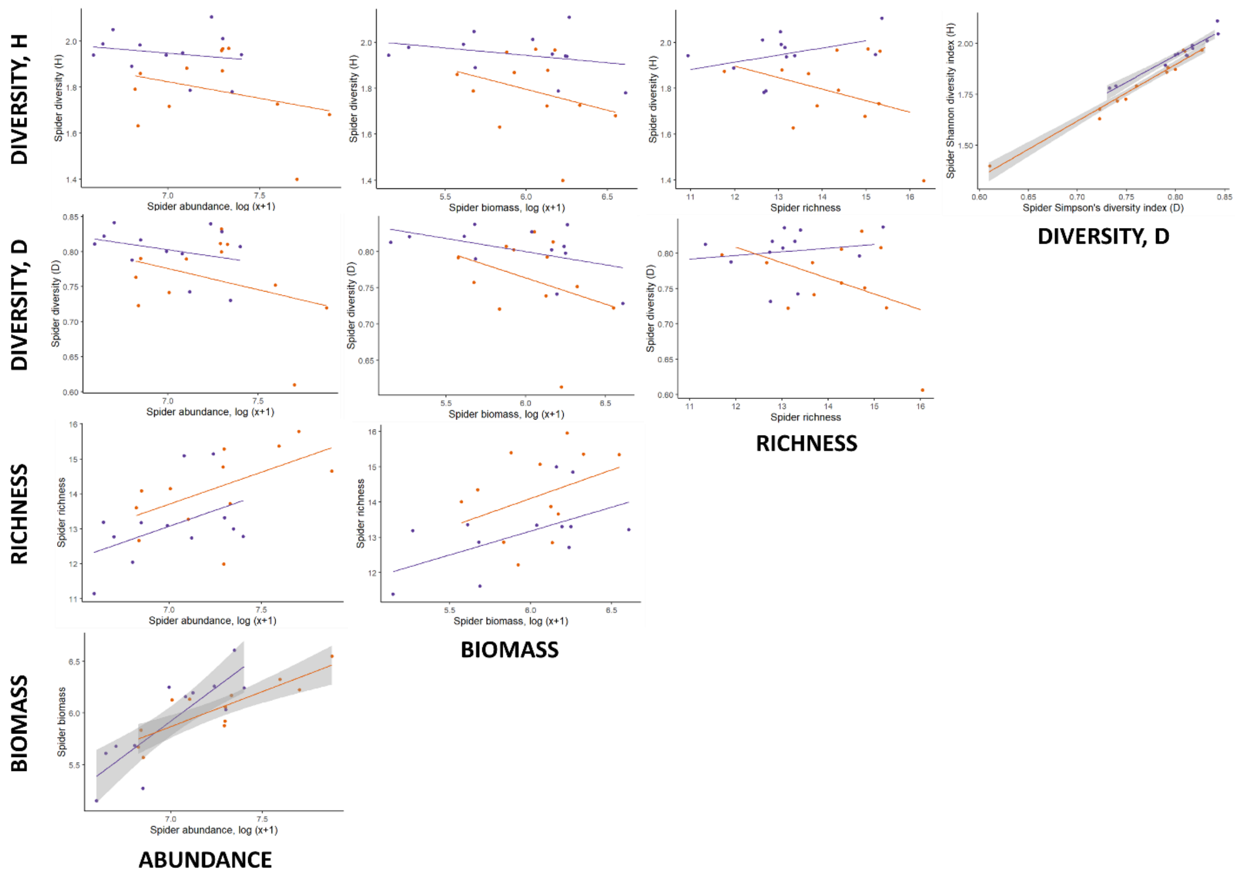


Figure 3.6. *Linear regressions between spider abundance, biomass, richness, Shannon diversity index (H), and Simpson's diversity index (D). Raleigh communities are shown in orange and Newark communities are shown in purple. Trend lines with 95% confidence intervals are significant.*

CHAPTER 4

Nonnative plant invasion increases urban forest structure and affects arthropod communities

ABSTRACT

Ecological theory and empirical evidence indicate that greater structural complexity and diversity in plant communities increases arthropod abundance and diversity. Nonnative plants are typically associated with low arthropod abundance and diversity due to lack of evolutionary history. However, nonnative plants increase the structural complexity of forests, as is common in urban forests. Therefore, urban forests are perfect ecosystems to determine whether structural complexity associated with nonnative plants will increase abundance and diversity of arthropods, as predicted by complexity literature, or whether structural complexity associated with nonnative plants will be depauperate of arthropods, as predicted by nonnative plant literature. We sampled 24 urban forests in two cites, Raleigh, NC and Newark, DE, to determine how nonnative plant complexity affects arthropods, and whether arthropods in different regions respond similarly to understory complexity and nonnative plant invasion. We quantified ground cover vegetation and shrub layer vegetation in each forest and created structural complexity metrics to represent total, nonnative, and native understory vegetation structural complexity. We vacuum sampled arthropods from vegetation and quantified non-spider arthropod and spider abundance, biomass, richness, and diversity. Our results confirm that nonnative plants increase understory vegetation complexity in urban forests. In Raleigh and Newark, we found support for, and against, the hypotheses that dense vegetation will increase arthropods and that nonnative vegetation will decrease arthropods. Urban forest arthropod abundance and biomass, but not diversity, increased with greater nonnative and native structural complexity. Arthropod richness and diversity

decreased with greater nonnative structural complexity. Our results suggest invaded urban forests may provide adequate food in the form of arthropod biomass to transfer energy to the next trophic level, but likely fail to provide ecological services and functions required for healthy urban forests. Urban land managers should survey urban forests for nonnative and native plant communities, and prioritize nonnative plant removal when allocating vegetation maintenance resources.

INTRODUCTION

Ecological theory and empirical evidence indicate that vegetation structural complexity and plant diversity increase arthropod abundance and diversity (Root 1973, Andow 1991, Carmona & Landis 1999, Thomas & Marshall 1999, Tilman 1999, Haddad et al. 2009, Borer et al. 2012). Denser and more complexly-structured vegetation can provide more food and shelter resources for a greater abundance of arthropods (Tilman 1999, Landis et al. 2005). Diverse plant communities offer diverse resources to generalists and specialists and can increase arthropod richness and diversity (Thomas and Marshall 1999, Haddad et al. 2009, O'Brien et al. 2017). Changes in plant communities affect trophic levels differently, altering amounts of herbivore and predator species in arthropod communities (Southwood et al. 1982, Haddad et al. 2009, Schuldt et al. 2014, Ebeling et al. 2014, O'Brien et al. 2017). Together, changes in plant communities can drastically alter arthropod abundance, biomass, richness, and diversity.

Nonnative plant species can increase forest structural complexity and affect plant diversity (Hartman & McCarthy 2008, Trammell & Carreiro 2011, Dyderski & Jagodziński 2020). Nonnative plant invasion can increase plant diversity by adding novel species to an area (Maskell et al. 2006, Kowarik 2011), which may contribute to greater structural complexity and increase arthropod diversity (Borer et al. 2012, Landsman et al. 2020). Alternatively, nonnative plant invasion can reduce plant diversity by outcompeting native species and suppressing native species growth (Trammell et al. 2012, Tanner & Gange 2013), which can reduce food resources and subsequently arthropod diversity (Tallamy 2004, Tallamy & Shropshire 2009, Burghardt & Tallamy 2013, Ballard et al. 2013, Richard et al. 2018). Additionally, nonnative plant species are geographically separated from their native arthropod community and therefore lack an evolutionary history with arthropods native to the invaded area, which reduces arthropod diversity (Adams et al. 2009, Kadlec et al. 2018, Narango et al. 2018). Arthropods frequently encounter nonnative plants in human-dominated landscapes, as many nonnative plants from the ornamental plant trade escape cultivation (Reichard & White 2001, Lehan et al. 2013) and grow well in disturbed areas (Pickett & Cadenasso 2009, Dyderski & Jagodziński 2019). Nonnative plant invasions are common in urban forests which are often adjacent to managed landscapes and frequently disturbed by human activities (Pickett et al. 2001, Malkinson et al. 2018).

