THE EFFECTS OF NONNATIVE PLANTS ON FOOD WEBS IN RESIDENTIAL LANDSCAPES

by

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A dissertation submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Entomology and Wildlife Ecology

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DEDICATION

To my son, Finnley James Hallworth. I hope that my small contributions can help make the world a little better place for you to enjoy.

******

"If you can take care of birds, you can take care of most of the environmental problems in the world" -- Dr. Thomas Lovejoy

"When we see land as a community to which we belong, we may begin to use it with love and respect" – Aldo Leopold, *Sand County Almanac*

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ABSTRACT

One of the most rapidly expanding, and least understood, ecosystems is the urban landscape. Urban-associated changes to the biological and physical environment can have cascading impacts on the ability of these landscapes to support biodiversity. One major way that these landscapes have changed is through the individual decisions of homeowners on which plant species to maintain on privately-owned residential land. In my dissertation, I investigated whether nonnative plant species affected the tritrophic interactions between plants, foliage arthropods and insectivorous birds at three scales. In chapter 1, I speak to the importance of residential yards to the future of conservation, and call for more research in these ecosystems. In chapters 2, 3 & 4, I use the Carolina chickadee (*Poecile carolinensis*) as a model insectivorous bird to determine the effects of nonnative plants on chickadee behavior, diet and population growth. In chapter 5, I estimated the energy contributions of nonnative plants to predatory spiders and a broader insectivorous bird community. In chapter 2, I determined which plants produced the most caterpillar prey for birds and whether chickadees displayed preferences for some plant species over others. I also identified whether the proportion of nonnative plant biomass predicted chickadee occupancy, abundance or breeding probability. Native plants provided more caterpillar prey than nonnative species even when controlling for plant genus. In addition, chickadees

preferred foraging in native plants that supported the most caterpillars and bred in yards that had the highest proportion of native plant biomass. In chapter 3, I combined insect sampling, diet analysis, and used estimates of reproduction, adult survival and fledgling survival in a population growth model to determine whether yards dominated with nonnative plants were capable of supporting sustainable populations of chickadees. My models indicated that yards with >30% nonnative plant biomass had fewer prey items, chickadee diets were composed of more predatory arthropods and these yards did not support sustainable chickadee populations. In chapter 4, I questioned whether nonnative plants influenced the nestling period for chickadees. I specifically tested the effects of nonnative plants on nestling diet, parental effort and nestling growth & condition. I found that as nonnative plants increased, the proportion of caterpillar prey declined, and provisioning visits increased. Consequently, chickadee nestlings in nonnative yards were also in poorer condition, grew slower and required more days to fledge. In chapter 5, I used a nitrogen enrichment experiment to test whether more energy is transferred to food webs from native plants compared to nonnatives. I found that nitrogen enrichment in caterpillars and spiders were similar regardless of the origin of treated plants, however, total biomass was lower on nonnative plants. At the next trophic level, both facultative and obligate insectivorous birds received more nitrogen enrichment when native plants were treated compared to nonnative, indicating these species were acquiring more prey from native plants. Overall, my dissertation indicates that for a plant-arthropod-insectivorous bird food web, nonnative plants are not ecologically equivalent to native plant species that are

displaced. My results provide compelling evidence that homeowners should prioritize native plant species in residential landscapes in order to support local food webs and biodiversity.

Chapter 1

INTRODUCTION

"Ecologists must include residential land use in conservation"

An Increasingly Urban World

Urban landscapes are arguably the most rapidly expanding, and least understood ecosystems, in the natural world. As we dive deeper into the Anthropocene, it will become imperative for conservation ecologists to incorporate urban ecology and restoration into conservation objectives. It is predicted that 67% of the world will be urbanized by 2050 (United Nations Population Division 2012) and new housing developments are causing exponential growth in the interface between developed areas and wilderness (Radeloff et al. 2018). Currently, private land makes up 60% (Quinn & Wood 2017), and housing developments over 20% (Radeloff et al. 2018), of all the land in the United States. The consequences of widespread urbanization result in drastic changes to both the abiotic and biotic properties of these systems and the transformation of natural habitat into human-dominated novel systems. For example, homeowners may manage their land by applying fertilizer, watering & mowing lawns, removing natural substrates, adding impervious surface and including novel, nonnative species in horticultural landscaping. Moreover, urbanization and interactions with introduced nonnative species are some of the leading causes of global species endangerment (Czech et al. 2000).

Since the nineties, urban ecology has blossomed in an effort to understand how anthropogenic development impacts ecological interactions. Yet, despite a surge of growth there has been little consideration for the role of residential properties in providing urban green space and a dearth of information available on the features of green space that promote biodiversity (Lepczyk et al. 2018). For example, many studies that compare ecological responses between 'urban' and 'nonurban' areas, or along an urban gradient, primarily focus on data collected within city parks, nature reserves, remnant forest, and other public spaces. In a literature review of ecological studies that included the term 'urban ecology' in 2017, 171 studies were published in 38 journals on urban biodiversity, yet only 26% included privately managed properties as part of the land use being studied while 62% included only publically accessible green space (figure 1 .1). 12% did not provide enough information in study site descriptions to discern what type of urban land use was included and whether the study was conducted within private land or not.

Within developed areas, residential properties alone can contain 20-30% of the total urban landscape (Loram et al. 2007) and almost 50% of the green space and plant biomass (Mathieu et al. 2007) highlighting the strong potential of these landscapes to restoration efforts. Local features are often more important for predicting urban biodiversity than surrounding landscape features (Beninde et al. 2015) and within residential yards, land management is driven by the collective decisions of community. Thus for robust assessments of urban ecology and successful conservation in these systems, is it is imperative that ecologists increase the number of studies that incorporate private land and homeowner decisions and values. These

patterns also suggests that our current knowledge of the patterns of urbanization is restricted to public spaces which reduces our ability to determine which mechanisms are driving observed patterns, and from an applied standpoint, which features can be effectively managed to support habitat for biodiversity. It is possible that residential areas may be avoided in ecological studies because of the increased difficulty to gain access, increased interactions with the public or complexity of coupled human-ecological systems (Murgui & Hedblom 2017; Dyson et al. 2018). However, the benefits of considering private land in conservation action far outweighs the added challenges of working in these landscapes. Below I outline a few of these benefits from ecological and social perspectives.

The Power of Private Land; a Conservation Opportunity

Residential properties have the potential to supply resources to local flora and fauna, but restoration in urban areas can be challenging because the collective quality of the landscape is dependent on the additive effects of homeowner decisions on individual parcels of land. In addition, most species don't operate at the scale of a single yard, such that resource availability and connectivity must be improved at a larger scale for many mobile organisms like birds and pollinators (Goddard et al. 2010). Widespread conservation success in developed areas will be dependent on encouraging, and incentivizing, local action by individual land owners (Goddard et al. 2017). By studying the features of residential properties, ecologists can contribute to data-driven resources and tools to help guide the individual decisions of parcel owners to manage urban greenspace.

Conservation on private land can also have lasting influence on ecological interactions that go beyond a single yard. Residential areas support habitat for a wide breadth of taxa that provide important ecosystem services to humans like pollinators (Lowenstein et al. 2015), pest-controlling insectivores (Evans 2015; Philpott & Bichier 2017), and seed dispersers (Garcia et al. 2010). Improving residential properties within the matrix can also increase connectivity in the landscape for vagile species by connecting isolated habitat fragments (Rudd et al. 2002; Driscoll et al. 2013) and reduce the severity of edge effects to preserved land (Driscoll et al. 2013; Wood et al. 2014). By including the residential matrix into ecological studies, this will help embed urban conservation into broader conservation action across the landscape.

It is more apparent than ever that conservation science is linked to efforts that include both social values and ecosystem services (Soulé 1985). Importantly, including private land in restoration does not take away resources from the immediate needs of other conservation projects. The decisions of how to manage private land come primarily from land developers and homeowners themselves, which means restoration funding is almost entirely a private endeavor. Public awareness of biodiversity issues requires continuous contact biodiversity (Murgui & Hedblom 2017) yet preserved nature may be inaccessible to some urban communities (Lerman & Warren 2011). Fortunately, there is no place that nature and is more accessible to diverse communities than within our home. Ecological research on private land has the potential to increase educational and translational opportunities to communicate science, and the process of science, to the general public (Evans et al. 2005). This will increase the diversity of communities that have access to ecological knowledge which

may inspire increased participation in restoration action or political action that improve environmental outcomes (Murgui & Hedblom 2017).

Novel Plant Communities in Residential Yards

Although urban ecology has experienced a surge of attention, we lack investigations into the specific mechanisms that contribute to observed patterns (Lepczyk et al. 2018), such as how yard features affect resource availability (Faeth et al. 2005; Shochat et al. 2006, 2010). One of the most pronounced differences between residential communities is through the individual homeowner decisions to landscape with particular plant species. The plants found in residential areas can provide ecological, social, cultural and health services as well as provide important habitat for urban wildlife (Nesbitt et al. 2017). Understanding the identities and abundance of urban flora that are best able to provide resources for wildlife is imperative for effective conservation on private land (Stagoll et al. 2010).

The evolutionary novelty of nonnative plants to their introduced regions makes them poor substitutes for specialized insects that rely on one or a few host plants (Tallamy et al. 2010; Forister et al. 2015). Moreover, insects form the foundation for a wide breadth of consumers that rely on invertebrates as prey (Wilson, 1985). Recent work has shown that landscaping decisions that include native plants are related to an increase in richness of species that inhabit the yard (Daniels & Kirkpatrick 2006; Burghardt et al. 2009; Lerman & Warren 2011; Bates et al. 2014). Yet, no study yet has explored explicit connections between plant species, prey availability, and the birds that inhabit these areas, nor directly examined the relationships between nonnative vegetation and fitness consequences in higher-order predators. Of

comparable importance to the conservation of species, is the conservation of ecological interactions that support stable and complex food webs (Harvey et al. 2017) and sustainable populations (Lepczyk et al. 2018). A comprehensive understanding of how plants, insects and birds interact when plant assemblages are dominated by ornamental and invasive nonnative species will be essential to inform urban conservation.

In this dissertation, I investigate the role of nonnative plants in food webs by determining their impact on food resources for insectivorous birds. I investigate this question at three scales, the behavioral decisions and condition of individuals (Chapter 2, 4), consequences for the population (Chapter 3), and energetic contributions to a community of secondary consumers (Chapter 5). By investigating this important mechanism within the context of residential yards, this body of work advances our understanding of the ecological interactions between humans and biodiversity in a changing world.

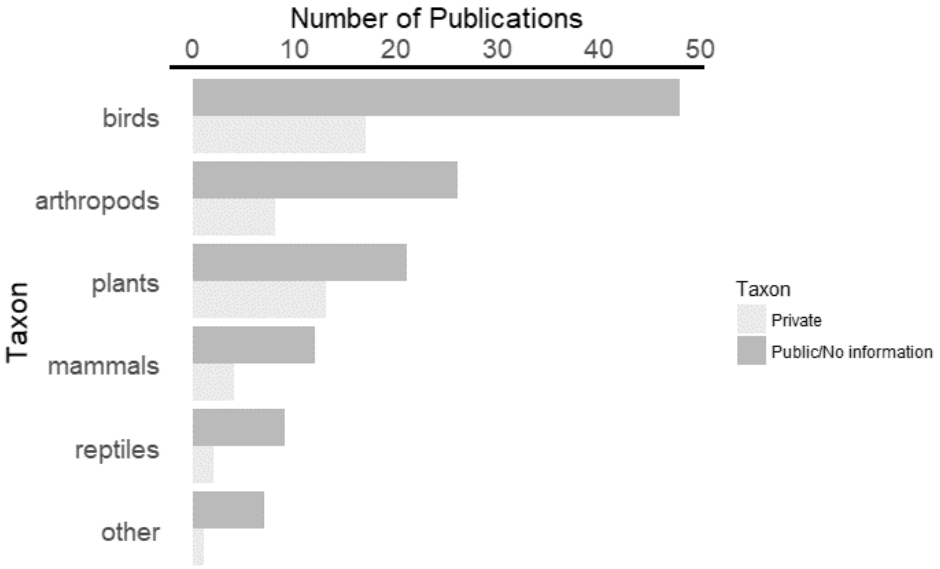

Figure 1.1 Number of biodiversity publications in 2017 using the term ‘urban ecology’ on public and private land. Public land included remnant habitat, nature reserves, city parks, botanical/community gardens, college campuses, roadsides, or public ‘right-of-ways’. Private land included residential neighborhoods, private gardens, green roofs, human settlements and citizen science datasets. Studies with ‘no information’ had study sites in urban areas but did not provide enough information to identify whether study locations were publically or privately owned.

REFERENCES

1. Bates AJ, Sadler JP, Grundy D, Lowe N, Davis G, Baker D, Bridge M, Freestone R, Gardner D, Gibson C. 2014. Garden and landscape-scale correlates of moths of differing conservation status: significant effects of urbanization and habitat diversity. PLoS One 9:e86925.

2. 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.

3. Burghardt KT, Tallamy DW, Shriver WG 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. Conservation Biology 23:219–224.

4. Czech B, Krausman PR, Devers PK. 2000. Economic associations among causes of species endangerment in the United States: associations among causes of species endangerment in the United States reflect the integration of economic sectors, supporting the theory and evidence that economic growth proceeds at the competitive exclusion of nonhuman species in the aggregate. BioScience 50:593–601.

5. Daniels GD, Kirkpatrick JB. 2006. Does variation in garden characteristics influence the conservation of birds in suburbia? Biological Conservation 133:326–335.

6. Driscoll DA, Banks SC, Barton PS, Lindenmayer DB, Smith AL. 2013. Conceptual domain of the matrix in fragmented landscapes. Trends in Ecology & Evolution 28:605–613.

7. Dyson K, Ziter C, Fuentes TL, Patterson MS. 2018. Conducting urban ecology research on private property: Advice and lessons learned in the field. PeerJ Preprints.

8. Evans BS. 2015. The ecology of birds in the urban landscape: Avian community composition, dispersal, and survival across the rural-to-urban gradient in Washington DC. The University of North Carolina at Chapel Hill.

9. Evans C, Abrams E, Reitsma R, Roux K, Salmonsen L, Marra PP. 2005. The Neighborhood Nestwatch Program: Participant Outcomes of a Citizen-Science Ecological Research Project. Conservation Biology 19:589–594.

10. Faeth SH, Warren PS, Shochat E, Marussich WA. 2005. Trophic dynamics in urban communities. BioScience 55:399–407.

11. Forister ML et al. 2015. The global distribution of diet breadth in insect herbivores. Proceedings of the National Academy of Sciences 112:442–447.

12. Garcia D, Zamora R, Amico GC. 2010. Birds as suppliers of seed dispersal in temperate ecosystems: conservation guidelines from real-world landscapes. Conservation biology 24:1070–1079.

13. Goddard MA, Dougill AJ, Benton TG. 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology & Evolution 25:90–98.

14. Goddard MA, Ikin K, Lerman SB. 2017. Ecological and social factors determining the diversity of birds in residential yards and gardens. Pages 371–397 Ecology and Conservation of Birds in Urban Environments. Springer International Publishing.

15. Harvey E, Gounand I, Ward CL, Altermatt F. 2017. Bridging ecology and conservation: from ecological networks to ecosystem function. Journal of Applied Ecology 54:371–379.

16. Lepczyk CA, Aronson MFJ, Evans KL, Goddard MA, Lerman SB, MacIvor JS. (2017). Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. BioScience 67(9), pp.799-807.

17. Lerman SB, Warren PS. 2011. The conservation value of residential yards: linking birds and people. Ecological Applications 21:1327–1339.

18. Loram A, Tratalos J, Warren PH, Gaston KJ. 2007. Urban domestic gardens (X): the extent & structure of the resource in five major cities. Landscape Ecology 22:601–615.

19. Lowenstein DM, Matteson KC, Minor ES. 2015. Diversity of wild bees supports pollination services in an urbanized landscape. Oecologia 179:811–821.

20. Mathieu R, Freeman C, Aryal J. 2007. Mapping private gardens in urban areas using object-oriented techniques and very high-resolution satellite imagery. Landscape and Urban Planning 81:179–192.

21. Murgui E, Hedblom M. 2017. Improving Research towards Conservation Objectives. Pages 491–507 Ecology and Conservation of Birds in Urban Environments. Springer, Cham.

22. Nesbitt L, Hotte N, Barron S, Cowan J, Sheppard SR. 2017. The social and economic value of cultural ecosystem services provided by urban forests in North America: A review and suggestions for future research. Urban Forestry & Urban Greening 25:103–111.

23. Philpott SM, Bichier P. 2017. Local and landscape drivers of predation services in urban gardens. Ecological Applications 27:966–976.

24. Quinn JE, Wood JM. 2017. Application of a coupled human natural system framework to organize and frame challenges and opportunities for biodiversity conservation on private lands. Ecology and Society 22

25. Radeloff VC, Helmers DP, Kramer HA, Mockrin MH, Alexandre PM, Bar-Massada A, Butsic V, Hawbaker TJ, Martinuzzi S, Syphard AD. 2018. Rapid growth of the US wildland-urban interface raises wildfire risk. Proceedings of the National Academy of Sciences 115:3314–3319.

26. Rudd, H, Vala, J and Schaefer, V. 2002. Importance of backyard habitat in a comprehensive biodiversity conservation strategy: a connectivity analysis of urban green spaces. Restoration ecology, 10(2), pp.368-375.

27. Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH. 2010. Invasion, Competition, and Biodiversity Loss in Urban Ecosystems. BioScience 60:199–208.

28. Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186–191.

29. Soulé ME. 1985. What is conservation biology? BioScience 35:727–734.

30. Stagoll K, Manning AD, Knight E, Fischer J, Lindenmayer DB. 2010. Using bird–habitat relationships to inform urban planning. Landscape and Urban Planning 98:13–25.

31. Tallamy DW, Ballard M, D'Amico V. 2010. Can alien plants support generalist insect herbivores? Biological Invasions 12:2285–2292.

32. Wilson EO. 1987. The little things that run the world (the importance and conservation of invertebrates). Conserv. Biol., 344-346.

33. Wood EM, Pidgeon AM, Radeloff VC, Helmers D, Culbert PD, Keuler NS, Flather CH. 2014. Housing development erodes avian community structure in U.S. protected areas. Ecological Applications 24:1445–1462.

Chapter 2

NONNATIVE PLANTS IMPROVE FORAGING AND BREEDING HABITAT FOR AN INSECTIVOROUS BIRD

Published in Biological Conservation
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Abstract

Understanding how introduced plants reduce food web complexity is critical to effective conservation management within human-dominated systems. In urban breeding birds, the paucity of dietary specialists suggests that a lack of food resources, such as arthropod prey essential for reproduction and survival, may contribute to bird declines. Local plant species composition and abundance is influenced by the landscaping decisions of private homeowners and may be contributing to differences in insect prey availability. In this study, we examined whether non-native plants are a limiting factor to a resident breeding insectivore, the Carolina chickadee (*Poecile carolinensis*). We used caterpillar counts, chickadee foraging observations and detection-corrected hierarchical models, to determine the influence of local landscaping features on insect food availability, chickadee tree preference, site occupancy, site abundance and breeding territory selection. Native plants were more likely to host a higher biomass of caterpillars compared to non-native plants, and chickadees strongly preferred to forage in native plants that supported the most

caterpillars. In addition, chickadees were less likely to breed in yards as the dominance of non-native plants increased. Chickadee occupancy increased with tree basal area and chickadee abundance declined as impermeable surface area increased and basal area decreased. Our results demonstrate that non-native plants reduce habitat suitability for chickadees by reducing insect food available for breeding. Improving human-dominated landscapes as wildlife habitat should include increasing native, and arthropod-producing, plant species to effectively support the life history needs of insectivorous birds.

Introduction

Worldwide, habitat is rapidly being converted from coevolved native ecosystems into novel assemblages of plants and animals (Radeloff et al., 2015). Nowhere are these changes more apparent than within the human-dominated residential matrix. Urban-associated declines in the abundance and richness of native organisms have been documented globally (Dolan et al., 2011; McKinney, 2008). Because conversion to 'urban' development includes a variety of concurrent changes to the local ecosystem, conservation ecologists have called for a mechanistic understanding of the drivers underlying species declines in these systems (Shochat et al., 2006).

One of the most ubiquitous threats to biodiversity today is the conversion of native plant communities into plant assemblages dominated by non-native species (Johnson, 2007). Such conversions have triggered debate about the benefit of managing non-native species particularly when it is unclear how well introduced plants support wildlife and management is financially and logistically challenging.

From a conservation perspective, this debate cannot be resolved without a clear understanding of both the positive and negative impacts of non-native plants. Unfortunately, there are few studies that have examined whether introduced plants provide ecological niches that are equivalent to the native species that are displaced (Tallamy, 2004). Needed are multi-trophic studies of native and non-native plants that elucidate how differences in bottom-up resources affects higher-order consumers in novel ecosystems (Faeth et al., 2005; Harvey et al., 2010).

Recent studies suggest that, on average, consumer biodiversity, particularly the abundance, richness and survival of herbivorous insects, is reduced by non-native plants (Burghardt et al., 2010; Holmquist et al., 2011; Litt and Steidl, 2010; Tallamy et al., 2010). This occurs in part because herbivorous insects have adapted to circumvent the phytochemical defenses of particular plant lineages, resulting in a radiation of specialized plant-insect associations (Forister et al., 2015). During urban conversion, native plants are replaced by non-native species with novel chemical, physical, and phenological features for which native herbivorous arthropods have few physiological or behavioral adaptations. This can result in reduced herbivory on introduced plants and a competitive advantage for these plants to spread (i.e. Enemy Release Hypothesis; Keane and Crawley, 2002).

It is well documented that the biomass of arthropods, particularly Lepidoptera larvae, support large and diverse trophic webs, and are an important component of the diets of insectivorous consumers such as birds (Cooper 1988; Holmes and Schultz, 1988). Even generalist bird species rely heavily on arthropods during the breeding season because these food items provide high protein, calcium, and carotenoids for nestling growth (Eeva et al., 2010; Razeng and Watson, 2014). Thus, landscaping with

non-native plants may negatively affect bird populations if individuals preferentially rely on herbivorous insects and non-native plants do not support adequate prey populations for breeding birds. In contrast, non-native plants could promote increases in other food items (e.g. non-native arthropods), keeping overall prey biomass similar between native and non-native plants (Cook and Talley, 2014; Mitchell and Litt, 2016) and bird populations unaffected. Exploring the trajectory of these relationships requires simultaneous study of insect communities and bird populations in the presence of both native and non-native plants.

Plant abundance and species composition in residential areas are primarily a result of landscaping decisions of homeowners and developers on private land (Lerman and Warren, 2011). Interest in 'rewilding suburbia' has sparked renewed public attention for landscaping that contributes to wildlife habitat (Marzluff, 2014; Tallamy, 2009). For example, population expansion of the rare *Eumaeus atala* butterfly resulted from increases in the horticultural sale of native Zamia sp., the sole genus of host plant for this species (Culbert 2010). If local factors that drive population persistence within a residential patch are identified, this information could assist landowners in providing additional resources for wildlife, and help increase native biodiversity in these systems (Goddard et al., 2010).

In this study, we used the Carolina chickadee (*Poecile carolinensis*; hereafter, 'chickadee') as a representative insectivorous bird to investigate how plant species origin influences foraging and breeding behavior in residential neighborhoods. Specifically, we followed foraging behaviors of individually marked birds to determine if chickadees exhibit a preference for native over non-native plants. In addition, we used hierarchical models to determine which local habitat features predict

occupancy, abundance and nesting activity of chickadees. Given their insectivorous diet during the breeding season, we tested the hypothesis that both plant species origin (native or non-native) and consumer productivity (i.e. the probability of supporting Lepidoptera prey) influences the occurrence of chickadees as well as their foraging and breeding decisions. We predicted that areas with more native plants would support more chickadees, and chickadees would forage more often in the most insect-producing native plants.

Methods

Study Species

Chickadees are year-round residents that inhabit Eastern deciduous forests as well as residential areas. During the breeding season (this region: April-early June) arthropod prey make up >90% of chickadee diet, particularly Lepidoptera larvae, Hemiptera, and Araneae (Mostrom et al., 2002). Chickadees are single-brooded, synchronous, cavity nesters that readily use artificial nest boxes.

Study Sites

Our study took place between March-June in 2013-2014 within private residential yards of homeowners who volunteered for the Smithsonian's Neighborhood Nestwatch program in the Washington D.C. metropolitan area (Evans et al. 2005, Yard Locations: appendix figure A.1). We selected 97 sites from a pool of 195 yards; most were separated by at least 1 km (Mean distance: 22.26 ± 0.16 km). Inclusion in this study was primarily driven by access permission; however, sites were distributed across a rural-urban landscape gradient and in areas of varying human

population density and socioeconomic status (Lerman and Warren, 2011). Prior to data collection, all sites received an artificial cavity nesting tube (modified from Grubb and Bronson, 1995) to assure that site occupancy would not be influenced by the availability of suitable nesting locations. Although our nest box and point count sampling took place within the focal yard, we aimed to conduct our plant, caterpillar and chickadee behavior at a larger, patch scale that was relevant to the size of a chickadee territory (Goddard et al., 2010). Thus, these samples took place within a 50-m radius surrounding the focal yard which included neighboring properties (appendix figure A.2). Caterpillar and chickadee foraging data was collected in both 2013 and 2014 and plant communities. Chickadee occupancy, abundance and chickadee breeding data were collected in 2014.

Caterpillar Sampling

To determine the caterpillar abundance on individual woody plant species, we conducted a timed-search sampling effort, designed for detection of Lepidoptera on woody plants, within a subset of yards where chickadees were present (Wagner 2010; Burghardt et al. 2010). Sampling was conducted between May and early June to encompass the period when chickadees were feeding young, and to only sample one peak of caterpillar biomass. Plants were selected by walking 25m from the center of the yard in each cardinal direction and sampling the four plant species encountered (total: 16 plants per site). For five minutes the observer meticulously searched foliage and stems counting and collecting all folivorous holometabolous larvae (mostly Lepidoptera but also Hymenoptera sawflies; hereafter 'Caterpillars') located in an area on the plant (approximately 1.5m x 1.5m) up to 4m high, and measured each caterpillar to the nearest 0.5mm. Each five-minute search period was repeated three

times per plant species per site on different areas of vegetation (total: 48 five-minute samples per yard).

Foraging Behavior

Adult chickadees breeding at the site were captured to attach unique color band combinations for re-identification. To quantify foraging effort on plants, observers systematically surveyed the focal yard, accessible neighboring yards, and adjacent public land to record foraging behavior of the breeding pair. Once a color-banded bird was located, plant species used for foraging were recorded every minute (2014) or every plant switch (2013) until the bird was lost; observations resumed when the focal individual was relocated. We confirmed active foraging by observing searching and/or probing behavior, and the absence of other non-feeding behavior (i.e. singing, preening, etc.). Sites were visited every 2-5 days while the nest was active, alternating observers, and observations were attempted for a minimum of one hour per visit.

Bird Surveys

Surveys were conducted from 15 Apr – 14 Aug 2014. We surveyed each site 2-3 times and all surveys were completed in the morning between 0630 and 1100 when bird activity is highest. During a 10-minute observation period, a trained observer identified all chickadees that were seen or heard within a 50m radius. The central point of the survey was located approximately 10m from the backside of the house in a location that maximized coverage of the focal residential yard. For occupancy analyses, we pooled abundance per survey into a binary response so that chickadees were either detected (=1) or not detected (=0) at each site per visit. For abundance analyses, we used the maximum number of individuals observed at each

site per visit. Because chickadee territories begin to break down and fledglings disperse in June and July in this region (Mostrom et al., 2002), we included only the 1st and 2nd survey visits (i.e. April-May) for these analyses.

Nest boxes were checked for breeding evidence about once per week by participant volunteers or trained observers. During each survey, we also searched for nests and breeding activity (e.g. nest building, nestling feeding) within the 50m-radius area to account for nests located in adjacent yards or inaccessible locations. Sites were designated as having active breeding (=1) or no breeding (=0). Nests abandoned during building (n=3) were not considered active.

Plant Surveys

We quantified woody plant availability using a modified i-Tree protocol for forest communities to determine habitat quality for wildlife (www.itreetools.org, Lerman et al., 2014). We focused on woody plants, rather than all plants, because these were most relevant to bird habitat (Lerman et al. 2014), support the most caterpillar prey (Tallamy and Shropshire, 2009), and represent the majority of plant biomass in residential areas. We surveyed vegetation at each site with five, non-overlapping 0.04 ha plots including one centered on the nest box and four additional plots randomly located within a 50m-radius area (0.79 ha) using ArcGIS software. This area was chosen because other Paridae species respond strongest to local plant cues within 50m of the nest (Hinks et al. 2015), and the 50m-radius area corresponded with the area covered by our bird and caterpillar surveys. Within each plot, we estimated % ground cover type (e.g. pavement, buildings) and measured and identified all woody plants >0.5m high. We measured diameter at breast height (dbh; when applicable, for multiple stems), height, & canopy area for trees and volume (length,

width and height) on individual shrubs. Plant origin (native or non-native) was determined using USGS distribution maps for each plant species (Little 2013). We defined native plants as any species with an historical distribution within the Eastern US region (i.e. east of the Mississippi River).

For each site we calculated basal area for each tree species by multiplying total dbh (sum of all tree stems)^2 by 7.854 x 10^{-5} (i.e. foresters constant). We also calculated relative dominance (basal area/total basal area) and relative density (tree count/total tree count) for each tree species in order to create a relative importance value which is the sum of relative density and relative dominance (hereafter: *importance value*, Holmes and Robinson, 1981). Because of the rich plant diversity and high dissimilarity between sites, we combined species into groups of respective genera and origin, hereafter: *plant groups*. For example 'Native *Acer'* consisted of *A. rubrum, A. saccharinum, A. saccharum, A. negundo* and 'Non-native *Acer'* contained *A. palmatum, A. campestre, A. ginnala,* and *A. platanoides*. We calculated importance values for each plant group on a site-by-site basis and then combined values to represent the total relative availability of all native and non-native trees. Because the origin importance value is a proportion of only two groups (native/non-native), we used only non-native values for all subsequent analyses. Shrub importance values were calculated separately but using volume (Thorne et al. 2002) in place of dbh.

Caterpillar Analysis

We first tested whether native and non-native plants differed in caterpillar abundance and biomass. Because of the large number of samples (n=3731), and few caterpillars found per sample (2.36% samples >1 caterpillar found) we reclassified each 5-min sampling event into a binary outcome of 'no caterpillar found' (=0) or

'caterpillar found' (=1) to reduce model dispersion. To account for differences among plant genera, we also included a scaled term representing the total number of caterpillar species that use a genus as a host plant (gleaned from host plant databases in Tallamy and Shropshire, 2009 and Robinson, et al. 2013; hereafter: '*Lepidoptera Index')*. We determined if plant origin and the Lepidoptera index predicted caterpillar probability using a logistic model. We also obtained biomass of caterpillars by using our measurements in a length-weight regression equation from Rodenhouse (1986). We then compared mean biomass of caterpillars from native and non-native plants within the same site using a non-parametric Wilcoxon signed rank test.

Foraging Behavior

We tested whether chickadees preferred native or non-native plants using a chi-square test on foraging observation frequencies. Because each site had different proportions of native/non-native plants available for foraging, we conducted an independent test for each site, and then tested for overall significance using Fisher's method of combining p-values using the sum of logs method (Mosteller and Fisher, 1948). We also calculated foraging preference for individual plant groups (i.e. Native *Acer* sp., Non-native *Prunus* sp., etc.) using methods from Holmes and Robinson (1981) and Wood et al. (2012). This method calculates preference values as the difference between the % observations in a plant group and the % importance value for that plant group at the site; where positive values indicate preference for a plant species, and negative values indicate avoidance. We compared chickadee foraging preference with the capacity of a tree species to produce caterpillar food, by using the Lepidoptera Index values for the plant group, and the plant origin (native/non-native) as fixed factors and their interaction in a generalized linear mixed model (GLMM)

using site as a random effect to control for local plant availability. We used this behavioral model to validate whether our measurements of food availability are correlated with actual food perception by our focal species (Hutto, 1990). Finally we derived a total non-native plant preference by summing the combined preference values for all non-native plant groups. Because our summed metric of non-native preference is just the inverse of native plant preference, we only used non-native values for our analysis. We tested whether chickadee tree preference for non-native plants changed as non-natives became more dominant within the territory, by comparing non-native tree preference with non-native importance values with a simple linear regression.

Chickadee Occupancy, Abundance, and Breeding.

To test what variables predict occupancy and abundance of chickadees, we used hierarchical models in package 'unmarked' (Fiske et al., 2011) using Program R (R Core Team, 2015) to compare fit of nested models in an AIC framework (variables used, appendix table A.1). We modeled occupancy using occurrence models (function: 'occu') and abundance using binomial mixture models (function: 'pcount') on repeated count data. To quantify the capacity of each site to produce caterpillars, we created a 'productivity' variable by multiplying the 'Lepidoptera Index' by the basal area for each plant species and then taking the sum of all plants at the site. Prior to analyses, all missing covariate values were replaced with the mean of that covariate. Several non-normal variables, including BASAL, VOLUME, and PRODUCTIVITY, were log transformed to reduce skew. All variables were scaled prior to running models (supplementary information).

Using ‘unmarked’, we simultaneously modeled detection because birds could be detected imperfectly over the sites and covariates of urbanization may be simultaneously influencing occupancy and our ability to detect individuals (MacKenzie et al., 2003). We first compared a list of models with observation-specific variables that could conceivably influence detection, and used covariates from the top model for detectability in our site-specific models. Detection models that did not fit *a priori* assumptions of true detection relationships, (e.g. detection increasing rather than decreasing with number of trees) were assumed to be driven by raw abundance and were not used. Variables in models were designed based on local habitat features of each survey site that could affect either occupancy or abundance. ‘Unmarked’ estimates occurrence and abundance using the likelihood based approach (MacKenzie et al., 2002) and ranks models using AIC (Burnham and Anderson, 2002). Model fit was tested by assessing goodness of fit via Pearson chi-square statistic with bootstrapping (1000 simulations, MacKenzie and Bailey, 2004).

Evidence of breeding was modeled using a generalized linear model with logit link function with ‘Chickadee-not breeding’ and ‘Chickadee-breeding’ as responses and the same site covariates. Breeding models were ranked using AICc and model averaged over the entire candidate model set using package ‘AICcmodavg’ (Mazerolle 2014). All covariate models were also ranked against a ‘global’ and ‘null’ (no covariates) model.

Results

In 2014, chickadees were detected at least once in 69.07% of 97 sites. The number of chickadees observed ranged from 0-6 with an average 0.80 ± 1.04 SD

chickadees per survey. Chickadee breeding evidence was confirmed within the 50m point count radius in 33 sites (36.67%).