Forests in urban areas are being recognized for their potential to conserve native species and natural resources (Mcdonald et al. 2008, Kowarik 2011, Aronson et al. 2014, Ives et al. 2016). Urban forests can contain diverse native biotic communities, including plants (Kϋhn et al. 2004, Aronson et al. 2014, Ives et al. 2016, Pregitzer et al. 2019, Trammell et al. 2020), arthropods (Croci et al. 2008, Tonietto et al. 2011, Agra Iserhard et al. 2018, de Andrade et al. 2019, Landsman et al. 2019), birds, mammals, reptiles, and amphibians (Croci et al. 2008, Aronson et al. 2014, Nielsen et al. 2014, MacGregor-Fors et al. 2016, Lerman et al. 2021), but are often degraded by city infrastructure expansion and development, ecosystem disturbances like the urban heat island effect and pollution, and nonnative species invasions (McDonnell et al. 1997, Pickett et al. 2001, Mcdonald et al. 2008, Seto et al. 2012, Beninde et al. 2015, Malkinson et al. 2018). Nonnative plants are particularly common in urban forests (McKinney 2002, Burton & Samuelson 2008, Aronson et al. 2015, Malkinson et al. 2018, Mitchell Chapter 1). Therefore, urban forests are perfect ecosystems with which to address the question: will structural complexity associated with nonnative plants increase arthropod abundance and diversity, as predicted by plant complexity literature, or will structural complexity associated with nonnative plants be depauperate of arthropods, as predicted by nonnative plant literature? To address this question, we sampled plant and arthropod communities from 24 urban forests to determine how nonnative plants affect structural complexity and plant diversity and how structural complexity and plant diversity affect arthropod communities. Within the eastern US, we collected plant and arthropod data from 12 forests around Raleigh, North Carolina and 12 forests around Newark, Delaware to determine if relationships between plant and arthropod communities are consistent in different regions with different nonnative plant communities.

METHODS

Site selection and vegetation sampling

This research was conducted in Raleigh, North Carolina (35.780˚N, 78.642˚W) and Newark, Delaware (39.683˚N, 75.753˚W) USA as part of the FRAME (FoRests Among Managed Ecosystems, https://sites.udel.edu/frame/) network of forests used to study urban forest ecology. We sampled 12 urban forests in each city for a total of 24 forests. We sampled plant communities at established sampling locations (N = 239, Trammell et al. 2020, Mitchell Chapter 1) in Newark forests in 2015 and in Raleigh forests in 2017. Plant communities with the FRAME have been extensively described, including overstory and understory trees and understory woody and herbaceous vegetation (Landsman et al. 2019, Trammell et al. 2020, Mitchell Chapter 1).

Briefly, we measured understory vegetation at two scales within a 2.5-m radius (19.6-m^2 area) circle surrounding sampling locations; we estimated percent cover by ground layer vegetation, and we counted stems in the shrub layer vegetation. We also estimated percent cover by nonnative ground vegetation, and identified dominant nonnative and native species. We identified and categorized the stems we counted as native or nonnative, and we combined ground cover and stem density species identifications to determine understory plant richness.

Arthropod collecting and processing

We collected arthropods at the same established locations within each forest using the vacuum sampling method described in Mitchell Chapter 3 (Figure 4.1). Vacuum samples were collected twice in 2019, in Raleigh between June 14-19 and July 17-19 and in Newark between June 22-24 and July 22-25. All non-arthropod material was removed from vacuum samples (Mitchell Chapter 3). Non-spider arthropods were identified to order and placed in a pre-weighed 1.5 ml vial (VWR® Micro Centrifuge Tubes, Cat. No. 10025-724) with 95% ethanol. If present (N = 213), caterpillars were placed in a second pre-weighed vial with 95% ethanol. Spiders were identified to family and placed in a third pre-weighed vial with 95% ethanol. All arthropod samples were dried and weighed in milligrams (Mitchell Chapter 3).

Statistical analyses

All analyses were conducted in R version 4.0.5 (R Core Team, 2021). We pooled arthropod data by sampling location and calculated abundance, biomass, richness, and Shannon diversity index (H) for non-spider arthropods and spiders. We separated caterpillar abundance and biomass from non-spider arthropod abundance and biomass in some analyses to determine if a strict herbivore group responded differently than arthropods combined. We created 3 similar structural complexity metrics to separate the effects of total, nonnative, and native structural complexity on arthropods. We created a total structural complexity metric first from percent total ground cover and total stem counts. We used data from both cities combined to determine the full data range for total ground cover and total stem counts and assigned 5 bins, labeled 1-5, to equally span each variable's range and represent increasing structural complexity in each vegetation layer. Each true data value was then attributed to a bin, and we added corresponding bin numbers representing ground cover and stem count structural complexity together to quantify understory structural complexity for each sampling location. This method was then repeated to create a nonnative structural complexity metric using percent nonnative ground cover and nonnative stem counts, and a native structural complexity metric using percent native ground cover and native stem counts. The nonnative and native complexity metrics used the same bin ranges as the total complexity metric, to ensure they were at comparable scales for analyses.

We used linear regressions to determine how total, nonnative, and native structural complexity affects arthropods in urban forests. We log (x + 1) transformed arthropod abundance and biomass data but did not transform arthropod richness or diversity (Zuur et al. 2010, Ives 2015). We used the glm function from the 'stats' package to create models for each city to determine the effects of nonnative structural complexity, native structural complexity, and their interaction, on the abundance, biomass, richness, and diversity of non-spider arthropods and spiders. Forest site was included in all models as a random variable.

RESULTS

Effects of plant origin on understory structural complexity

In both cities, total structural complexity increased as nonnative understory plant richness increased (Figure 4.2). The total structural complexity metric was positively correlated with the nonnative structural complexity metric. In Raleigh, total structural complexity decreased as native understory plant richness increased, while the total structural complexity metric was positively correlated with the native structural complexity metric. In Newark, total structural complexity increased as native understory plant richness increased, and the total structural complexity metric positively correlated with the native structural complexity metric.

Effects of understory structural complexity on arthropod communities

In both cities, non-spider arthropod abundance and biomass, with caterpillars removed, increased as total structural complexity increased (Figure 4.3). In Raleigh, non-spider arthropod richness increased as total structural complexity increased. In Newark, non-spider arthropod richness decreased as total structural complexity increased. In both cities, spider biomass increased as total structural complexity increased. In Newark, spider abundance increased as total structural complexity increased. In both cities, caterpillar abundance and biomass had no significant relationship with total structural complexity (Figure 4.4).

Effects of nonnative and native structural complexity on arthropod communities

In Raleigh, non-spider arthropod abundance increased as nonnative structural complexity increased (Figure 4.5). Non-spider arthropod biomass increased as nonnative and native structural complexity increased. Non-spider arthropod diversity decreased as nonnative structural complexity increased. Spider biomass increased as nonnative and native structural complexity increased. Spider diversity decreased as nonnative structural complexity increased. In Newark, non-spider arthropod abundance increased as native structural complexity increased (Figure 4.6). Non-spider arthropod biomass increased as nonnative and native structural complexity increased. Spider biomass increased as native structural complexity increased. Spider richness and spider diversity both decreased as nonnative structural complexity increased, and there were significant positive interactions between nonnative and native metrics in each model. Raleigh was the only city in which caterpillars had a significant response to nonnative or native structural complexity; caterpillar abundance increased as native structural complexity increased.

DISCUSSION

In urban forests, nonnative understory plant richness and nonnative structural complexity were more highly correlated with total structural complexity than native understory plant richness and native structural complexity. This indicates urban forest structural complexity is composed more by nonnative plant structure than native plant structure and that plant structure increases the amount of arthropods regardless of plant origin, suggesting nonnative plants in urban forests can support some arthropod populations and may provide food resources for higher trophic levels, like birds (Frank et al. 2019, Long & Frank 2020, Parsons et al. 2020). Total structural complexity generally increased arthropod abundance, biomass, and richness, but decreased diversity. This indicates the increase in arthropod abundance was not evenly distributed (Gotelli 2008), suggesting only certain non-spider orders and spider families increased in abundance as total structural complexity increased. Nonnative and native structural complexity both increased arthropod abundance and biomass, but only nonnative structural complexity decreased arthropod richness and diversity. This suggests that arthropod communities on structurally complex nonnative plants are abundant but dominated by a few common taxa, while structurally complex native plants have more abundant arthropods evenly distributed across taxa. We found caterpillar abundance, but not biomass, increased with greater native structural complexity in Raleigh forests. However, we found no effect of native structural complexity on caterpillars in Newark forests. This discrepancy questions expectations that native plants host more abundant caterpillar communities (Tallamy & Shropshire 2009, Burghardt & Tallamy 2013, Burghardt & Tallamy 2015). We acknowledge our arthropod collection protocol was not designed to describe urban forest caterpillar communities specifically, but feel our results still represent a sample of urban forest understory caterpillars.

Effects of plant origin on understory structural complexity

Responses of total structural complexity to nonnative and native understory plant richness differed by city. Raleigh forests had more nonnative understory vegetation and Newark forests had more native understory vegetation (Mitchell Chapter 1). The most abundant understory species in Raleigh were primarily nonnative (*Hedera helix*, *Ligustrum sinense*, *Lonicera japonica*, *Microstegium vimineum*, *Smilax rotundifolia*, *Vinca sp.*, *Vitis rotundifolia*) with vining and low-growing herbaceous structure, while Newark's most abundant understory species were primarily native (*Clethra alnifolia*, *Lindera benzoin*, *Lonicera japonica*, *Rosa multiflora*, *Thelypteris noveboracensis*, *Toxicodendron radicans*, *Viburnum dentatum*) with a combination of shrub and vining or low-growing herbaceous structure (Mitchell Chapter 1, Table 1.5). In rural Maryland forests the presence of a nonnative shrub (*Rosa multiflora*), also common in our Newark forests, increased forest structure (Landsman & Bowman 2017).

Effects of understory structural complexity on arthropod communities

Our results showed responses of arthropods to total structural complexity were generally positive, but specific relationships differed by city. Non-spider arthropod and spider biomass increased with greater understory structure in Raleigh and Newark, but caterpillar biomass did not. Greater understory structural complexity increased insect and spider abundance in rural Maryland forests (Landsman & Bowman 2017) and arthropod occupancy in Australian urban green spaces (Threlfall et al. 2017). Greater forest complexity was correlated with greater butterfly richness in Brazil (Orlandin & Carneiro 2021), reduced ant richness in Australia (Lassau & Hochuli 2004), and reduced spider richness in rural Maryland (Landsman & Bowman 2017). From our results, non-spider arthropod diversity in Newark was the only arthropod response metric to respond negatively to increased structural complexity. These results are similar to a study in France that found dense shrub layer vegetation in urban forests reduced carabid beetle diversity (Croci et al. 2008) but differ from a study in Argentina that measured reduced arthropod diversity in low structural complexity forest vegetation (Gardner et al. 1995). We found greater non-spider arthropod diversity in Raleigh compared to Newark, and non-spider arthropod diversity was different between cities while spider diversity was similar among cities. This may indicate some influence of Raleigh's greater proportion of nonnative plant species on non-spider arthropod diversity, as Landsman & Bowman (2017) found greater spider diversity in areas of dense nonnative ground cover compared to structurally less complex control areas.

Effects of nonnative and native structural complexity on arthropod communities

Responses of arthropods to nonnative and native structural complexity differed by city, but in general, structurally complex vegetation increased abundance and biomass and decreased richness and diversity. Nonnative plant richness in rural Maryland forests reduced insect abundance and biomass (Landsman & Bowman 2017). Plots invaded by a nonnative grass (*Microstegium vimineum*), also common in our Raleigh forests, had greater invertebrate abundance and greater spider diversity compared to uninvaded reference plots (Landsman et al. 2020). In Raleigh, insect predator abundances were similar on native trees and nonnative congeners (*Acer* spp. and *Quercus* spp.), but predator communities on nonnative congeners differed from those on native trees (Frank et al. 2019). In the UK, arthropod biomass was greater on two native trees (*Quercus* spp.) compared to two nonnative trees in the same genus

(Southwood et al. 2004). Native plant richness in rural Maryland increased abundance and biomass of some insect orders (Landsman & Bowman 2017) and greater native vegetation in Australian urban green spaces increased arthropod occupancy (Threlfall et al. 2017). Native or drought-tolerant plants in Los Angeles County urban sites increased insect abundance, richness, and diversity (Adams et al. 2020). In a replicated, planted field trial conducted in Newark, arthropod abundance, biomass, and richness were greater on native plants than nonnative plants (Ballard et al. 2013).

Conclusions and management implications

In Raleigh and Newark, we found support for, and against, the hypotheses that more vegetation will increase arthropods and that nonnative vegetation will decrease arthropods. Urban forest arthropod abundance and biomass increased with greater nonnative and native structural complexity, but we found no evidence that increased structure increased arthropod diversity, as predicted by plant complexity literature. Arthropod richness and diversity decreased with greater nonnative structural complexity, but nonnative plants were not depauperate of arthropods, as predicted by nonnative plant literature. This suggests urban forests invaded by nonnative plants may still provide adequate food biomass to transfer energy to the next trophic level, but may fail to provide ecological services and functions required for healthy urban forests. Urban land managers could consider plant species origin when managing urban green space and prioritize the removal of nonnative structure when allocating vegetation maintenance resources. Here, we detail relationships between urban forest arthropods and understory vegetation structural complexity and demonstrate that changes in arthropod diversity are not predictable from arthropod abundance, biomass, or richness.

ACKNOWLEDGEMENTS

Thank you to the City of Raleigh, Town of Cary, North Carolina State University, US Forest Service, City of Newark, and University of Delaware for providing access to research sites. Thank you to Annemarie Nagle, Lawrence Long, Michael Just, Kristi Backe, Sarah Parsons, Elsa Youngsteadt, Samantha Larsen, Nora Lahr, Caleb Wilson, Jane Petzoldt, Sophia Copeman, Catherine Crofton, Doua Jim Lor, Logan Tyson, Kyle Sozanski, Hannah Frank, Maggie Hamilton, Alyanna Wilson, R. Kevin Aiken, Laney Kimble, Owen Cass, Molly Carlson, Chandler Purser, Shawn Janairo for assistance in Raleigh. Thank you to Vince D'Amico and Tara Trammell for collaboration and access to FRAME sites and protocols. Thank you to Covel McDermot, Eric Moore, Carl Rosier, Zach Ladin, Matt McDermitt, Nathaly Rodriguez, Andrew Adams, and R. David Mitchell for field help in Newark. Thank you to the US Department of Agriculture, US Geological Survey, NC Forest Service, and NC Invasive Plant Council for funding.