Plant Diversity and Productivity

Plant diversity was highly variable among sites. During surveys, we detected >230 different plant species representing 63 different families. The average number of plant species per site was 29 ± 10 (range: 12-58 sp.). Plants that could not be identified (2.38% of shrubs and 0.40% of trees), due mostly to property access difficulties, were considered unknown and excluded. Proportions of non-native plants (based on importance values) varied among sites from 0.60% to 94.94% with a mean of 39.30% ± 23.56% SD. Basal area varied from 1.12 m^2 to 160.98 m^2 with a mean of 22.09 m^2 ± 30.67 SD.

The probability of finding a caterpillar during a search period was positively related to the Lepidoptera index of the plant genus (Scaled Lepidoptera Index: β 0.43 ± 0.05 SE, $p<0.001$, CI=0.33, 0.53, figure 2.1), and negatively related to plant origin (Non-native: β -0.65 ± 0.12 SE, $p<0.001$, CI=-0.88, -0.42, figure 2.1). When comparing only congeneric species of differing origin, non-native plant species had a significantly lower caterpillar occurrence per sample than native plants in the same genus (Non-native congeners: β -0.66 ± 0.16 SE, $p<0.001$, CI=-0.98, -0.35). Average caterpillar biomass was also significantly lower on non-native plants compared to native plants at the same site (Wilcoxon signed rank test: v=1218, p=0.005, appendix figure A.2).

Foraging Activity

In 2013, 618 foraging observations of chickadees at specific plants were collected at 22 sites (mean: 33.00 ± 19.03 SD points per pair) and in 2014, 2,398 foraging observations at 33 different sites were collected (77.10 ± 48.10 SD). Plant preferences at the same site in both years were highly correlated ($r>0.8$); therefore, for sites with data for both years, only 2014 data were used for analyses (n=13 sites). Sites with < 10 observations were excluded from analyses (both years: n=3 sites). Average foraging height was 16.90m ± 9.71 SD (range: 0-40m). Unknown or unidentifiable plants made up 3.88% of the observations and other foraging locations (snags, feeders, ground, etc.) made up 1.89% of the observations. Without taking into account plant abundance, the plant groups foraged in most frequently across all sites were native *Quercus* (28% of observations), followed by native *Acer* (16%), native *Carya* (4%), native *Liriodendron* (3%), native *Ulmus* (3%) and native *Pinus* (3%).

According to our Fisher's method of combined chi-square tests, native plants were preferred by chickadees disproportionately to their availability (Fisher's Test: chi-square = 1636.08, $p<0.001$, appendix figure A.3). Moreover, as the proportion of non-native plants increased, chickadees significantly increased their preference for native plants (β -0.42 ± 0.05 SE, $p<0.001$, R^2: 0.68, CI: -0.52,-0.31, figure 2.2). Native plant groups were more preferred in 97% of chickadee territories observed and native *Quercus* sp. was the most preferred group in 61% territories (appendix table A.2). Chickadees also had the highest preference for plant groups that supported the most caterpillars (highest Lepidoptera index) relative to availability within the survey (Scaled Lepidoptera Index: β 6.27 ± 0.72 SE, $p<0.001$, figure 2.3), however preferences were lower (Non-native: β -3.53 ± 1.47 SE, $p=0.02$, CI: -6.43, -0.63) and

the relationship weaker for non-native plants (Non-native: β -5.17 ± 1.42 SE, $p<0.001$, CI: -7.96, -2.38).

Detectability

For detection of chickadee occupancy, the confidence intervals of all detection variables overlapped zero and the null model was included within the most parsimonious models (ΔAIC<2, appendix table A.3). Therefore, no variables were included in occupancy models to account for detection; however, detection was allowed to be imperfect. Chickadee detection probability of abundance was negatively related to BUILDING (model averaged: β -0.39 ± 0.14, CI: -0.67, -0.12, appendix table A.3; appendix figure A.4), and this variable was included in subsequent abundance models.

Chickadee Occupancy and Abundance

For chickadee occupancy, all top models included the variable BASAL (ΔAIC<4, w=0.76, appendix table 4). The relative importance of BASAL accounted for the majority of the weight across models (w=0.87, appendix figure A.5). BASAL was significantly positively related to occupancy (β 1.47 ± 0.64, CI: 0.21, 2.73, figure 2.4a). Chickadee occupancy was also negatively related to EXOTIC TREE (β -0.80 ± 0.44) however the confidence interval slightly overlaps zero when holding BASAL constant (CI: -1.67, 0.06).

For chickadee abundance, the most parsimonious models included both IMPERVIOUS and BASAL (ΔAIC<4, w=0.74, appendix table A.4). The relative importance of IMPERVIOUS accounted for 0.75 of the weight and BASAL accounted for 0.72 (appendix table 5). Chickadee abundance was negatively related to

IMPERVIOUS (β -0.32 ± 0.12, CI: -0.55, -0.08, figure 2.4b), and positively related to BASAL (β 0.34 ± 0.10, CI: 0.14, 0.53) when accounting for the influence of BUILDING on abundance detection.

For the presence of breeding activity, all eight parsimonious models contained the variable EXOTIC TREE (ΔAIC<4, w=0.94, appendix table A.4). The probability of nesting chickadees was negatively related to EXOTIC TREE (β -1.49 ± 0.3, CI: -1.49, -0.3, figure 2.4c). Overall, the relative importance of EXOTIC TREE accounted for 0.95 of the weight (appendix table A.5).

Discussion

Urbanization drastically alters the abiotic and biotic properties of the landscape including large conversions of regional floristics due to horticultural preferences for non-native plants on residential properties. Despite the potential for global ecological impact, no study has considered whether non-native plants negatively affect habitat for individual breeding birds occupying residential areas. Here, we demonstrate that native plants are superior to non-native species at supporting the abundance and biomass of caterpillars required for chickadee reproduction. Accordingly, in yards where chickadees occur, non-native plants are avoided as a foraging substrate and chickadee plant preferences are highest for native genera that support the most caterpillars. In addition, using point count surveys and behavioral observations, we found that the amount of non-native vegetation, in conjunction with reduced tree biomass and increased impervious surface, reduces the presence and breeding activity of chickadees in residential areas over a wide urban landscape.

Our caterpillar sampling confirmed that native plant species produced numerically more and greater biomass of Lepidoptera larvae than plant species from both non-native genera and non-native congeneric species. This complements several studies across regions and plant taxa that show non-native vegetation reduces insect herbivore diversity (Burghardt and Tallamy, 2013; Fiedler and Landis, 2007; Flanders et al., 2006; Litt and Steidl, 2010). Our study builds on this work by showing that non-native plants also reduce the *amount* of caterpillar food available, which is a feature critical to bird conservation. Also unique to our study is that we measured the probability of caterpillar occurrence between congeneric species (e.g. native vs. non-native *Acer*). This is particularly important considering the popularity and invasive qualities of congeneric species in this region such as *A. platanoides* and *Q. accutissima*. Although non-native congeners support more caterpillars in comparison to plants unrelated to any native species, congeners had a 47% (CI: 34%-59%) lower probability of having caterpillars compared to native species. Thus, homeowners interested in increasing the native bird food available in their yard should still prioritize the planting of productive native plant species as well as genera. In this study, native trees were composed of planted species, as well as self-seeded trees that were allowed to remain within residential development. Our results reinforce the suggestion that conserving native vegetation within a residential landscape can benefit local breeding birds by increasing important foraging substrates for phytophagous insects that comprise the prey that support higher order consumers.

Our behavioral data demonstrate that chickadees avoid foraging in non-native plant species. Aslan and Rejmánek (2010) also reported very few observations of birds gleaning insects from non-native vegetation and most bird/non-native plant

interactions involved foraging on fruit-producing plant species. During the time of our observations (April-June), most available fruit was from the previous fall on non-native *Ilex* sp. and *Nandina domestica*, and were avoided by all breeding birds. In sites with a low proportion of non-native plants, preference values were close to zero, suggesting that foraging activity on non-natives was consistent with plant availability within the landscape. It is possible that chickadees may forage less discriminately when prey availability is reliable, and switch to more directed foraging on preferred plants when prey is unreliable and/or in short supply (i.e. risk-sensitive foraging; Stephens et al., 2007). Although we were unable to determine what arthropod taxa adult chickadees were consuming, or the plant signal birds use to preferentially forage, caterpillars are one of the most commonly provisioned food items for nestling chickadees (Brewer, 1961; D. Narango, unpublished data) and are likely targeted prey. In sites dominated with non-native plants, foraging insectivores disproportionately selected native plants, potentially resulting in higher inter- and intra-specific competition among birds for food and stronger top-down pressures on prey populations. High predation rates on insects in the spring may suppress prey populations on native plants later in the breeding season. Increasing the abundance of native and insect-producing plant genera in urban areas is predicted to reduce competition and increase resources available for birds during both breeding and migratory stopover.

Within our study region in the mid-Atlantic, chickadees preferred to forage on native plants and selected the most productive native plant genera for Lepidoptera. In this study and others, bird predation on insects appears to be density dependent; the plants that support the most Lepidoptera also support the most bird foraging. For

example, in four studies that looked at bird predation on plants, the most preferred plant tended to also support very high numbers of Lepidoptera species (e.g. *Prunus*, 456 spp., Singer et al., 2012; *Betula*, 411 spp., Holmes and Robinson 1981; *Quercus*, 532 spp., Wood et al. 2012, this study). In agreement, we also show that our index based on Lepidoptera host plant use can be useful for predicting both caterpillar abundance on plants, as well as the plant preference of an insectivorous bird on native plants.

Currently, many 'wildlife-friendly' plant species are marketed to the public based on their ability to produce fruit or seed, well past the breeding season. In fact, several invasive shrubs (e.g. *Rosa multiflora*, *Lonicera maackii*, *Elaeagnus umbellata*) have been planted widely in part because they produced fruit for wildlife. Native horticultural plants should also be marketed for their ability to produce food for wildlife in the form of insect prey to support more diverse and complex food webs within residential neighborhoods. Because this index is based on plant genera, it is likely useful in other systems outside the Eastern United States. The Lepidoptera index used in this study could provide easy-to-use information to land managers and the public on which plant species best support breeding birds (available at https://nationalzoo.si.edu/migratory-birds/data). Several online databases already provide region-specific lists of native plants, but options are numerous and can be overwhelming (personal communications with homeowners). Including the Lepidoptera index may help guide consumers toward plant purchases that will be best able to serve as 'food hubs' for insectivorous birds.

For consumers that rely on specialized resources like insect prey, bottom-up resources via plant communities are predicted to limit populations in altered habitats

like residential yards. Here we found that chickadees avoided breeding in areas with high proportions of non-native plants, even when nesting cavities were available, suggesting that these areas do not provide the food resources necessary for raising young and cavity-availability is not necessarily the primary driver of chickadee breeding. Homeowners who choose to landscape with non-native plants are not providing suitable habitat for species that require a specialized diet of arthropods during breeding. The fact that there were no nesting chickadees present at sites most dominated by non-native plants suggests there may be a minimal threshold of suitable foraging plants required for successful breeding. Although our study focused on the breeding activity of a single species, greater than 96% of the terrestrial bird species in North America rear nestlings primarily on arthropod prey (derived from Dickinson 1999) because of the amount and quality of nutrients needed for growth and reproduction (Martin, 1987; Nagy and Holmes, 2005). In addition, chickadees are known to lead other bird species to foraging locations (Morse 1970). Thus, chickadee breeding behavior may serve as a model for the relationship between plant quality and habitat for insectivorous birds in general.

We did not find support for our prediction that occupancy and abundance would be negatively related to non-native plants; instead, occupancy and abundance was positively related to basal area of plants and abundance was negatively related to impervious surface. There are several reasons why our occupancy and abundance patterns were not consistent with our predictions. In areas with a high proportion of non-native plants, remaining native plants may continue to support enough prey for foraging birds, albeit without breeding. Nestlings may require higher abundances or reliability of insect food resources than non-native vegetation can support. Indeed, our

foraging data supports this assertion for chickadees, which disproportionately selected native plants in the most non-native sites. Furthermore, in sites where we were able to follow breeding chickadees, *Quercus*, the genus with the highest Lepidoptera Index, tended to be present and highly preferred.

In this system, the basal area of plants was the best predictor of chickadee occupancy with a weaker negative effect of non-native plants. The correlation between vegetation volume and chickadee presence is documented in other *Poecile* species (Brennan et al., 1999), and it is not surprising that Carolina chickadees behave similarly in a residential environment. However, non-native plants also had a negative effect on chickadee occupancy, albeit not statistically significant. Non-native plants may be biologically relevant to chickadee occupancy if non-breeding chickadees tend to, but may not always, avoid non-native plants for foraging and dispersal through the developed matrix. Our sample size may not have been large enough to detect a significant difference in occupancy given the variation in our data although our model estimates suggest that non-native trees may have a biological effect on chickadee occupancy. Regardless, individuals are not contributing to population growth until they initiate breeding, which is when the negative effect of non-native plants is most pronounced.

Chickadee abundance also declined with percent impervious surface and increased with tree basal area within 50 meters. Abundance may be directly impacted by factors not measured in this study, or changes in demographic parameters of chickadees over large scale variation in vegetation volume. Typically, chickadee counts were rarely more than two individuals encountered during each survey period. When counts exceeded 2 individuals it may have reflected a neighboring breeding pair

reacting to a territorial intrusion. Non-breeding, second-year individuals were frequently captured between April-June across all landscapes but were particularly common near breeding territories in areas with low urbanization and high mature tree densities (D. Narango, personal observation). Unmated non-breeding birds may result from a surplus of adults from source populations combined with a lack of suitable cavities or uneven sex ratios (Marra and Holmes, 1997). Demographic data across urban and plant origin gradients will elucidate which landscapes are more reproductively successful for breeding chickadees.

The general patterns that distinguish urban wildlife communities are often based on differences in the degree of development within the landscape, but local habitat differences, such as native plant availability, have received less attention. Our study suggests caution before generalizing 'urban' features and assuming 'adaptation' in breeding birds. First, despite similar amounts of development, plant communities were highly variable among neighborhoods due to landscaping decisions of homeowners and developers. Secondly, although chickadees were present in many yards during bird surveys, presence did not predict local breeding, and not every yard supported breeding individuals. Generalist synanthropes are thought to "thrive" in residential habitats (Donnelly and Marzluff, 2004), possibly because of increases in resources such as bird feeders and fruit availability (Gleditsch and Carlo, 2011). However, studies that rely on count data document presence but not necessarily reproduction. In this study, had we relied on only count data, we would have failed to find a strong effect of non-native plants. Instead, the strongest effects of non-native plants were on individually-based decisions of where chickadees chose to raise young, and the microhabitat they used to search for food.

Conclusions

Encouraging landscaping that has positive benefits for biodiversity has tremendous potential to restore human-dominated areas to wildlife-friendly and ecologically-stable habitat. This study complements accumulating evidence that the ecological quality of private properties influences the biodiversity residing in residential neighborhoods (Belaire et al., 2014; Burghardt et al., 2009; Lerman and Warren, 2011). Here, we provide evidence that residential areas can be improved for bird habitat by incorporating productive native plant species because non-native plants do not support sufficient prey resources, foraging substrates or breeding locations for an insectivorous breeding bird. Interestingly, the general decline of avian species in urban systems is driven by a loss in insectivorous specialists, and an increase in the abundance of disturbance-tolerant, and generalist omnivores (Blair, 1996). Our results suggest that the high proportion of non-native plants in these environments is contributing to these patterns by reducing habitat quality for consumers that rely on arthropod prey.

Across all urban systems, plants provide many essential ecosystem services in addition to enhancing biodiversity (e.g. carbon sequestration, watershed management, microclimate moderation, pollinator support, etc.) and also increase residential market values (USDA Forest Service, 2016). For example, in xeric areas, native landscaping, embraced by homeowners for water conservation, has simultaneously supported habitat for native desert bird communities (Lerman and Warren, 2011). Preserving natural, native habitat patches is a good strategy for improving landscapes for wildlife habitat. However, our study suggests that also improving habitat potential *between*

natural areas via sharing the residential matrix with flora and fauna is just as important. Future landscape planning for human-dominated landscapes should consider increasing plantings of native species that maximize ecosystem services as well as provide habitat for wildlife. Homeowners will benefit from such approaches while supporting local food webs and increasing landscape connectivity across urban areas.