REFERENCES

Adams, J. M., Fang, W., Callaway, R. M., Cipollini, D., Newell, E., & TRAIN. (2009). A cross-continental test of the Enemy Release Hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. *Biological Invasions*, 11, 1005-1016. DOI 10.1007/s10530-008-9312-4

Adams, B. J., Li, E., Bahlai, C. A., Meineke, E. K., McGlynn, T. P., & Brown, B. V. (2020). Local- and landscape-scale variables shape insect diversity in an urban biodiversity hot spot. *Ecological Applications*, *30*(4). https://doi.org/10.1002/eap.2089

Agra Iserhard, C., Duarte, L., Seraphim, Noemy, V. A., & Freitas, L. (2018). How urbanization affects multiple dimensions of biodiversity in tropical butterfly assemblages. *Biodiversity and Conservation*. https://doi.org/10.1007/s10531-018-1678-8

Andow, D. A. (1991). Vegetational diversity and arthropod population response. *Annu. Rev. Entomol*, 36, 561-586.

Aronson, M. F. J., La Sorte, F. A., Nilon, C. H., Katti, M., Goddard, M. A., Lepczyk, C. A., … Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2013.3330

Aronson, M. F. J., Handel, S. N., La Puma, I. P., & Clemants, S. E. (2015). Urbanization promotes non-native woody species and diverse plant assemblages in the New York metropolitan region. *Urban Ecosystems*, *18*(1), 31–45. https://doi.org/10.1007/s11252-014-0382-z

Ballard, M., Hough-Goldstein, J., & Tallamy, D. (2013). Arthropod Communities on Native and Nonnative Early Successional Plants. *Environmental Entomology*. https://doi.org/10.1603/EN12315

Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*, 18, 581-592.

Borer, E. T., Seabloom, E. W., & Tilman, D. (2012). Plant diversity controls arthropod biomass and temporal stability. *Ecology Letters*, 15, 1457-1464.

Burghardt, K. T., & Douglas W. T. (2013). Plant Origin Asymmetrically Impacts Feeding Guilds and Life Stages Driving Community Structure of Herbivorous Arthropods. *Diversity and Distributions.* https://doi.org/10.1111/ddi.12122

Burghardt, K. T., & Douglas W. T. (2015). Not all non-natives are equally unequal: reductions in herbivore β-diversity depend on phylogenetic similarity to native plant community. *Ecology Letters.* https://doi.org/10.1111/ddi.12122

Burton, M. L., & Samuelson, L. J. (2008). Influence of urbanization on riparian forest diversity and structure in the Georgia Piedmont, US. *Plant Ecology*, 195(1), 99–115. https://doi.org/10.1007/s11258-007-9305-x

Carmona, D. M, & Landis, D. A. (1999). Influence of Refuge Habitats and Cover Crops on Seasonal Activity-Density of Ground Beetles (Coleoptera: Carabidae) in Field Crops. *Environ. Entomol.*, 28. https://academic.oup.com/ee/article/28/6/1145/451198.

Croci, S., Butet, A., Georges, A., Aguejdad, R., & Clergeau, P. (2008). Small urban woodlands as biodiversity conservation hot-spot: A multi-taxon approach. *Landscape Ecology*, *23*(10), 1171–1186. https://doi.org/10.1007/s10980-008-9257-0

de Andrade A. C., Dellefrate Franzini, L., & Mesquita, D. O. (2019). Assessing the effect of urbanization on tropical forest dwelling teiid lizards. *Ecological Indicators*. https://doi.org/10.1016/j.ecolind.2018.12.037

Dyderski, M., & Jagodziński, A. (2019). Context-Dependence of Urban Forest Vegetation Invasion Level and Alien Species' Ecological Success. *Forests*. https://doi.org/10.3390/f10010026

Dyderski, M. K., & Jagodziński, A. M. (2020). Impact of invasive tree species on natural regeneration species composition, diversity, and density. *Forests*, *11*(4). https://doi.org/10.3390/F11040456

Ebeling, A., Meyer, S. T., Abbas, M., Eisenhauer, N., Hillebrand, H., et al. (2014). Plant Diversity Impacts Decomposition and Herbivory via Changes in Aboveground Arthropods. *PLoS ONE*, 9(9). doi:10.1371/journal.pone.0106529

Frank, S. D., Backe, K. M., McDaniel, C., Green, M., Widney, S., & Dunn, R. R. (2019). Exotic urban trees conserve similar natural enemy communities to native congeners but have fewer pests. https://doi.org/10.7717/peerj.6531

Gardner, S. M., Cabido, M. R., Valladares, G. R. & Diaz, S. (1995). The Influence of Habitat Structure on Arthropod Diversity in Argentine Semi-Arid Chaco Forest. *Journal of Vegetation Science*, 6(3), 349–356. https://doi.org/10.2307/3236234.

Gotelli, N. J. (2008). *A Primer of Ecology (fourth)*. Sinauer Associates, Inc.

Haddad, N. M., Crutsinger, G. M., Gross, K., Haarstad, J., Knops, J. M. H., & Tilman D. (2009). Plant Species Loss Decreases Arthropod Diversity and Shifts Trophic Structure. *Ecology Letters*, 12(10), 1029–39. https://doi.org/10.1111/j.1461-0248.2009.01356.x.

Hartman, K. M. & McCarthy, B. C. (2008). Changes in Forest Structure and Species Composition following Invasion by a Non-Indigenous Shrub, Amur Honeysuckle (Lonicera maackii). *The Journal of the Torrey Botanical Society*, 135(2), 245-259.

Ives, A. R. (2015). For testing the significance of regression coefficients, go ahead and log-transform count data. *Methods in Ecology and Evolution*, *6*(7), 828–835. https://doi.org/10.1111/2041-210X.12386

Ives, C. D., Lentini, P. E., Threlfall, C. G., Ikin, K., Shanahan, D. F, et al. (2016). Cities are hotspots forthreatened species. *Global Ecology and Biogeography*, 25, 117-126.

Kadlec, T., Štrobl, M., Hanzelka, J. Hejda, M., & Reif, J. (2018). Differences in the community composition of nocturnal Lepidoptera between native and invaded forests are linked to the habitat structure. *Biodiversity and Conservation*, 27(10), 2661-2680.

Kowarik, I. (2011). Novel urban ecosystems, biodiversity, and conservation. *Environmental Pollution*, 159, 1974–1983. https://doi.org/10.1016/j.envpol.2011.02.022

Kühn, I., Brandl, R., & Klotz, S. (2004). The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, 6, 749-764.

Landis, D. A., Menalled, F. D., Costamagna, A. C., & Wilkinson, T. K. (2005). Manipulating plant resources to enhance beneficial arthropods in agricultural landscapes. *Weed Science*, 53(6), 902–908. https://doi.org/10.1614/ws-04-050r1.1

Landsman, A. P., & Bowman, J. L. (2017). Discordant response of spider communities to forests disturbed by deer herbivory and changes in prey availability. *Ecosphere*, 8(2). https://doi.org/10.1002/ecs2.1703

Landsman, A. P., Ladin, Z. S., Gardner, D., Bowman, J. L., Shriver, G., D'Amico, V., & Delaney, D. A. (2019). Local landscapes and microhabitat characteristics are important determinants of urban–suburban forest bee communities. *Ecosphere*, *10*(10). https://doi.org/10.1002/ecs2.2908

Landsman, A. P., Burghardt, K. T., & Bowman, J. L. (2020). Invasive grass (Microstegium vimineum) indirectly benefits spider community by subsidizing available prey. *Ecology and Evolution*, 10(20), 11133–11143. https://doi.org/10.1002/ece3.6752

Lassau, S. A., & Hochuli, D. F. (2004). Effects of habitat complexity on ant assemblages. *Ecography*, 27, 157-164.

Lehan, N. E., Murphy, J. R., Thorburn, L. P., & Bradley, B. A. (2013). Accidental introductions are an important source of invasive plants in the continental United States. *American Journal of Botany*, 100(7), 1287–1293. https://doi.org/10.3732/ajb.1300061

Lerman, S. B., Narango, D. L., Avolio, M. L., Bratt, A. R., Engebretson, J. M., Groffman, P. M., … Trammell, T. L. E. (2021). Residential yard management and landscape cover affect urban bird community diversity across the continental USA. *Ecological Applications*. https://doi.org/10.1002/eap.2455

Long, L. C., & Frank, S. D. (2020). Risk of bird predation and defoliating insect abundance are greater in urban forest fragments than street trees. *Urban Ecosystems*. https://doi.org/10.1007/s11252-020-00939-x

MacGregor-Fors, I., Escobar, F., Rueda-Hernández, R., Avendaño-Reyes, S., Baena, M. L., Bandala, V. M., … Utrera-Barrillas, E. (2016). City "green" contributions: The role of urban greenspaces as reservoirs for biodiversity. *Forests*, 7(7). https://doi.org/10.3390/f7070146

Malkinson, D., Kopel, D., & Wittenberg, L. (2018). From rural-urban gradients to patch – matrix frameworks: Plant diversity patterns in urban landscapes. *Landscape and Urban Planning*, *169*, 260–268. https://doi.org/10.1016/j.landurbplan.2017.09.021

Maskell, L. C., Bullock, J. M., Smart, S. M., & Thompson, P. E. H. (2006). The distribution and habitat associations of non-native plant species in urban riparian habitats. *Journal of Vegetation Science*, 17(4).

Mcdonald, R. I., Kareiva, P., & Forman, R. T. T. (2008). The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141(6), 1695–1703. https://doi.org/10.1016/j.biocon.2008.04.025

McDonnell, M. J., Pickett, T. A., Groffman, P., Bohlen, P., Pouyat, R. V, Zipperer, W. C., … Medley, K. (1997). Ecosystem Processes Along an Urban-to-Rural Gradient. *Urban Ecosystems,* 1, 21-36.

McKinney, M. L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, *11*(2), 161–176. https://doi.org/10.1007/s11252-007-0045-4

Narango, D. L., Tallamy, D. W., & Marra, P. P. (2018). Nonnative plants reduce population growth of an insectivorous bird. *Proceedings of the National Academy of Sciences*, 115(45). https://doi.org/10.1073/pnas.1809259115

O'Brien, M. J., Brezzi, M., Schuldt, A., Zhang, J. Y., Ma, K., Schmid, B., & Niklaus, P. A. (2017). Tree diversity drives diversity of arthropod herbivores, but successional stage mediates detritivores. *Ecology and Evolution*, 7(21), 8753–8760. https://doi.org/10.1002/ece3.3411

Orlandin, E., & Carneiro, E. (2021). Classes of protection in urban forest fragments are effectiveless in structuring butterfly assemblages: landscape and forest structure are far better predictors. *Urban Ecosystems*. https://doi.org/10.1007/s11252-020-01086-z

Parsons, S. E., Kerner, L. M., & Frank, S. D. (2020). Effects of native and exotic congeners on diversity of invertebrate natural enemies, available spider biomass, and pest control services in residential landscapes. *Biodiversity and Conservation*. https ://doi.org/10.1007/s1053 1-020-01932 -8

Pickett, S. T. A., & Cadenasso, M. L. (2009). Altered resources, disturbance, and heterogeneity: A framework for comparing urban and non-urban soils. *Urban Ecosystems*, *12*(1), 23–44. https://doi.org/10.1007/s11252-008-0047-x

Pickett, S. T. A., Cadenasso, M. L., Grove, J. M., Nilon, C. H., Pouyat, R. V, Zipperer, W. C., & Costanza, R. (2001). Urban Ecological Systems: Linking Terrestrial Ecological, Physical, and Socioeconomic Components of Metropolitan Areas. *Annu. Rev. Ecol. Syst*., 16, 127-157.

Pregitzer, C. C., Charlop-Powers, S., Bibbo, S., Forgione, H. M., Gunther, B., Hallett, R. A., & Bradford, M. A. (2019). A city-scale assessment reveals that native forest types and overstory species dominate New York City forests. *Ecological Applications*, *29*(1). https://doi.org/10.1002/eap.1819

R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Reichard, S. H., & White, P. (2001). Articles Horticulture as a Pathway of Invasive Plant Introductions in the United States. *BioScience*, 51. https://academic.oup.com/bioscience/article/51/2/103/390610

Richard, M., Tallamy, D. W., & Mitchell, A. B. (2018). Introduced plants reduce species interactions. *Biological Invasions*. https://doi.org/10.1007/s10530-018-1876-z

Root, R. B. (1973). Organization of a Plant-Arthropod Association in Simple and Diverse Habitats: The Fauna of Collards (Brassica Oleracea). *Ecological Monographs*, 43(1), 95-124.

Schuldt, A., Baruffol, M., Bruelheide, H., Chen, S., Chi, X., Wall, M., & Assmann, T. (2014). Woody plant phylogenetic diversity mediates bottom-up control of arthropod biomass in species-rich forests. *Oecologia*, 176(1), 171–182. https://doi.org/10.1007/s00442-014-3006-7

Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences of the United States of America*, 109(40), 16083–16088. https://doi.org/10.1073/pnas.1211658109

Southwood, T. R. E., Moran, V. C., Kennedy, C. E. J., & Morant, V. C. (1982). The Richness, Abundance and Biomass of the Arthropod Communities on Trees. *Journal of Animal Ecology*, 51.

Southwood, T. R. E., Wint, G. R. W., Kennedy, C. E. J., & Greenwood, S. R. (2004). Seasonality, abundance, species richness and specificity of the phytophagous guild of insects on oak (Quercus) canopies. *European Journal of Entomology*, 101(1), 43–50. https://doi.org/10.14411/eje.2004.011

Tallamy, D. W. (2004). Do alien plants reduce insect biomass? *Conservation Biology*. https://doi.org/10.1111/j.1523-1739.2004.00512.x

Tallamy, D. W., & Shropshire, K. J. (2009). Ranking lepidopteran use of native versus introduced plants. *Conservation Biology*. https://doi.org/10.1111/j.1523-1739.2009.01202.x

Tanner, R. A., & Gange, A. C. (2013). The impact of two non-native plant species on native flora performance: Potential implications for habitat restoration. *Plant Ecology*, 214(3), 423–432. https://doi.org/10.1007/s11258-013-0179-9

Thomas, C. F. G., & Marshall, E. J. P. (1999). Arthropod abundance and diversity in differently vegetated margins of arable fields. *Agriculture, Ecosystems, and Environment*, 72, 131–144.