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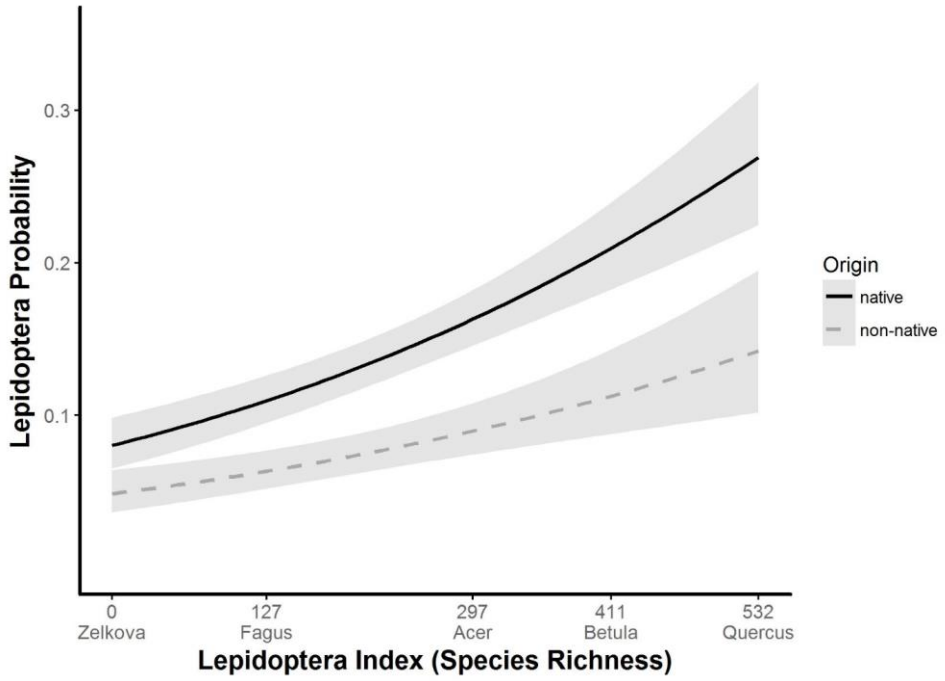


Figure 2.1 A model of the probability of Lepidoptera being found on a 5-minute search period for native and non-native plant species. When controlling for the diversity of Lepidoptera found on a given genus, non-native species had a lower probability of having caterpillars than native species (Non-native: β -0.65 ± 0.12, $P<0.001$, CI=-0.88, -0.42).

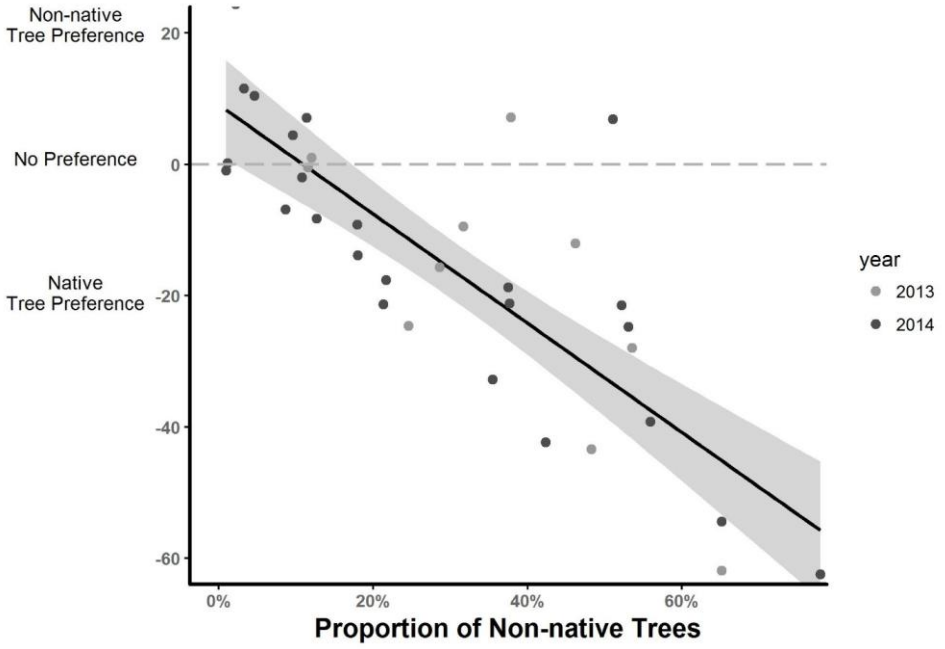


Figure 2.2 Relationship between chickadee non-native plant aversion (negative values) and proportion of non-native plants within 50m of the nest box (β: -0.42 ± 0.05, P<0.001, R^2: 0.68, CI: -0.52,-0.31). Plant preferences at the same site in both years were highly correlated (r>0.8); therefore, for sites with data for both years, only 2014 data were used for analyses. Values close to zero should be interpreted as foraging that is consistent with the availability within the territory.

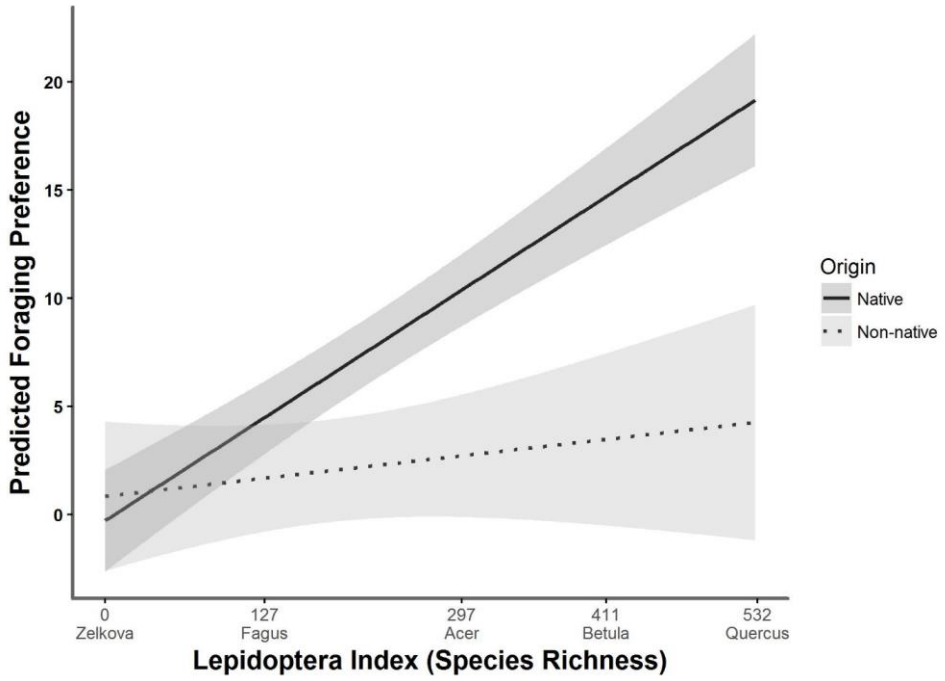
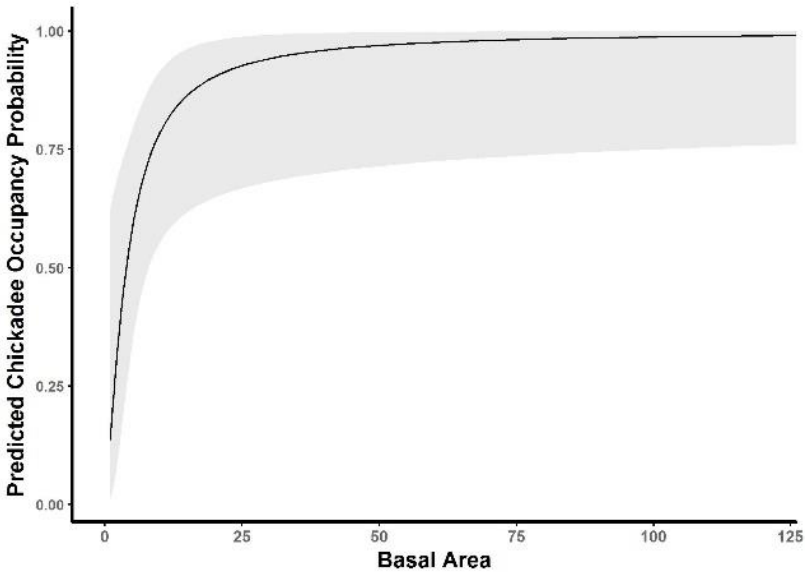
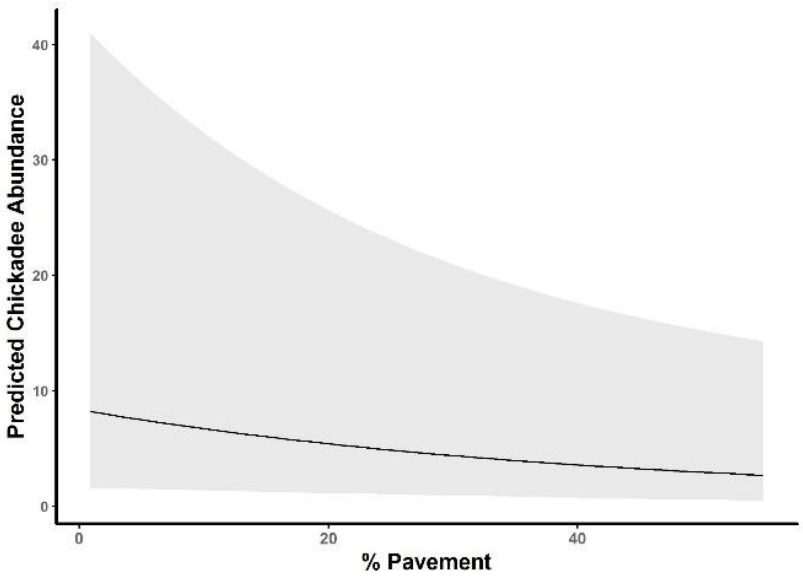


Figure 2.3 Relationship between the Lepidoptera Index and predicted foraging preference of chickadees in Washington, D.C. residential yards. Relative to the plant availability at the yard level (random effect), foraging preferences are positively related to the Lepidoptera Index (β: 6.27 ± 0.72, P<0.001, CI: 4.85, 7.70), a proxy for both prey diversity and availability. However, this relationship is weaker for non-native plants (Lepidoptera Index*Origin: β: -5.17 ± 1.42, P<0.001, CI: -7.96, -2.38) and foraging preferences are lower for non-native plants (Origin: β: -3.53 ± 1.47, P=0.02, CI: -6.43, -0.63).

(a)


Predicted Chickadee Occupancy Probability
1.00
0.75
0.50
0.25
0.00
0
25
50
75
100
125
Basal Area

(b)


Predicted Chickadee Abundance
40
30
20
10
0
0
20
40
% Pavement

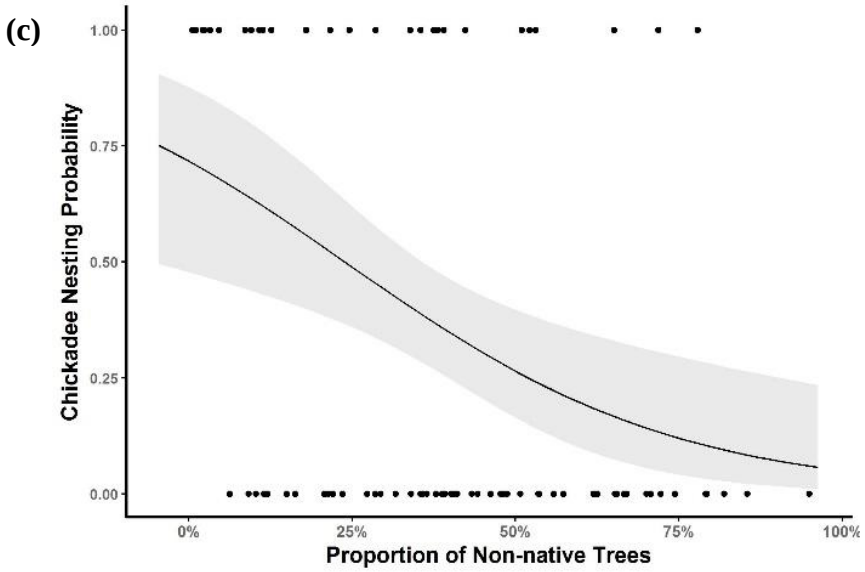


Figure 2.4 Relationships between local variables and chickadee occupancy, abundance and breeding activity. Estimates shown are model-averaged. (a) The probability of chickadee occupancy is positively related to the basal area of trees at the 50m-radius site (BASAL: β 1.47 ± 0.64, CI: 0.21, 2.73). (b) The abundance of chickadees is negatively related to the average % impervious surface at the 50m-radius site (IMPERVIOUS: β -0.32 ± 0.12, CI: -0.55, -0.08). (c) The probability of chickadee nesting is negatively related to the proportion of non-native trees at the territory (EXOTIC TREE: β -0.90 ± 0.30, CI: -1.49, -0.30).

REFERENCES

1. Aslan, C.E., Rejmánek, M., 2010. Avian use of introduced plants: ornithologist records illuminate interspecific associations and research needs. Ecol. Appl. 20, 1005–1020.

2. Belaire, J.A., Whelan, C.J., Minor, E.S., 2014. Having our yards and sharing them too: the collective effects of yards on native bird species in an urban landscape. Ecol. Appl. 24, 2132–2143.

3. Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. Ecol. Appl. 6, 506–519.

4. Brennan, L.A., Morrison, M.L., Dahlsten, D.L., 1999. Influence of Vegetation on Occupation of Nest Boxes by Chestnut-Backed and Mountain Chickadees. Northwest. Nat. 80, 90–98. doi:10.2307/3536655

5. Brewer, R., 1961. Comparative Notes on the Life History of the Carolina Chickadee. Wilson Bull. 73, 348–373.

6. Burghardt, K.T., Tallamy, D.W., 2013. Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. Divers. Distrib. doi:10.1111/ddi.12122

7. Burghardt, K.T., Tallamy, D.W., Shriver, W.G., 2009. Impact of native plants on bird and butterfly biodiversity in suburban landscapes. Conserv. Biol. 23, 219–224.

8. Burghardt, K.T., Tallamy, D.W., Philips, C., Shropshire, K.J., 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere 1, art11. doi:10.1890/ES10-00032.1

9. Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

10. Cook, R.W., Talley, T.S., 2014. The invertebrate communities associated with a Chrysanthemum coronarium-invaded coastal sage scrub area in Southern California. Biol. Invasions 16, 365–380.

11. Cooper, R.J., 1988. Dietary relationships among insectivorous birds of an eastern deciduous forest. West Virginia University PhD Dissertation

12. Culbert, D.F. 2013. Florida Coonties and Atala Butterflies. Environmental Horticulture Department, Florida Cooperative Extension Service, Institute of Food and Agricultural Sciences, University of Florida. https://edis.ifas.ufl.edu/mg347#FOOTNOTE_1 (Accessed March 17, 2016).

13. Dickinson, M.B. 1999. Field Guide to the Birds of North America. ed. 3. National Geographic Society. Washington, D.C.

14. Dolan, R.W., Moore, M.E., Stephens, J.D., 2011. Documenting effects of urbanization on flora using herbarium records. J. Ecol. 99, 1055–1062. doi:10.1111/j.1365-2745.2011.01820.x

15. Donnelly, R., Marzluff, J.M., 2004. Importance of Reserve Size and Landscape Context to Urban Bird Conservation. Conserv. Biol. 18, 733–745. doi:10.1111/j.1523-1739.2004.00032.x

16. Eeva, T., Helle, S., Salminen, J.-P., Hakkarainen, H., 2010. Carotenoid Composition of Invertebrates Consumed by Two Insectivorous Bird Species. J. Chem. Ecol. 36, 608–613. doi:10.1007/s10886-010-9796-0

17. Evans, C., Abrams, E., Reitsma, R., Roux, K., Salmonsen, L., Marra, P.P., 2005. The Neighborhood Nestwatch Program: Participant Outcomes of a Citizen-Science Ecological Research Project. Conserv. Biol. 19, 589–594.

18. Faeth, S.H., Warren, P.S., Shochat, E., Marussich, W.A., 2005. Trophic dynamics in urban communities. BioScience 55, 399–407.

19. Fiedler, A.K., Landis, D.A., 2007. Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. Environ. Entomol. 36, 751–765.

20. Fiske, I., Chandler, R., others, 2011. Unmarked: An R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.

21. Flanders, A.A., Kuvlesky Jr, W.P., Ruthven III, D.C., Zaiglin, R.E., Bingham, R.L., Fulbright, T.E., Hernández, F., Brennan, L.A., Vega Rivera, J.H., 2006. Effects of invasive exotic grasses on South Texas rangeland breeding birds. The Auk 123, 171–182.

22. Forister, M.L., Novotny, V., Panorska, A.K., Baje, L., Basset, Y., Butterill, P.T., Cizek, L., Coley, P.D., Dem, F., Diniz, I.R., others, 2015. The global distribution of diet breadth in insect herbivores. Proc. Natl. Acad. Sci. 112, 442–447.

23. Gleditsch, J.M., Carlo, T.A., 2011. Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. Divers. Distrib. 17, 244–253. doi:10.1111/j.1472-4642.2010.00733.x

24. Goddard, M.A., Dougill, A.J., Benton, T.G., 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends Ecol. Evol. 25, 90–98. doi:10.1016/j.tree.2009.07.016

25. Grubb, T.C., Bronson, C.L., 1995. Artificial snags as nesting sites for chickadees. The Condor 97, 1067–1070.

26. Harvey, J.A., Bukovinszky, T., van der Putten, W.H., 2010. Interactions between invasive plants and insect herbivores: A plea for a multitrophic perspective. Biol. Conserv. 143, 2251–2259. doi:10.1016/j.biocon.2010.03.004

27. Holmes, R.T., Robinson, S.K., 1981. Tree Species Preferences of Foraging Insectivorous Birds in a Northern Hardwoods Forest. Oecologia 48, 31–35. doi:10.2307/4216265

28. Holmes, R.T., Schultz, J.C., 1988. Food availability for forest birds: effects of prey distribution and abundance on bird foraging. Can. J. Zool. 66, 720–728. doi:10.1139/z88-107

29. Holmquist, J.G., Schmidt-Gengenbach, J., Slaton, M.R., 2011. Influence of invasive palms on terrestrial arthropod assemblages in desert spring habitat. Biol. Conserv. 144, 518–525.

30. Hutto, R.L., 1990. Studies of foraging behavior: central to understanding the ecological consequence of variation in food abundance. Stud. Avian Biol. 13, 389–390.