Threlfall, C. G., Mata, L., Mackie, J. A., Hahs, A. K., Stork, N. E., Williams, N. S. G., & Livesley, S. J. (2017). Increasing biodiversity in urban green spaces through simple vegetation interventions. *Journal of Applied Ecology*, 54(6). https://doi.org/10.1111/1365-2664.12876

Tilman, D. (1999). The ecological consequences of changes in biodiversity: a search for general principles. *Ecology*, 80(5), 1455-1474.

Tonietto, R., Fant, J., Ascher, J., Ellis, K., & Larkin, D. (2011). A comparison of bee communities of Chicago green roofs, parks and prairies. *Landscape and Urban Planning*, 103(1), 102-108.

Trammell, T. L. E., & Carreiro, M. M. (2011). Vegetation composition and structure of woody plant communities along urban interstate corridors in Louisville, KY, U.S.A. *Urban Ecosystems*. https://doi.org/10.1007/s11252-011-0193-4

Trammell, T. L. E., Ralston, H. A., Scroggins, S. A., & Carreiro, M. M. (2012). Foliar production and decomposition rates in urban forests invaded by the exotic invasive shrub, Lonicera maackii. *Biological Invasions*. https://doi.org/10.1007/s10530-011-0093-9

Trammell, T. L. E., D'Amico, V., Avolio, M. L., Mitchell, J. C., & Moore, E. (2020). Temperate deciduous forests embedded across developed landscapes: younger forests harbor invasive plants and urban forests maintain native species. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.13400

Zuur, A. F., Ieno, E. N., & Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14. https://doi.org/10.1111/j.2041- 210x.2009.00001.x

FIGURES

Figure 4.1. *Differences between (a) high structural complexity and (b) low structural complexity, as found within one urban forest in Newark.*

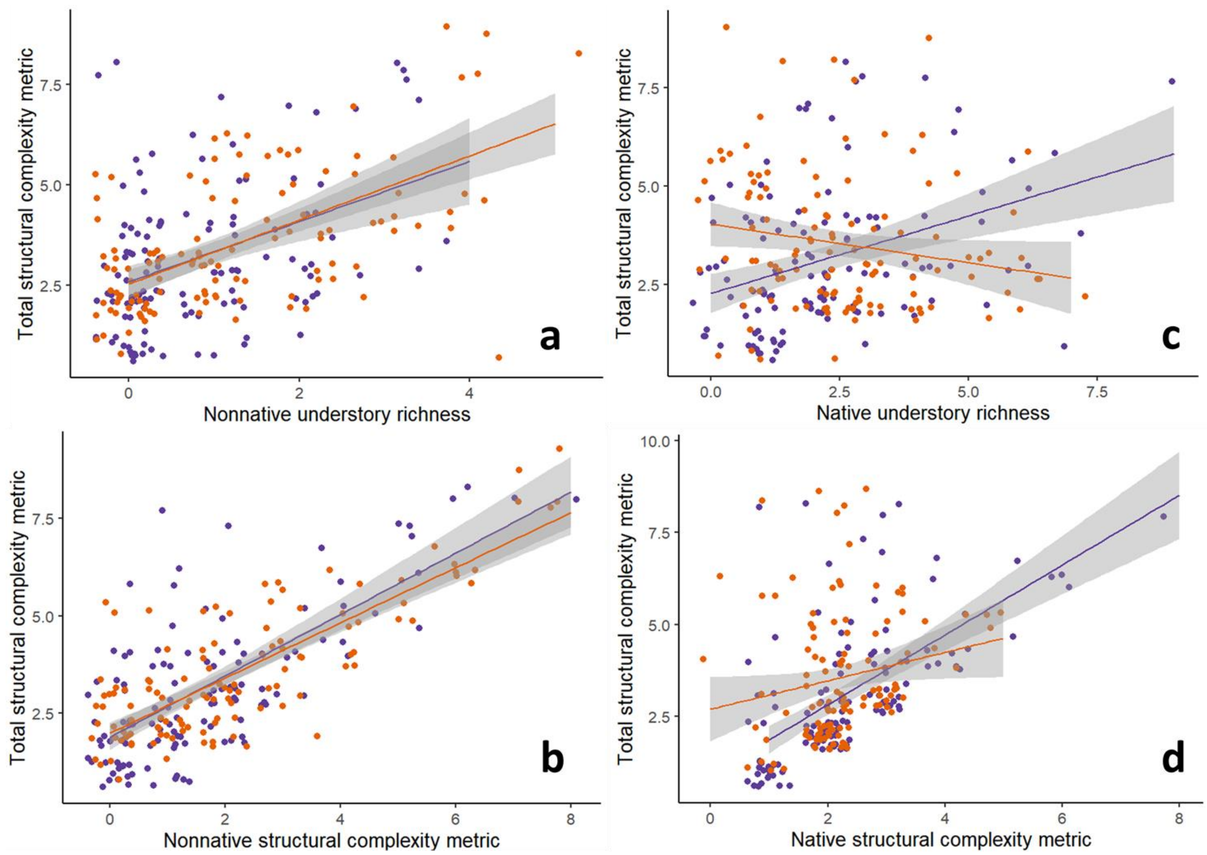
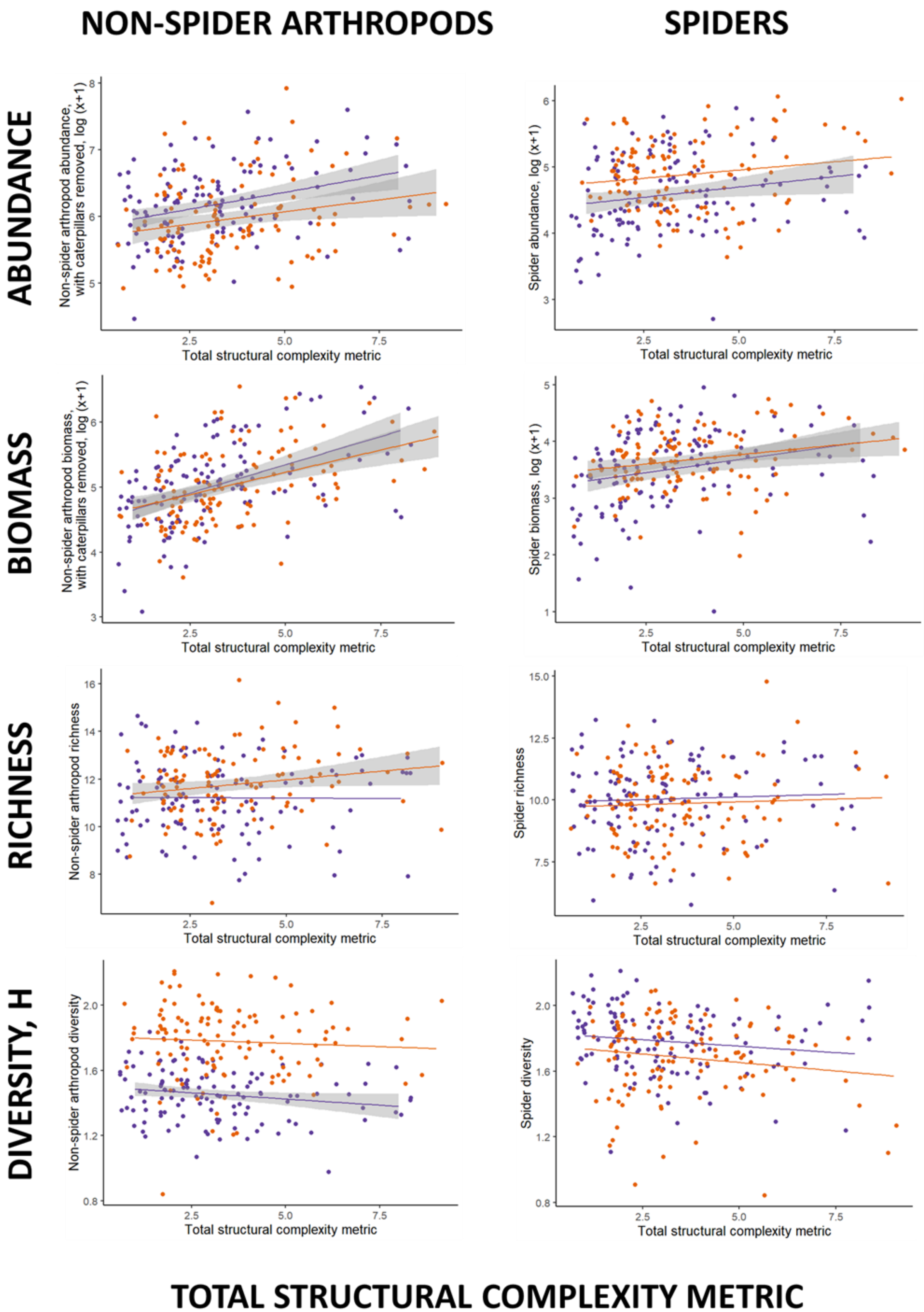


Figure 4.2. *Effects of (a) nonnative understory plant richness, (b) nonnative structural complexity, (c) native understory plant richness, and (d) native structural complexity on total understory structural complexity. Raleigh sites are shown in orange and Newark sites are shown in purple, trend lines with 95% confidence intervals are significant. Data points were jittered to reduce overlap.*

Figure 4.3. *Effect of total structural complexity on non-spider arthropod and spider abundance, biomass, richness, and diversity. Non-spider arthropod abundance and biomass does not include caterpillars. Non-spider arthropod richness and diversity include caterpillars with adult Lepidoptera. Raleigh sites are shown in orange and Newark sites are shown in purple, trend lines with 95% confidence intervals are significant. Data points were jittered to reduce overlap.*



NON-SPIDER ARTHROPODS
SPIDERS
ABUNDANCE
BIOMASS
RICHNESS
DIVERSITY, H
Non-spider arthropod abundance, with caterpillars removed, log (x+1)
Spider abundance, log (x+1)
Non-spider arthropod biomass, with caterpillars removed, log (x+1)
Spider biomass, log (x+1)
Non-spider arthropod richness
Spider richness
Non-spider arthropod diversity
Spider diversity
Total structural complexity metric
TOTAL STRUCTURAL COMPLEXITY METRIC

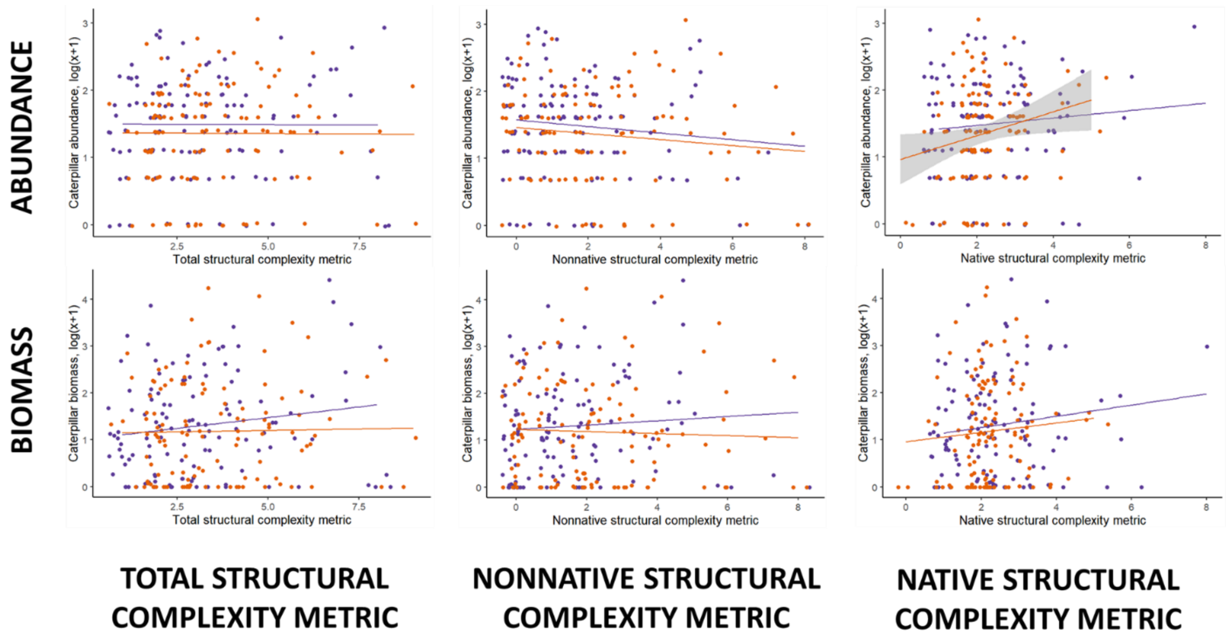


Figure 4.4. *Effect of total structural complexity, nonnative structural complexity, and native structural complexity on caterpillar abundance and biomass. Raleigh sites are shown in orange and Newark sites are shown in purple, trend lines with 95% confidence intervals are significant. Data points were jittered to reduce overlap.*

Figure 4.5. *Effect of nonnative (orange) and native (pale orange) structural complexity metrics on non-spider arthropod, including caterpillars, and spider abundance, biomass, richness, and diversity in Raleigh. Trend lines with 95% confidence intervals are significant. Data points were jittered to reduce overlap.*