31. Johnson, M.D., 2007. Measuring Habitat Quality: A review. The Condor 109, 489–504. doi:10.1650/8347.1

32. Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17, 164–170. doi:10.1016/S0169-5347(02)02499-0

33. Lerman, S.B., Nislow, K.H., Nowak, D.J., DeStefano, S., King, D.I., Jones-Farrand, D.T., 2014. Using urban forest assessment tools to model bird habitat potential. Landsc. Urban Plan. 122, 29–40. doi:10.1016/j.landurbplan.2013.10.006

34. Lerman, S.B., Warren, P.S., 2011. The conservation value of residential yards: linking birds and people. Ecol. Appl. 21, 1327–1339. doi:10.1890/10-0423.1

35. Litt, A.R., Steidl, R.J., 2010. Insect assemblages change along a gradient of invasion by a nonnative grass. Biol. Invasions 12, 3449–3463.

36. MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. 9, 300–318. doi:10.1198/108571104X3361

37. MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., Franklin, A.B., 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84, 2200–2207. doi:10.1890/02-3090

38. MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255. doi:10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

39. Marra, P.P., Holmes, R.T., 1997. Avian removal experiments: Do they test for habitat saturation or female availability? Ecology 78, 947–952.

40. Martin, T.E., 1987. Food as a limit on breeding birds: a life-history perspective. Annu. Rev. Ecol. Syst. 453–487.

41. Marzluff, J.M., 2014. Welcome to Subirdia: Sharing Our Neighborhoods with Wrens, Robins, Woodpeckers, and Other Wildlife. Yale University Press.

42. McKinney, M.L., 2008. Effects of urbanization on species richness: a review of plants and animals. Urban Ecosyst. 11, 161–176.

43. Mitchell, A.B., Litt, A.R., 2016. Nonnative plant shifts functional groups of arthropods following drought. Biol. Invasions 18, 1351–1361. doi:10.1007/s10530-016-1072-y

44. Mosteller, F., Fisher, R.A., 1948. Questions and Answers. Am. Stat. 2, 30–31. doi:10.2307/2681650

45. Mostrom, A.M., Curry, R.L., Lohr, B.S., 2002. Carolina Chickadee: *Poecile Carolinensis*. Birds of North America.

46. Nagy, L.R., Holmes, R.T., 2005. Food limits annual fecundity of a migratory songbird: an experimental study. Ecology 86, 675–681. doi:10.1890/04-0155

47. Radeloff, V.C., Williams, J.W., Bateman, B.L., Burke, K.D., Carter, S.K., Childress, E.S., Cromwell, K.J., Gratton, C., Hasley, A.O., Kraemer, B.M., Latzka, A.W., Marin-Spiotta, E., Meine, C.D., Munoz, S.E., Neeson, T.M., Pidgeon, A.M., Rissman, A.R., Rivera, R.J., Szymanski, L.M., Usinowicz, J., 2015. The rise of novelty in ecosystems. Ecol. Appl. 25, 2051–2068. doi:10.1890/14-1781.1

48. Razeng, E., Watson, D.M., 2014. Nutritional composition of the preferred prey of insectivorous birds: popularity reflects quality. J. Avian Biol. n/a-n/a. doi:10.1111/jav.00475

49. Rodenhouse, N.L., 1986. Food limitation for forest passerines: effects of natural and experimental food reductions.

50. Shochat, E., Warren, P.S., Faeth, S.H., McIntyre, N.E., Hope, D., 2006. From patterns to emerging processes in mechanistic urban ecology. Trends Ecol. Evol. 21, 186–191.

51. Singer, M.S., Farkas, T.E., Skorik, Mooney, K.A., 2012. Tritrophic Interactions at a Community Level: Effects of Host Plant Species Quality on Bird Predation of Caterpillars. Am. Nat. 179, 363–374. doi:10.1086/664080

52. Stephens, D.W., Brown, J.S., Ydenberg, R.C., 2007. Foraging: behavior and ecology. University of Chicago Press.

53. Tallamy, D.W., 2007. Bringing nature home: How native plants sustain wildlife in our gardens. Timber Pr.

54. Tallamy, D.W., 2004. Do Alien Plants Reduce Insect Biomass? Conserv. Biol. 18, 1689–1692. doi:10.1111/j.1523-1739.2004.00512.x

55. Tallamy, D.W., Ballard, M., D'Amico, V., 2010. Can alien plants support generalist insect herbivores? Biol. Invasions 12, 2285–2292. doi:10.1007/s10530-009-9639-5

56. Tallamy, D.W., Shropshire, K.J., 2009. Ranking lepidopteran use of native versus introduced plants. Conserv. Biol. 23, 941–947.

57. Thorne, M.S., Skinner, Q.D., Smith, M.A., Rodgers, J.D., Laycock, W.A., Cerekci, S.A., 2002. Evaluation of a Technique for Measuring Canopy Volume of Shrubs. Journal of Range Management 55, 235–241. doi:10.2307/4003129

58. Wagner, D.L., 2010. Caterpillars of eastern North America: a guide to identification and natural history. Princeton University Press.

59. Wood, E.M., Pidgeon, A.M., Liu, F., Mladenoff, D.J., 2012. Birds see the trees inside the forest: The potential impacts of changes in forest composition on songbirds during spring migration. For. Ecol. Manag. 280, 176–186. doi:10.1016/j.foreco.2012.05.041

Chapter 3

NONNATIVE PLANTS REDUCE POPULATION GROWTH OF AN INSECTIVOROUS BIRD

Abstract

Human-dominated landscapes are the most rapidly expanding ecosystems on earth, yet we know little about which features sustain or enhance their wildlife populations. Nonnative plants dominate most urban areas, but these species do not support insects critical for higher-order consumers. Despite the logical connection among plants, insects and vertebrate consumers, no study has examined the impact of nonnative plants on vertebrate consumer populations. Here, we demonstrate that residential yards dominated by nonnative plants had lower arthropod abundance, forcing Carolina chickadees to switch diets to less preferred prey. This diet shift leads to lower reproductive success and declining population trajectories compared to residential yards with >70% native plant biomass. Our results reveal that properties landscaped with nonnative plants are population sinks for insectivorous birds and emphasize the importance of promoting sustainable food webs by encouraging land owners to prioritize native plant species.

One Sentence Summary: Insectivorous bird populations and their prey are not sustained by nonnative plants in residential yards.

Main Text

E.O. Wilson has called insects "the little things that rule the world," underscoring their contribution to the maintenance of ecosystems (*1*). Unfortunately, recent studies have documented drastic declines in insect abundance following decades of human land-use (*2*); declines that may also compromise higher order trophic levels. One probable cause of insect declines in human-modified landscapes is the shift from native plant communities to those dominated by nonnative species. Over 90% of herbivorous insects specialize on one or a few native plant lineages (*3*) – thus, ecosystems dominated by nonnative plants are characterized by reduced insect diversity, abundance, and biomass (*4–7*). Given that the majority of terrestrial birds rely on insects as a primary food source for reproduction and survival, the persistence of insectivorous bird populations is inextricably linked to insect conservation. Nevertheless, the impact of landscapes dominated by nonnative plants on the population growth of insectivorous birds has never been measured, despite the global prevalence of nonnative plants (*8–10*) and the decline of biodiversity (*11*) in built landscapes.

One of the challenges of urban ecology is to understand how novel ecosystems change biotic communities and whether remaining species are filtered according to biological traits (*12*). To do this we must understand how organisms that have not evolved together interact at both individual and population levels and determine which features promote sustainable populations. Contemporary urban restoration aims to rebuild ecological function by prioritizing species that support important ecosystem services which may or may not include nonnative species. Considering that nonnative plants tend to dominate urban landscapes (*10*), it is imperative that we evaluate the contribution of nonnative plants to ecosystems relative to the native species that are displaced (*13*). Here, we measure how nonnative plants influence insectivorous birds by

quantifying arthropod abundance, avian diet, reproductive success, and adult & juvenile survival of Carolina chickadees (*Poecile carolinensis*) in private yards across a metropolitan area that varied in proportion of nonnative plant biomass (*14*, appendix figure B.1). We then incorporated our reproductive and survival confidence intervals into an iterative population growth model to estimate how population growth (λ) varied with the proportion of nonnative plants.

Arthropod sampling indicated that mean abundance of both caterpillars and spiders declined as nonnative plant biomass increased (n=202, Generalized Linear Model with quasi-Poisson regression (GLM-QP: β -1.33 ± 0.40, p=0.001, CI: -2.11, -0.56, Figure 3.1). Chickadee diets, estimated by $\delta^{15}N$ within blood plasma, shifted along this nonnative plant gradient from caterpillar dominated at sites with low nonnative plant cover to predatory arthropods (e.g. spiders) where nonnative plants became more dominant (n=60, Generalized Linear Model: β 2.14 ±0.69, p=0.002, CI: 0.79, 3.49, Figure 3.1). There was no difference between adult and nestling chickadees in $\delta^{15}N$ (GLM: β -0.02 ±0.25, p>0.1, CI:-0.50, 0.47), nor between years in levels of $\delta^{15}N$ in blood plasma (GLM: β 0.10 ± 0.25, p>0.1, CI: -0.39, 0.58). Our threshold models indicated that the slope of prey decline leveled off at 33.5% nonnative plants, and that chickadees ate more predatory arthropods such as spiders when yards were composed of 37.6% or more nonnative plant cover.

We used life history aster models (*15*) to simultaneously test the effect of nonnative plants on chickadee reproduction as a whole, as well as model the effect on each conditional stage of reproduction. We considered plant foliage biomass and year as plausible factors that might improve model fit; however, the model with the best fit included only the nonnative plant term. Reproductive success, defined as the number of

young produced by chickadees within the site per season, declined as nonnative plant biomass increased within the site (Aster model (AM): β -0.31 ± 0.06, p<0.001, Figure 3.2, appendix table B.1). Estimates from all stages of breeding were negative, indicating reproductive declines as nonnative plants increased. The model was influenced most strongly by negative effects of nonnative plants on the probability of chickadee settlement (AM: β -3.31 ± 0.64, p<0.001, Likelihood Ratio Test (LRT) deviance: 30.19, p<0.001, appendix figure B.2), and decline in the probability of nesting (AM: β –2.50 ± 0.774, p=0.001, LRT deviance: 10.93, p<0.001, appendix figure B.3). Additional negative effects of clutch size (AM: β -0.10 ± 0.23, p>0.1, LRT deviance: 0.18, p>0.1, appendix figure B.4), nest survival (AM: β -1.70 ± 0.97, p=0.08, LRT deviance: 3.88, p=0.07, appendix figure B.5) and fledgling number (AM: β -0.28 ± 0.29, p>0.1, LRT: 0.90, p>0.1, Figure 3.2) were modest when controlling for earlier components. Combined, nonnative yards were less attractive to reproductive individuals (i.e. "habitat quality hypothesis", settlement + breeding model, LRT deviance: 32.73, p<0.001), and individuals that did attempt to reproduce in nonnative yards had lower reproductive success (i.e. "habitat sink hypothesis", nest success + number of young fledged, LRT deviance: 4.00, p=0.04). Although chickadees are flexible enough to modify their diet when preferred prey are unavailable, and appear to judge habitat quality accurately, their flexibility is not sufficient to fully compensate for prey declines; thus, the reproductive performance of birds breeding in suboptimal habitat declines.

We used a Bayesian Cormack-Jolly-Seber model (*16*) to estimate apparent adult chickadee survival using 806 individuals across 132 sites. We found that nonnative plants had no detectible effect on apparent annual survival of adult females (CJS: β -0.08 ± 0.18 SD, appendix figure B.6) nor males (CJS: β 0.04 ± 31.61). Large

uncertainty in estimates at the highest end of the gradient was due to low sample sizes given that chickadees are unlikely to occupy sites with high proportions of nonnative plants. Mean female and male survival across the gradient were similar (Female: φ 0.62 ± 0.02 SD, range: 0.53-0.65; male: φ 0.62 ± 0.02 SD, range: 0.55-0.65).

For juvenile survival, our model revealed that mean daily survival for 88 juveniles was φ: 0.94 ± 0.01 SD. For each iteration, we took the product of daily survival from day 1-21 (i.e. number of days before independence), and then took the mean of all iterations, to determine that mean survival for the fledgling period was φ: 0.24 ± 0.06 SD (95% credible interval: 0.13-0.35, appendix figure B.7).

Using confidence intervals from our reproduction and survival models, we ran an iterative, female-centered population growth simulation to model change in λ over the nonnative plant gradient. We found that as the proportion of nonnative plant biomass increased within landscapes, chickadee population growth declined (Figure 3.4). Mean population growth in our residential system was only sustainable at <6% nonnative plant biomass (λ>0); however, confidence intervals overlapped replacement when nonnative plants were <30% of plant biomass. This simulation revealed that mean chickadee population growth was typically unsustainable in residential areas under the current landscaping paradigm but sites with a low percentage of nonnative plants (<30%) have potential to provide sufficient insect prey so that chickadees may source young to the regional population including areas that act as population sinks.

Residential areas are often characterized by vegetation loss relative to natural areas, but they also harbor diverse floral communities due to commercial availability and the personal choices of homeowners (*17–19*). This is critically important given that the widespread preference for nonnative plants in the horticultural industry has globally

transformed millions of hectares from potential habitat into ‘food deserts’ for native insects, with the unintentional consequence of reducing the abundance and distribution of birds. Until recently, urban habitat restoration has operated on the premise that all green spaces including residential landscapes and city parks are ecologically equivalent despite a poor understanding of the features determining whether a space functions as a source or sink for resident species (*17*). Our results identified the evolutionary origin of the plants used in urban landscaping as a key factor determining the ecological viability of such landscapes. Because many nonnative plants popular in horticulture are not currently invasive, it has been suggested that their negative ecological impacts are minimal (*13*) and that they may even benefit biodiversity by increasing plant diversity. Our study challenges this notion; our residential plant communities contained >200 different nonnative woody plant species, yet their evolutionary novelty created a trophic dead end for insectivorous consumers.

Our work demonstrates that even a common ‘urban-adapted’ bird species is food limited when nonnative plants dominate landscapes, but food limitation may be even more pronounced for diet-sensitive bird species. At least 310 bird species in North America are known to prey extensively on caterpillars (*20*), and the majority of terrestrial birds rely on insects at some point in their annual cycle. Specialist guilds that include numerous insectivores of conservation concern tend to be lost as habitats become increasingly urbanized (*21*). Thus, our findings for chickadees are likely to apply broadly to insectivorous birds and may partially explain the local extinction of these species from human dominated habitats. If bird species are eliminated from urban areas because they are intolerant of nonnative plants and concomitant declines in prey abundance, our recommendation for <30% nonnative plant biomass in landscape

designs represents a maximum limit for sustaining avian insectivores in these landscapes.

Our work adds to the growing body of evidence that native plants are essential for providing ecosystem services and resources for wildlife in human-modified landscapes (*7*, *22–24*). Nevertheless, even within sites with predominately native plant communities, there was substantial variation in potential population growth of chickadees. This may be influenced by the large differences among native plant species in the ability to support insect prey (*7*, *25*). Thus, future habitat restoration in residential landscapes should involve not just blanket prioritization of native species, but a nuanced consideration of the native plants that maximize stable food webs with the highest number of trophic interactions (*26*). Simultaneous study of which plant species support the most trophic interactions and whether their abundance influences consumer demography will reveal whether some native plants are disproportionately important for sustaining wildlife populations in residential systems.

We recognize that nonnative plants are extremely popular in the horticultural industry and are unlikely to be removed from commercial sale in the future (*8–10*, *19*). They can provide an aesthetically pleasing alternative to native species and many tolerate degraded urban conditions. Yet these plant species are clearly not the ecologically equivalents of the native plants they replace, especially in terms of meeting nutritional needs of native fauna that rely on insect populations for food. We recommend that ecological function be added to criteria used when choosing plants for local landscapes. Our study suggests that to conserve insect communities, sustain insectivorous bird populations, and support viable food webs in human-dominated

landscapes, productive, locally native flora should be prioritized for landscaping over nonnative species.

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Materials and Methods

Study Sites and Species

Carolina chickadees (*Poecile carolinensis*) were studied within *Neighborhood Nestwatch*, a citizen science program that monitors breeding birds in residential yards across the Washington D.C. metropolitan area (*27*, appendix figure B.1). Because birds operate at a patch rather than a yard scale (*18*), each 'site' was composed of a focal yard that contained a chickadee nest box as well as a 50-m radius (0.79 Ha) area around the center of the yard that contained other properties. A 50-m radius was chosen because this area is approximately the territory size of breeding chickadees (*28*). Sites were separated by at least 1km, located within a residential landscape and no sites were located within publically-owned parkland.

We chose chickadees as a study species because of their cosmopolitan presence in urban environments and predominantly insectivorous diet throughout most of the year such that caterpillars and spiders are disproportionately important prey relative to other invertebrate taxa (*29, 30*). We placed chickadee nest boxes into the yards of 159 Nestwatch participants, quantified each plant community, monitored arthropod abundance, and assessed chickadee site occupancy and reproduction as well as diet using the ratio of $^{15}N/^{14}N$ in blood plasma ($\delta^{15}N$). We also used a 17-year capture-resight dataset of individually-marked adult chickadees from Nestwatch to estimate apparent annual survival of adults and used radio-telemetry to monitor family groups after fledging for juvenile survival.

Field Methods

Arthropod Abundance

In 2013-2014 we quantified arthropod abundance using a timed-search approach on sixteen woody plants per site. In each cardinal direction, we randomly chose four plant species 25m from the center of the yard and conducted three, 5-minute searches per plant for all arthropods within a 2.25m^2 area (48 samples per site). Because of the large number of zeros in our dataset and high variation among plant species, we calculated the average abundance of caterpillars and spiders per sample, for each site.