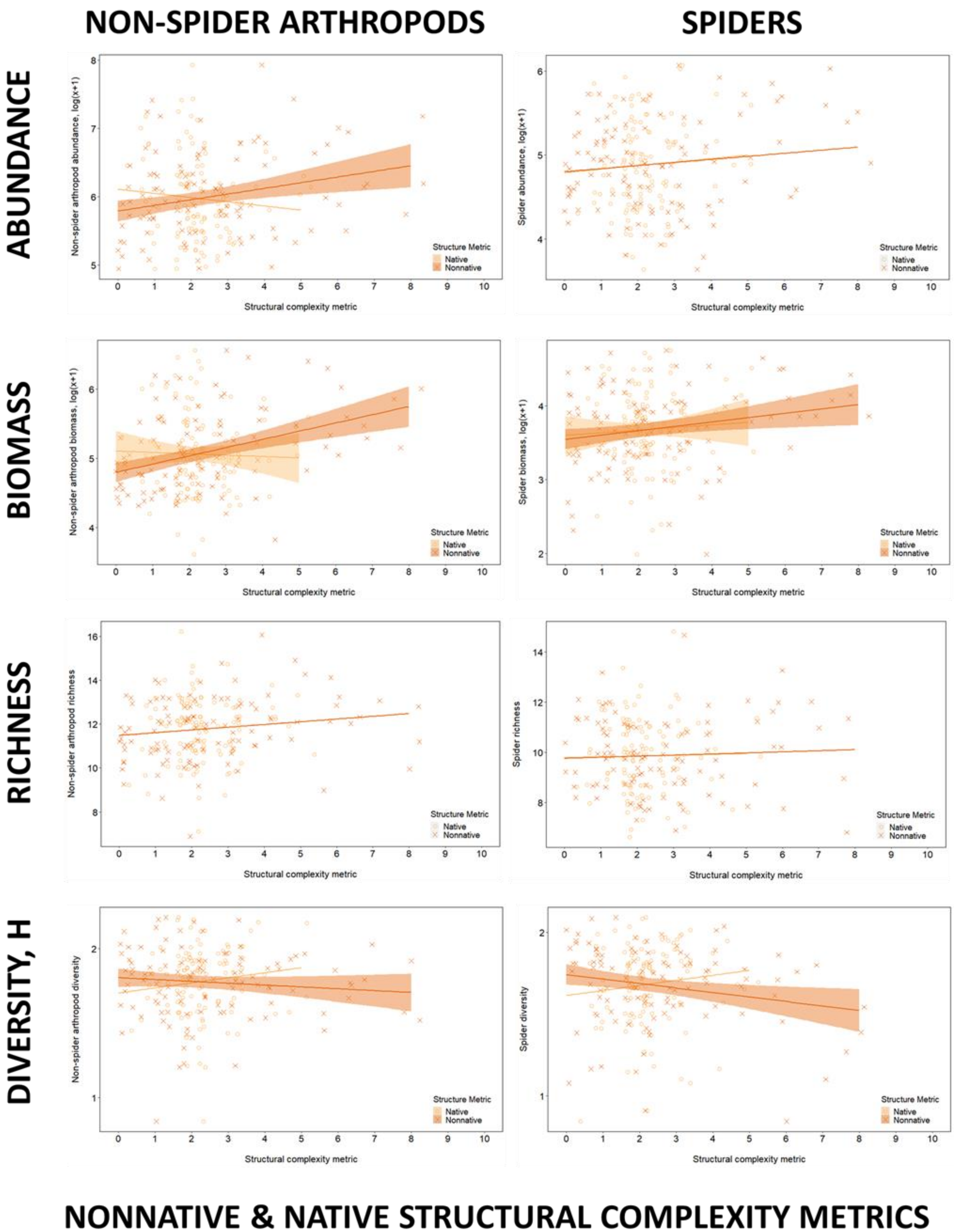
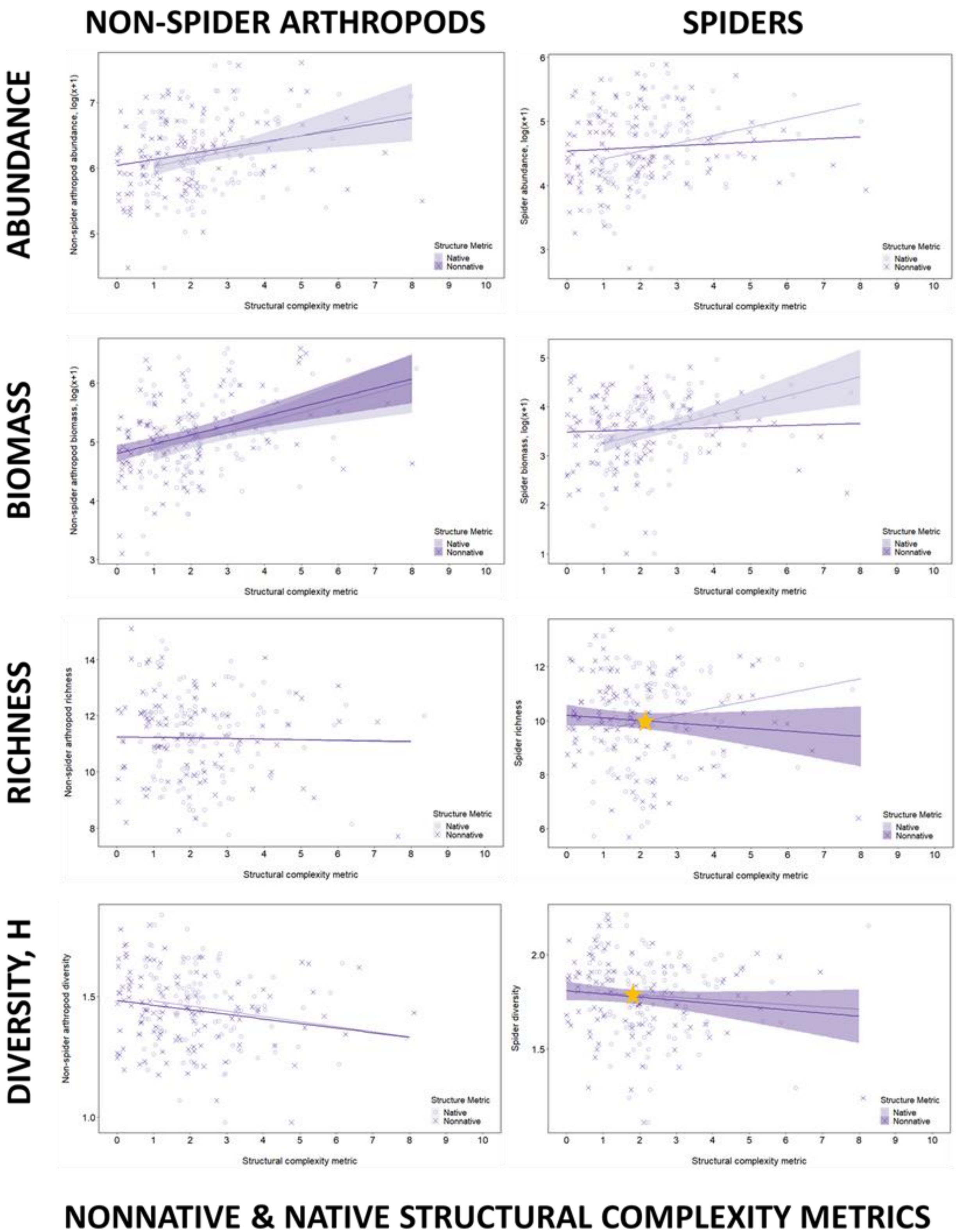

NON-SPIDER ARTHROPODS
SPIDERS
ABUNDANCE
BIOMASS
RICHNESS
DIVERSITY, H
Non-spider arthropod abundance, log(x+1)
Spider abundance, log(x+1)
Non-spider arthropod biomass, log(x+1)
Spider biomass, log(x+1)
Non-spider arthropod richness
Spider richness
Non-spider arthropod diversity
Spider diversity
Structural complexity metric
Structure Metric
Native
Nonnative
NONNATIVE & NATIVE STRUCTURAL COMPLEXITY METRICS

Figure 4.6. *Effect of nonnative (purple) and native (pale purple) structural complexity metrics on non-spider arthropod, including caterpillars, and spider abundance, biomass, richness, and diversity in Newark. Yellow star indicates a significant interaction. Trend lines with 95% confidence intervals are significant. Data points were jittered to reduce overlap.*


NON-SPIDER ARTHROPODS
SPIDERS
ABUNDANCE
BIOMASS
RICHNESS
DIVERSITY, H
Non-spider arthropod abundance, log(x+1)
Spider abundance, log(x+1)
Non-spider arthropod biomass, log(x+1)
Spider biomass, log(x+1)
Non-spider arthropod richness
Spider richness
Non-spider arthropod diversity
Spider diversity
Structural complexity metric
Structure Metric
Native
Nonnative
NONNATIVE & NATIVE STRUCTURAL COMPLEXITY METRICS