Diet

Within these years we also determined the trophic level of individual adult and nestling chickadees using stable isotope ratios of $\delta^{15}N$ found in the blood plasma of captured birds. We used values of $\delta^{15}N$ to assign trophic position of individual birds where lower values indicate a higher consumption of herbivorous arthropods (such as caterpillars) and higher values indicate higher consumption of predatory arthropods (such as spiders) (*31*). We collected blood samples from birds via brachial veins, spun samples in a centrifuge to separate plasma from hematocrit and stored in a freezer at -80^{o}C. Prior to isotopic analysis, we freeze-dried samples for at least 24 hours and weighed 0.5-0.7mg into tin capsules. For nestlings, individuals within a nest are non-independent; therefore, we randomly selected a sample from one individual from each nest for processing. All samples were analyzed for isotopic analysis at the Smithsonian Stable Isotope Mass Spectrometry Laboratory in Suitland, MD. In each run, we included acetanilide and urea standards every 13 samples. We calculated δ units in parts per thousand (‰) as the ratio of ^{15}N:^{14}N based on international standards of atmospheric nitrogen.

Reproduction

From 2013-2016 we collected data on chickadee reproduction and occupancy by monitoring nest boxes during the chickadee breeding season (March-June, for more details see *7*). Nest box monitoring was completed by both technicians and volunteer homeowners trained in monitoring protocol by DLN. Nest boxes were checked approximately once per week and presence of a nest, number of eggs and number of nestlings were recorded. In addition, technicians visited sites at least once per month regardless of nesting status to search for nests or breeding evidence in natural cavities or adjacent properties, as well as confirm clutch and brood sizes from our citizen science data. Following successful completion of the nest, boxes were checked again to collect any deceased nestlings. At the end of the season, each site was assigned whether a chickadee was present, whether a nest was active, total eggs laid, whether the nest was successful (at least 1 young fledged) and total number of young produced. Nests were not considered active until at least one egg was laid.

In each month we also conducted timed point-counts to survey chickadee occupancy. A trained technician recorded every chickadee seen or heard within 50m from the center of the yard during a 10-minute survey. Most chickadee nesting occurs between late March-Mid June in this region (>99% of nests observed). In addition, after mid-June territories break down and dispersal occurs such that birds occupying yards in late summer may be only transient individuals. Thus, in order to capture birds that were occupying territories during the breeding season, we only included surveys between April-June. We created a binary variable for each site where 1 indicated a chickadee was present during a survey within 50m and 0 if no chickadee was observed during surveys. If a nest was monitored without a chickadee being detected on a survey we considered that site as occupied.

Adult Survival

We quantified annual survival using a 17-year capture-resight dataset on individually-marked chickadees caught at sites for which we also had recorded plant community data. Sites were visited at least once each year between April-August to color-band chickadees and re-sight returning individuals (for more details see *32*). Our data set included birds captured from 2000-2016; however, 2006 and 2011 were not included because no data were collected in these years. Birds were captured opportunistically, using mist nets and conspecific playback and individuals were marked with a unique combination of colored plastic bands, as well as a US Fish and Wildlife Service aluminum band. All birds were aged using plumage characteristics (e.g. molt limits, *33*) and skull ossification and sexed via breeding evidence. During yearly visits, technicians systematically covered a 200m radius area to re-sight previously captured individuals that were not present in the focal area. Homeowners were also trained on re-sighting techniques and instructed to report opportunistic observations of color-banded individuals throughout the year.

Juvenile Survival

In 2016, we determined juvenile survival by following family groups with radio-telemetry and monitoring the daily survival of 88 fledglings after leaving the nest. We placed transmitters on adults in order to monitor survival of the young by proxy, because of nestling sensitivity to premature fledging once they were old enough to carry transmitters, and the difficulty of recovering transmitters from deceased birds on private land. In all, transmitters were successfully placed on adults from 20 nests just prior or immediately after fledging. Transmitters have been successfully used to monitor the

survival of young and are shown to have no effect on behavior or mortality on similar species (*34*).

Transmitters were placed on adults between days 14-16 of the nestling period, or immediately after fledging. We used the PicoPip Ag337 transmitter from Lotek Wireless Inc. (www.lotek.com) with 12 millisecond pulse length and 30 pulses per minute. We attached transmitters using the Rappole and Tipton harness method (*35*) using 1mm elastic beading cord. The total weight of transmitter and harness was <5% of the total weight of all individuals (total weight: ~0.4g). All transmitters had a battery life of >21 days. For most nests, all nestlings were banded with one federal band and one color-band so that all individuals could be uniquely identified. Nestlings from some nests could not be accessed because of the design (2 nests) or height (1 nest) of the nest box. For these nests, we counted the number of individual fledglings that were observed being fed by the adult with the transmitter.

Our resighting of fledglings occurred the first visit after the nest had successfully fledged. We confirmed the number of nestlings that fledged by inspecting nest boxes for deceased individuals. We assumed that any nestlings not present in the box had successfully fledged. We monitored family groups by locating the individual with the transmitter and determining the number and identity of all fledglings in its care. Chickadee families remain intact with both adults regularly caring for young together. In general, all fledglings remain in the same proximate area while being cared for and make conspicuous begging calls that allow for relocation. Once the adult was found we followed the family group for at least 30 minutes in order to record the location of foraging and fledglings being cared for. We monitored family groups for at least 21 days; after which remaining fledglings began to reach independence and disperse.

On some visits, adults could not be visually relocated due to 1) a homeowner denying access to the property, 2) interference with the signal, 3) personal safety of the technician or 4) behavior of the adults. On these occasions we spent at least one hour traversing the surrounding neighborhood attempting to relocate and resight the family group and triangulate the approximate location. If the group could not be visually relocated after at least 1 hour, the number of fledglings was not recorded for that visit.

Plant Communities

We determined proportion of nonnative plant biomass at the site level, using a modified i-Tree protocol for assessing wildlife habitat (*36*). We surveyed 5 non-overlapping 0.04 Ha circular plots including one centered on the nest box and 4 additional plots located randomly within the site area. Within each plot, we measured and identified all woody trees and shrubs, calculated foliage biomass, and determined the importance value for each plant species. *Importance value* is a forestry metric for how dominant a species is at a site by summing the relative density and relative biomass for each plant species.

In order to combine the biomass of both trees and shrubs to use in our importance value calculations, we used the foliage volume of each individual plant. We calculated foliage volume using the following formula from Thorne et al. (*37*) based on the basic ellipsoid volume formula:

$$FoliageVolume = \frac{2}{3}\pi H\left(\frac{A}{2}*\frac{B}{2}\right)$$

Where *H* is the height, *A* is the width at the widest point, and *B* is the width perpendicular to *A*. For shrubs, we used the height and width of the full shrub. For trees, we used the height and width of the canopy.

On a small subset of trees (8% of the total dataset), we collected data on the diameter at breast height (dbh) but were unable to acquire full canopy data in order to calculate foliage volume. To include these trees in our calculations, we used our known canopy volumes and dbh relationship to estimate canopy volumes for these trees. Using the function 'glmer' from package 'lme4' (*38*). We ran a generalized linear mixed model with a Poisson distribution using canopy volume as our response variable, dbh as a fixed effect, and tree species as a random effect to allow different species to grow at different rates. We used the function 'r.squaredGLMM' in package 'MuMIn' (*39*) to calculate the variance that was explained by our fixed and random effects. This model had a conditional pseudo R^2 of 0.70 indicting that tree species and dbh strongly explained the variation in canopy volume. With this model, we used the 'predict' function in R to estimate canopy volume according to both dbh and species identity for each individual tree that was missing canopy data prior to calculating importance values.

We determined plant origin using USGS (*40*, *41*) and USDA (*42*) range maps and information from the Missouri Botanical Garden (*43*). We designated nonnative plants as any taxon with a distribution that does not include the Eastern United States (i.e. east of the Mississippi river). Importance values for all nonnative plants were summed to obtain total importance value of nonnative species at the site. Because plant biomass may also be an important feature for foliage-gleaning birds, we also calculated foliage volume by summing total volume for each plant species.

Statistical Analysis

Arthropod Abundance and Chickadee Diet

To determine whether arthropod abundance and diets may be altered by changes in the plant community, we used generalized linear regression. Our prey model included nonnative plants and arthropod type (i.e. caterpillar or spider) as predictors (n=220) and our error distribution was quasi-Poisson. Our diet model included nonnative plants, age (i.e. adult, nestling) and year (n=60) and a Gaussian error distribution. Diets comprised of herbivorous consumers (e.g. caterpillars) occupy a lower trophic level, and thus, have low $\delta^{15}N$; therefore, chickadees in areas dominated by nonnative vegetation were predicted to have higher values of $\delta^{15}N$ because of increased consumption of alternative prey such as predatory arthropods (e.g. spiders). To calculate thresholds we refit both our prey and diet models with a squared nonnative plant term and used the coefficients in the following equation: $\frac{-b}{2*a}$ where *a* represents the coefficient of our linear term, and *b* represents the coefficient of our quadratic term.

Reproduction

We used life history 'aster' models (*15, 44*) to test whether nonnative plants influence several related and conditional levels of reproductive success (n=411 site/year combinations). The benefit of using ASTER models is that these models allow you to test for the effect of your variable of interest on reproductive fitness as a whole, as well as test for the influence on conditional levels of reproduction within one joint model without sacrificing degrees of freedom. The conditional levels included in the model were reproductive elements with a Bernoulli distribution (settlement, nest initiation, and

nest survival) and two with a zero-truncated Poisson distribution (number of eggs, number of fledglings; figure 3.1). In our model we tested three variables we were primarily interested in and had the most justification: proportion of nonnative plant biomass, foliage volume (to represent plant biomass), and year to account for annual variation. To obtain significance of our predictor terms, we compared our full model with nested models with one of our three fixed effects removed using likelihood ratio tests. We also compared a full additive model with models that included interaction terms. Our best fit model included all significant fixed and interaction terms. With this model, we then used the "predict.aster" function to estimate conditional mean value parameters of each stage over our nonnative plant gradient from 0-100% nonnative plants.

With our best fit model, we assessed the magnitude of the effect of nonnative plants on each node in the reproductive model. To determine whether the effect of nonnative plants at each stage improved our predictions of total reproductive success, we created a binary pseudo-covariate for each stage, and then used likelihood ratio tests to assess whether including that stage in our total reproduction model significantly affected fitness relative to other stages. Here, if inclusion of an interaction between nonnative plants and our reproductive stage of interest improved the fit of our model compared to a null model with prior stages, then nonnative plants had a strong impact on total reproductive success at this stage independent of prior stages. We also compared two additive models, a 'habitat quality' model that included the effects of nonnative plants on settlement and nesting probability, and a 'habitat sink' that included the effects on nest survival and number of fledglings.

Some minor changes were made to the reproduction dataset prior to the analysis. First, we removed all sites in years where the nest fate was unknown because the nest was either not monitored to completion, or we did not receive permission from the homeowner to monitor (n=15). For nests which number of fledglings was unknown (n=8), we included the mean number of fledglings produced across all sites (4 fledglings). For nests which the number of eggs laid was unknown (n=9) we included the same number of fledglings that were produced under the assumption that all eggs had hatched and survived. For nests which the pair failed during laying (n=5), and thus the potential number of eggs the female would have laid was unknown, we included the mean number of eggs laid (6 eggs). We assessed models with and without these modified nests and found that including them did not have any significant effect on the results, effect sizes or interpretation, therefore we chose to retain them in the final model.

Adult and Juvenile Survival

To estimate apparent adult survival, we fit our capture-resight data using a Cormack-Jolly-Seber model (CJS) to determine the relationship between our covariate of interest (nonnative plants) and chickadee apparent survivorship, as well as account for detection probability (*16*). Because transient individuals are not breeding and may not be relevant to the local plant community (*45*) we truncated our dataset to only include adults that were captured or resighted to avoid biasing our estimates low by including younger birds that are potentially dispersing (n=806 individuals). Males are also more conspicuous because of singing behavior; therefore, we fit sex-specific detection and survival. Survival was allowed to vary by each year (n=17, 2000-2016).

Using our telemetry data, we constructed a dataset that included each individual fledgling and the days it was resighted up until 21 days. To estimate apparent juvenile survival we used CJS models that allowed daily survival to change across time (1–21 days) to determine mean daily survival of fledglings while accounting for detection. Because fledglings in each family group are non-independent, and only one family was followed for each site, we used site as a random effect. All family groups left their natal territories to forage in habitats that were outside of the area that we assessed plant communities. Therefore, we determined mean daily survival across all sites and did not allow survival to vary with nonnative plants. With this model we derived the mean survival at each daily time interval and then took the product of the mean cumulative survival and credible interval over the 21-day period.

We fit both survival models using a Bayesian approach with uninformative prior distributions for our unknown parameters and our nonnative plant term. We performed Markov Monte Carlo simulations to estimate posterior distributions using JAGS (*46*) called by package "jagsUI" (*47*) in program R (*48*) . We used 500,000 iterations with a burn-in of 50,000 iterations, a thinning rate of six and three chains. We assessed convergence by confirming that R^ was <1.1 for all parameters estimated.

Population Growth Model

We used the estimates obtained from the aster model and the apparent survival model in an equation to calculate female-centered stochastic population growth across a gradient of nonnative plants:

$$\lambda = \ln\left(N_{t+1}\right) = \ln\frac{\left(\left[N_{t0} * 0.5 * R_s\right] * N_p * N_s * J_s\right) + N_{t0} * A_s}{N_{t0}}$$

We included parameters for reproduction (R_s: number of young fledged), nest survival (N_s: the probability of the nest surviving), nesting probability (N_p: probability of an active nest), adult survival (A_s: the probability of the female surviving the year) and juvenile survival (J_s: the probability of a fledgling reaching independence). For our reproduction and adult survival parameters we pulled a random number from a uniform distribution within the confidence intervals calculated from the models between 0 to 100% nonnative plants. From the aster model, we used 0.5 times the predicted fledged young (to represent female fledglings assuming equal sex ratios) and the probability estimates. From the survival model, we used apparent survival of adult females. For juvenile survival, we pulled from the same uniform distribution of survival estimates across the nonnative plant gradient. For each run of the population model we simulated the change in a population of 1000 individuals after t+1. To obtain a confidence interval around our growth estimates, we ran 10000 iterations. We plotted the mean population growth and confidence intervals across the nonnative plant gradient and determined where in the gradient the population becomes unsustainable by the point at which confidence intervals do not overlap replacement ($\lambda=0$).

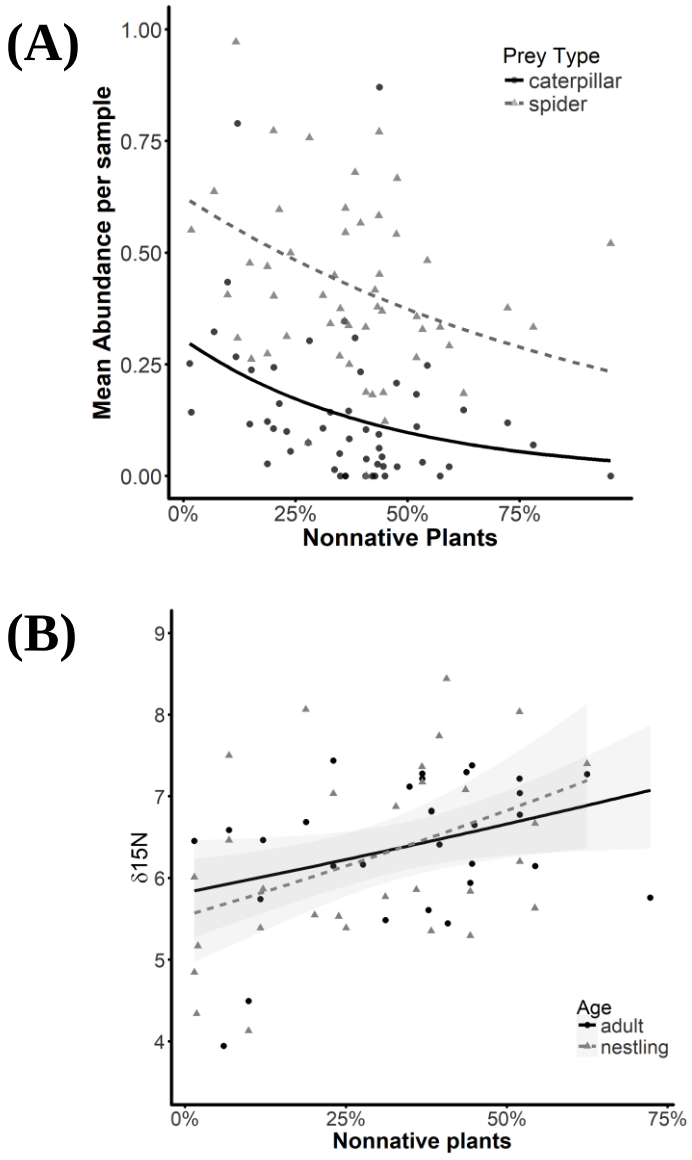


Figure 3.1 Prey availability and chickadee diet across a gradient of nonnative plants. (A) Abundance of caterpillars and spiders declined as yards become more dominated by nonnative plants; spiders tended to be more abundant than caterpillars irrespective of plant communities. (B) As nonnative plants increased within the territory, blood plasma $\delta^{15}N$ also increased, suggesting a decline in herbivorous arthropods and increase in predatory arthropods within diet.

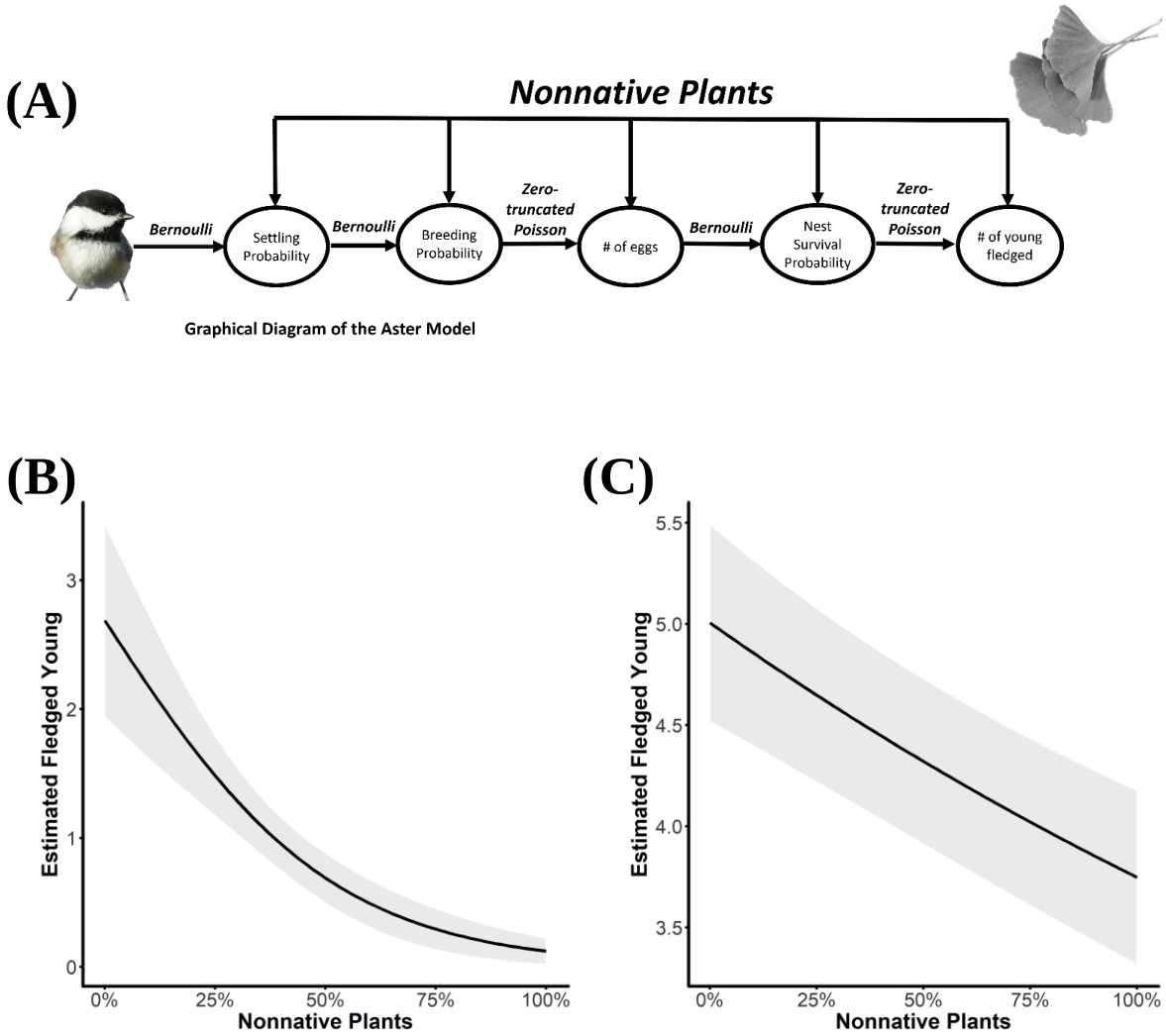


Figure 3.2 Predicted chickadee reproduction produced by sites across a gradient of nonnative plants as predicted by our top aster model. (A) Graphical depiction of the aster model for reproduction. Our model included the reproductive components of settlement probability, breeding probability, number of eggs, nest survival probability and number of fledglings. For each conditional component of the model, we included different error distributions. (B) Unconditional mean value predictions of reproductive success (cumulative effects across all nodes). (C) Conditional predictions for number of young fledged (conditional on nest success). Reproductive success, and all included nodes, declined as proportion of nonnative plants increased (appendix figure B.2-5).

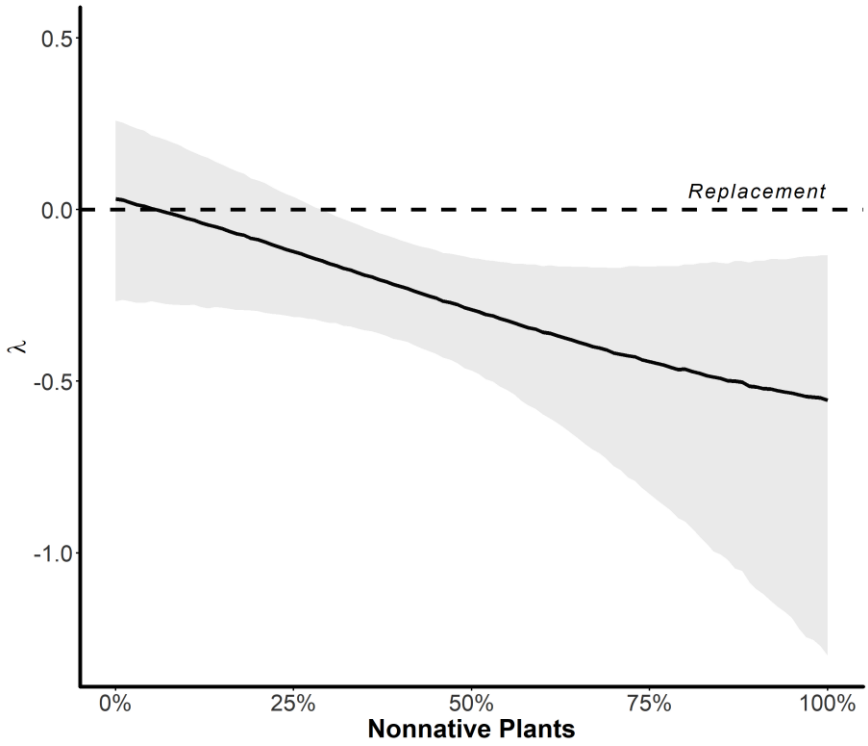


Figure 3.3 Population growth of Carolina chickadees over a nonnative plant gradient. As nonnative plants increased within the territory, population growth (λ) declined. Mean estimates were below replacement (λ<0) when yards were <6% nonnative plants; however, yards with <30% nonnative plants had confidence intervals that overlapped replacement indicating these locations have the potential to source chickadees to the regional population. Yards with plant communities >30% nonnative plants are functioning as population sinks.

REFERENCES

1. E. O. Wilson, The little things that run the world (the importance and conservation of invertebrates) Conserv. Biol., 344-346 (1987).

2. C. A. Hallmann et al., More than 75 percent decline over 27 years in total flying insect biomass in protected areas. PloS One. 12, e0185809 (2017).

3. M. L. Forister et al., The global distribution of diet breadth in insect herbivores. Proc. Natl. Acad. Sci. 112, 442–447 (2015).

4. A. R. Litt, E. E. Cord, T. E. Fulbright, G. L. Schuster, Effects of invasive plants on arthropods. Conserv. Biol. 28, 1532–1549 (2014).

5. K. T. Burghardt, D. W. Tallamy, C. Philips, K. J. Shropshire, Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere. 1, 1–22 (2010).

6. K. T. Burghardt, D. W. Tallamy, Plant origin asymmetrically impacts feeding guilds and life stages driving community structure of herbivorous arthropods. Divers. Distrib. 19, 1553–1565 (2013).

7. D. L. Narango, D. W. Tallamy, P. P. Marra, Native plants improve breeding and foraging habitat for an insectivorous bird. Biol. Conserv. 213, 42–50 (2017).

8. M. L. McKinney, Measuring floristic homogenization by non-native plants in North America. Glob. Ecol. Biogeogr. 13, 47–53 (2004).

9. R. W. Dolan, M. E. Moore, J. D. Stephens, Documenting effects of urbanization on flora using herbarium records. J. Ecol. 99, 1055–1062 (2011).

10. H. Qian, R. E. Ricklefs, The role of exotic species in homogenizing the North American flora. Ecol. Lett. 9, 1293–1298 (2006).

11. M. F. Aronson et al., in Proc. R. Soc. B (The Royal Society, 2014), vol. 281, p. 20133330.

12. P. M. Groffman et al., Ecological homogenization of residential macrosystems. Nat. Ecol. Evol. 1 (2017).

13. M. A. Davis et al., Don’t judge species on their origins. Nature. 474, 153 (2011).

14. Materials and methods are available as supplementary materials.

15. C. J. Geyer, S. Wagenius, R. G. Shaw, Aster models for life history analysis. Biometrika. 94, 415–426 (2007).

16. M. Kéry, M. Schaub, Bayesian population analysis using WinBUGS: a hierarchical perspective (Academic Press, 2012).

17. C. A. Lepczyk et al., Biodiversity in the city: fundamental questions for understanding the ecology of urban green spaces for biodiversity conservation. BioScience. 67, 799–807 (2017).

18. M. A. Goddard, A. J. Dougill, T. G. Benton, Scaling up from gardens: biodiversity conservation in urban environments. Trends Ecol. Evol. 25, 90–98 (2010).

19. M. L. Avolio, D. E. Pataki, T. L. Trammell, J. Endter-Wada, Biodiverse cities: the nursery industry, homeowners, and neighborhood differences drive urban tree composition. Ecol. Monogr. (2018).

20. J. H. Poelen, J. D. Simons, C. J. Mungall, Global biotic interactions: an open infrastructure to share and analyze species-interaction datasets. Ecol. Inform. 24, 148–159 (2014).

21. V. Devictor, R. Julliard, D. Couvet, A. Lee, F. Jiguet, Functional homogenization effect of urbanization on bird communities. Conserv. Biol. 21, 741–751 (2007).

22. S. B. Lerman, P. S. Warren, The conservation value of residential yards: linking birds and people. Ecol. Appl. 21, 1327–1339 (2011).

23. C. H. Greenberg, S. T. Walter, Fleshy fruit removal and nutritional composition of winter-fruiting plants: a comparison of non-native invasive and native species. Nat. Areas J. 30, 312–321 (2010).

24. R. Isaacs, J. Tuell, A. Fiedler, M. Gardiner, D. Landis, Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. Front. Ecol. Environ. 7, 196–203 (2009).

25. D. W. Tallamy, K. J. Shropshire, Ranking lepidopteran use of native versus introduced plants. Conserv. Biol. 23, 941–947 (2009).

26. E. Harvey, I. Gounand, C. L. Ward, F. Altermatt, Bridging ecology and conservation: from ecological networks to ecosystem function. J. Appl. Ecol. 54, 371–379 (2017).

27. C. Evans et al., The Neighborhood Nestwatch Program: Participant outcomes of a citizen-science ecological research project. Conserv. Biol. 19, 589–594 (2005).

28. R. Brewer, Ecological and Reproductive Relationships of Black-Capped and Carolina Chickadees. The Auk. 80, 9–47 (1963).

29. R. J. Cooper, Dietary relationships among insectivorous birds of an eastern deciduous forest. Dissertation, West Virginia University (1988).

30. A. C. Martin, H. S. Zim, A. L. Nelson, American wildlife & plants: a guide to wildlife food habits: the use of trees, shrubs, weeds, and herbs by birds and mammals of the United States (Courier Corporation, 1961).

31. E. Pagani-Núñez, M. Renom, F. Mateos-Gonzalez, J. Cotín, J. C. Senar, The diet of great tit nestlings: Comparing observation records and stable isotope analyses. Basic Appl. Ecol. 18, 57–66 (2017).

32. B. S. Evans, T. B. Ryder, R. Reitsma, A. H. Hurlbert, P. P. Marra, Characterizing avian survival along a rural-to-urban land use gradient. Ecology. 96, 1631–1640 (2015).

33. P. Pyle, S. N. G. Howell, D. F. DeSante, R. P. Yunick, M. Gustafson, Identification guide to North American birds. Part I. Columbidae to Ploceidae. Braun-Brum. Inc Ann Arbor MI (1997).

34. B. Naef-Daenzer, F. Widmer, M. Nuber, A test for effects of radio-tagging on survival and movements of small birds. Avian Sci. 1, 15–23 (2001).

35. J. H. Rappole, A. R. Tipton, New harness design for attachment of radio transmitters to small passerines. J. Field Ornithol., 335–337 (1991).

36. S. B. Lerman et al., Using urban forest assessment tools to model bird habitat potential. Landsc. Urban Plan. 122, 29–40 (2014).

37. M. S. Thorne et al., Evaluation of a technique for measuring canopy volume of shrubs. J. Range Manag., 235–241 (2002).

38. D. Bates, M. Maechler, B. Bolker, S. Walker, lme4: Linear mixed-effects models using Eigen and S4. R Package Version. 1, 1–23 (2014).

39. K. Bartoń, MuMIn: multi-model inference. R package version 1.10. 0. package MuMIn (2014).

40. A. M. Prasad, L. R. Iverson, Little's range and FIA importance value database for 135 eastern US tree species (2003).

41. E. L. Little, Atlas of United States trees, volume 4, minor Eastern hardwoods (1977).

42. USDA, NRCS. 2018. The PLANTS Database (http://plants.usda.gov, 24 February 2018). National Plant Data Team, Greensboro, NC 27401-4901 USA.

43. Missouri Botanical Garden, (http://www.missouribotanicalgarden.org/plantfinder/plantfindersearch.aspx, 24 February 2018).

44. C. J. Geyer, R package aster (Aster Models), version 0.8-31 (2015).

45. S. Snell, B. Evans, E. White, A. Hurlbert, The prevalence and impact of transient species in ecological communities. bioRxiv, 163816 (2017).

46. M. Plummer, JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling (2003).

47. K. Kellner, jagsUI: a wrapper around rjags to streamline JAGS analyses. R Package Version. 1 (2015).

48. R Core Team, R: A language and environment for statistical computing. (R Foundation for Statistical Computing, Vienna, Austria, 2015; http;//www.R-project.org/).

Chapter 4

RESIDENTIAL PLANT COMMUNITIES INFLUENCE DIET, PARENTAL EFFORT AND NESTLING CONDITION IN CAROLINA CHICKADEES

Abstract

In urban areas, plant communities are often determined by the individual landowner preferences for certain horticultural species. Attractive nonnative plants dominate most residential landscapes and can have cascading influences on the availability of important insect prey for consumers. Despite declines in food abundance there is little information available on the costs associated with breeding in areas dominated by nonnative plants species. To fill this gap, we quantified Carolina chickadee (*Poecile carolinensis)* diet, parental effort and nestling condition in residential yards that varied in nonnative plant biomass. Specifically, we video-taped nests to determine the proportion of high-quality prey (i.e. caterpillars) in nestling diet, and the number of provisioning visits. We also collected morphological measurements to monitor nestling growth as well as mass and hematocrit ratios to assess nestling condition and number of days to fledging. Our data showed that as yards increased in nonnative plant biomass, the proportion of caterpillars in the nestling diet declined and the number of provisioning visits increased. Despite increases in parental effort, nestlings in nonnative yards had slower feather growth, were in poorer condition, and took longer to fledge the nest. These results reveal that parental effort, prey choice, and fledging success are a function of the native plant biomass in the local area. This

suggests that plant communities used in landscaping are a driving force that limits both the colonization of urban habitat, and successful breeding by insectivorous birds. Urban restoration that aims to provide habitat for insectivorous consumers should prioritize locally native plant species that support high insect prey biomass to improve residential landscapes for urban birds.

Introduction

Providing high quality prey to growing young can ultimately improve a bird's fitness if diet selection translates into higher nestling survival (Ricklefs 1974). Across many species and landscapes, caterpillars are a disproportionately important food item for woodland passerine birds (Wilkin et al. 2009; Burger et al. 2012) in part because of their high protein (Razeng and Watson 2014), carotenoid content (Eeva et al. 2010), low proportion of chitin, as well as high biomass and caloric content (Bell 1990). As expected, caterpillar-rich diets can improve nestling condition or size (Blondel et al. 1991; Wilkin et al. 2009) and heavier nestlings are more likely to recruit into the breeding population (Both et al. 1999). High quality diets can have positive effects on adult fitness, either directly by improving juvenile survival (Naef-Daenzer et al. 2001) or indirectly by improving the quality of communicative signals in offspring (Hõrak et al. 2000) or reducing reproductive costs in adults (Martin 1987). However, high quality prey can be patchy and uncommon; thus, provisioning adults should assess the quality and quantity of available food and make adjustments to foraging behavior and diet breadth to maximize fitness by way of nestling production (i.e. risk-sensitive foraging, Brown et al. 2007). Parents may bring low quality foods when the abundance of high-quality food is low (Arnold et al. 2010) or the time to find and

handle high-quality food is high (Sauter et al. 2006; Stephens et al. 2007). When the search time outweighs the quality of prey or the probability of finding high quality prey, provisioning adults will switch strategies. These patterns hold true in the field, where blue tits (*Cyanistes caeruleus*) provision more often (García-Navas and Sanz 2011) and with more spiders (Bańbura et al. 1994) when caterpillar abundance is low, suggesting that spiders are a lower quality food item and caterpillars may be the preferred food source.

While most studies have assessed how bird foraging decisions change with respect to variation at the scale of the individual, few have determined how individuals adapt to changes in the prey landscape. Because the majority of herbivorous insect prey are host plant specialists (Forister et al. 2015), prey availability can be heavily influenced by the plant species within the surrounding community. To maximize prey resources, adults should nest near productive tree species to increase the availability of caterpillars for provisioning in order to maximize growth with the least amount of effort (Wilkin et al. 2009).

Previous work in urban landscapes has suggested that birds may be food limited. Urban birds tend to have higher rates of provisioning (Isaksson and Andersson 2007; Newhouse et al. 2008) and lower nestling growth rates and mass (Hinsley et al. 2008; Newhouse et al. 2008; Chamberlain et al. 2009). One feature of urban landscapes that may influence prey availability and nestling condition is the abundance of nonnative plants in landscaping preferences (Avolio et al. in press). Nonnative plants produce lower abundance and diversity of caterpillars (Burghardt et al. 2010; Litt et al. 2014; Narango et al. 2017) and the reduction of caterpillars in the diet may have cascading effects on nestling growth if alternative food quality is poor

or lower quality food is more reliable (Mägi et al. 2009). However, chickadees are flexible enough to use multiple prey types (Martin 1951) that may, or may not be negatively affected by plant origin. To date, most urban studies have ignored differences in prey type and none have considered whether the productivity and origin of trees within the territory influence provisioning behavior and nestling condition.

Here, we used a tritrophic approach to test whether nonnative plants influence patterns of provisioning behavior. Specifically, we tested whether the amount of nonnative plant biomass influences the composition of provisioned prey, parental effort, and nestling condition for an insectivorous bird, the Carolina chickadee (*Poecile carolinensis*). To do this we measured prey items and feeding visits using video cameras at the nest and measured nestling growth and mass in nests located within residential yards that varied in the surrounding plant community. Because nonnative plants support lower abundance and biomass of high quality prey (i.e. caterpillars), we predicted that adults in nonnative yards would feed fewer caterpillars to their young and make more visits to the nest. Because nestling growth is a function of prey quality and quantity, we also predicted that nestlings in nonnative yards would grow slower and be in poorer condition.

Methods

Field Data Collection

Study Area and Species

This study was conducted within the *Neighborhood Nestwatch* Project (Evans et al. 2005), from 2013-2016. In >200 yards across the Washington DC metropolitan

area, we set up nest boxes designed to attract Carolina chickadees. Homeowners assisted in monitoring nest boxes to assess the reproductive success of breeding chickadees (Narango et al. in review) while technicians banded and resighted previously color-banded individuals for adult survival (Evans et al. 2015). Chickadees are an ideal species for testing these questions because they are primarily insectivorous during the breeding season, and diets consist primarily of caterpillars (Lepidoptera), spiders (Aranae) and true bugs (Hemiptera) (Martin 1951; Mostrom et al. 2002). Moreover, their time of peak resource demands for breeding (this region, April-May) coincides with the migratory period of many species of conservation concern and may serve as a proxy for insectivorous bird habitat in general.

Video Analysis

At sites with breeding chickadees, we assessed provisioning behavior and diet by video recording visits by adults to feed nestlings between days 4-12 of the nestling period. Nests were videotaped with a video camera (Sony Handycam CX405) at 60 frames/sec. To obtain the best images of prey items brought to the nest, we placed a temporary perch in front of cavity entrance to increase the probability that food items and color-band combinations would be captured on video. After positioning the camera, adults were monitored to ensure that the presence of the perch or video camera did not alter provisioning behavior or cause agitation. If adults hesitated to enter the nest box, or exhibited stressed behavior (e.g. mobbing, agitated calls), we adjusted the location of the perch or camera and tried again. If the adults would not cooperate after multiple tries, we took down our camera to avoid any negative effects on nestlings and attempted the following day. Our goal was to place our video camera <3m from each nest in order to obtain the best quality photo; however, nest box

location, available camouflage, adult tolerance to the cameras, and yard permissions caused some cameras to be farther away.

At each nest, we recorded feeding events during the early (days 4-6) and late (days 9-11) stages of the nestling period. We transcribed videos to quantify feeding visits of each adult, and identified nestling food items when possible. Because our ability to identify food items was affected by individual bird behavior, camera position, and prey size, we were unable to identify every food item that was brought. However, because caterpillars are generally conspicuous and larger than chickadee bill size, all visits with caterpillars could be identified. Thus, we coded each provisioning visit as a binary event (caterpillar or non-caterpillar) and determined the proportion of visits that contained caterpillars. We also recorded the number of total provisioning visits, sex of the bird if known (determined by color-bands) and the amount of time spent at the nest. For each nest we determined the number of visits per nestling, per hour and the proportion of visits with caterpillars.

Nestling Growth and Condition

Immediately following our video recordings, we measured nestling growth and condition on three randomly selected nestlings. Each nestling was color-banded, weighed to the nearest 0.1g, and measured for body size and feather extension. We collected the following measurements to assess body growth: mass (in g) and the length of the right tarsus (in mm). For feather growth we measured the length of the full right wing, the full length of primary feather R9, the full length of rectrix feather R6 as well as the amount of these feathers that were exposed from quill (all in mm).

We revisited each nest exactly five days after initial banding (days 9-12) to record a second sample of provisioning behavior, measure nestlings, as well as collect

a small sample of blood. After our last measurements, we revisited nests approximately every two days to determine the day that nestlings successfully fledged. Observations of successful nestling fledging were also supplemented by opportunistic observations by homeowners when needed. We defined the total nestling period as the number of days that nestlings remained in the nest from the date of hatching.

Plant Communities

At sites where we collected nest provisioning data, we assessed plant communities around each nest using five, non-overlapping modified i-TREE surveys (Lerman et al. 2014). Within each 11.3-m radius plot (0.05 ha), we measured and identified to species all woody plants. Using these data, we calculated plant biomass (foliage volume via Thorne et al. 2002) and importance values of each species (Holmes and Robinson 1981, see Narango et al. 2017 for more details). Importance values are a term representing the sum of the relative biomass and relative density of a particular plant species. For each site, we summed the value of all nonnative species to obtain a proportion of nonnative plant biomass. We designated plants as nonnative if they had a natural distribution that did not contain the Eastern United States (i.e. east of the Mississippi river) based on published USGS and USDA range maps (Little 1977 and PLANT database). To control for total plant biomass, we summed the foliage volume of all plants for each site.

Statistical Analysis

Diet and Parental Effort

To assess the effect on diet, we tested whether the proportion of caterpillars declined over the nonnative plant gradient using beta regression. To test for differences in parental effort, we used a generalized linear model with number of visits per nestling, per hour as our response. For both models we used both nonnative plants and total plant biomass as fixed effects.

Nestling Condition

We determined body condition of nestlings by using the mass-size residuals of a linear regression model that contained weight as the dependent variable, and tarsus length as independent variables (Schulte-Hostedde et al. 2005). We considered including time of day as an additional covariate, however, including this term did not improve model fit, and was therefore removed. From our residuals positive values indicate nestlings in good condition relative to their size and negative values indicate poor condition. We tested for differences in nestling mass condition by using our condition residuals as a response variable in a linear model with nonnative plants and plant biomass as fixed effects and the random effect of nestling and nest identity.

Our second indicator of condition was nestling hematocrit ratios. The ratio of packed red blood cells to blood plasma can be used as an indicator of condition in birds, because hematocrit is known to decrease when birds exhibit high energetic activity and/or are under nutritional stress (Jenni et al 2006). We determined the proportion of hematocrit by dividing our measurement of the amount of packed red blood cells by the total amount of blood collected. This proportion was used as a response variable in linear regression with proportion of nonnative plants and plant

biomass as fixed effects and both nestling and nest as random effects. Although hematocrit ratio is a percentage, mean hematocrit ratio was 0.43±0.06 (range: 0.25-0.66) and did not approach the upper and lower bounds of 0 and 1. Because the distribution of our response variable did not violate assumptions of normality, we did not transform our response or use a different error distributions in our generalized linear model.

Nestling Growth

We assessed differences in nestling growth rate trajectories by using nonlinear mixed effect models (Sofaer et al. 2013) with a logistic function from (Stark and Ricklefs 1998 and Sofaer et al. 2013):

$$M_t = \frac{A}{1 + e^{(K+ (I - t))}} + \varepsilon$$

Where M_t= Measurement at time t, A = asymptotic measurement, K = growth rate constant, I=the inflection point of the curve (in days) and t= nestling age (in days). Following methods from Sofaer et al. (2013), we also included random effects of nest and nestling where A_i, K_i, and I_i represent the random effect of the nest; A_{ij}, K_{ij}, J_{ij}, represent the random effect of the nestling, nested within the nest; ε_{ijk} is normally distributed random error of the *k*th measurement.

We tested changes in nestling growth curves by including proportion of nonnative plants and plant biomass as fixed effects. Each measurement of each individual was used as a unique sample. Including all random effects of nest and nestling on A, K, and I over-parameterized our model, therefore we first considered what random effects best fit our data using Akaike's Information Criterion (AIC, Burnham and Anderson 2003). We considered candidate models of combinations of

random effects with either nest, nestling or both nest and nestling as random effects on our three parameters of interest, A, K or I. We fit our candidate models using function 'nlme' (Pinheiro et al. 2014) and used AICc to rank models. We used the top model to inform our model specification for running subsequent Bayesian predictions. We fit separate models for tarsus, wing, mass and exposed primary. For each model, we specified the following starting values: A= the largest value observed in nestling chickadees for each measurement; inflection point=8 (in days, assuming a minimum fledge date of day 16), K=0.5.

Nestling Period

Finally, we tested whether the nestling period (number of days from hatch to fledge day) changed as nonnative plants increased. We used a linear model with a Poisson distribution with number of days as a response variable and both nonnative plants and plant biomass as fixed effects.

For all models, we determined β coefficients, credible intervals and predictions for all of our analyses by fitting each model with a Bayesian analysis using JAGS (Plummer 2003; Hildebrandt and Schaub 2018). We used Markov chain Monte Carlo simulations to model change in our response as both nonnative plants and plant biomass increased. For each analysis we used 50,000 iterations with a thinning rate of 5, a 10,000 iteration burn-in and three chains. We assessed convergence by confirming that all P^ values were <1.1. We plotted mean growth curves, subsampled 100 pulls from the posterior distribution of the predictions and both 90% and 95% credible intervals.

Results

Diet, Parental Effort and Nonnative Plants

We quantified diet information from 46 videos across 23 individual nests. The majority of prey chickadee adults brought to the nest were caterpillars (primarily Geometridae and Noctuidae) and spiders (Salticidae, Aranidae, Linyphiidae and others, figure 4.1). The majority of alternative prey were too small to be consistently and reliably identified, however, other prey observed in the diet included aphids (Aphidae), scale insects (Coccoidea), dipteran larvae and adults (Syrphidae and others), ants (Formicidae), beetles (unknown), hemipteran nymphs (Flatidae and others), and insect egg sacs. We also recorded rare incidents of chickadees feeding bird seed to young.

For our diet analysis we only included sites for which we had > 10 observations where prey could be identified as a caterpillar or not (n=35 videos). Our final dataset had 48.29 ± 5.56 SE visits per video with caterpillars making up between 0% and 96.67% of the visits. The proportion of caterpillars declined as nonnative plants increased when controlling for total plant biomass (β: -3.21 ± 0.91, CI: -5.08, -1.53, figure 4.2). Proportion of caterpillars also decreased as plant biomass increased (β: -1.18 ± 0.47, CI: -2.11, -0.27).

For our analysis of parental effort, we included 44 videos across 22 different sites for which all visits could be reliably seen. Individual adults could not be identified for every nest, therefore we pooled all feeding visits for total visits per nest. We then divided the total number of visits by the number of nestlings, and the total time of the observation (in hours), to get visits per nestling per hour for each video. Videos ranged from 1.09 visits per nestling/hour up to 14.05 visits per nestling/per

hour (mean: 4.84 ± 0.42 SE). The number of visits per nestling/per hour increased as proportion of nonnative plant biomass increased (β: 12.81 ± 1.65, CI: 9.55, 16.07, figure 4.3). There was no relationship between feeding rates and total plant biomass (β: 0.42 ± 0.50, CI: -0.56, 1.40).

Nestling Condition and Nonnative Plants

Nestling mass was strongly related to tarsus length (β 0.80 ± 0.03, t=28.69, $p<0.001$, R^2: 0.59, figure 4.5). Additional inclusion of predictors such as time of day or year did not improve fit of this model (Likelihood ratio test: $p>0.1$) and were not included. The residuals of this model ranged from -3.49 to 4.33 g. Nestling condition, defined as the residuals of the mass-tarsus linear model, declined over the nonnative plant gradient (β -1.81 ± 0.38, CI: -2.57, -1.06, figure 4.6) when controlling for total plant biomass. Body condition also declined as total plant biomass increased (β -0.25 ± 0.06, CI: -0.37, -0.14).

When controlling for total foliage biomass, there was a modest decline in the amount of packed red blood cells per blood volume as nonnative plants increased, however our confidence intervals overlapped zero (β -0.05 ± 0.04, CI: -0.13, 0.03, figure 4.7). There was no relationship between foliage biomass and red blood cells (β -0.01± 0.01, CI: -0.02, 0.01).

Nestling period lengthened as nonnative plant biomass increased when controlling for foliage biomass (β 0.43 ± 0.17, CI: 0.11, 0.76, figure 4.8). There was no relationship between nestling period and foliage biomass (β 0.02 ± 0.03, CI: -0.05, 0.08).

Nestling Growth and Nonnative Plants

Our top model had both nest and nestling included as random effects on the inflection point variable. Two measurements showed meaningful changes as plant communities became more nonnative: mass and wing length. As yards became more nonnative, nestlings tended to gain mass at a faster rate but were at a lower mass at day 16 (Table 4.1, figure 4.10). Similarly, nestling wings also grew at faster rates as yards increased in nonnative plant biomass but were shorter overall than nestlings in native yards (Table 4.1, figure 4.10) at day 16. For tarsus length and primary exposed feathers, all growth parameters were similar and confidence intervals overlapped zero (table 4.1, figure 4.10). All confidence intervals overlapped zero for total plant biomass except for primary exposure, which tended grow slower and be longer as plant biomass increased.

Discussion

Our data show that increases in nonnative plants are associated with lower proportions of caterpillars in nestling diet, higher parental effort and reduced condition of nestlings. These results are consistent with previous findings that urban breeding birds are provisioning more often and nestlings are fledging at smaller weights (Newhouse et al. 2008; Chamberlain et al. 2009). However, we uniquely show here that even within an urban landscape, available prey quality can vary drastically depending on the evolutionary origin of the surrounding plant community and may explain differences between urban and non-urban habitats. Moreover, these negative impacts are more pronounced than effects of plant biomass overall. Thus, the identity

of plants within the urban community has far reaching implications for reproductive success in this species and perhaps others.

Here, we show that caterpillars are disproportionately important items for Carolina chickadees, and changes to the plant community can alter the availability of high-quality prey and parental effort. Our video data showed that, to some degree, chickadees are flexible enough to take advantage of alternative prey types when caterpillars are unavailable. Chickadees provisioned many types of prey, yet caterpillars remained a disproportionately important food item for growing nestlings, constituting 48.55% of all of our feeding observations. Spiders also made up a large number of observations but varied a great deal in size. At a few sites of high nonnative plant biomass, we also observed several chickadees feeding bird seed to young, despite the fact that nestlings are physiologically ill-equipped to digest seed and thus seed food sources are not ideal for growth. In fact, at nests where chickadees were feeding bird seed, nestling mortality was very high (Narango, personal observation). To our knowledge, our study is the first to document this maladaptive behavior of provisioning of bird seed to young. However, given that bird seed is ubiquitous in the suburban landscape, yet provisioning bird seed is relatively rare, we do not believe that seed is an 'ecological trap' that reduces nestling survival. Instead, we believe birds that are not able to find sufficient arthropod prey for nestlings adopt the risky behavior of feeding young the most easily available food source, albeit without any nutritional benefit to young.

Despite flexibility in prey types, many items were too small to be accurately identified to taxonomic resolution lower than order with the video technique used here. Ecologists have used many techniques to identify bird diets, such as throat

ligatures, fecal samples, emetics, stable isotopes and videography (Rosenberg and Cooper 1990). All of these techniques come with some element of bias given the differences in effort and taxonomic resolution. However, most caterpillars are specialized to feed on only a few host plants (Bernays and Graham 1988; Forister et al. 2015) and they are a primary food item of many insectivorous birds (Cooper 1988). Thus the presence of caterpillars would be most impacted by changes in plant community composition and have the strongest consequences to nestling condition. Future studies should combine traditional techniques with new molecular analyses (i.e. DNA barcoding and high throughput sequencing) to determine the abundance, diversity, and host specialization of important prey items and how local plant features can alter diet networks. New insights into bird diet with fine scale taxonomic resolution will reveal how nutrition plays a role in prey choice when food availability varies over time and space.

As nonnative plants increased in biomass, the proportions of caterpillars declined and subsequently, total feeding visits increased. Caterpillars appear to be a superior food item compared to other arthropod groups because of their high biomass and caloric density (Schroeder 1977; Scriber and Slansky Jr 1981), protein (Razeng and Watson 2014) and carotenoids (Eeva et al. 2010). Thus, diets high in caterpillar biomass may afford adults the ability to spend more time in self-maintenance or nest guarding, or opportunities to be more discriminating when seeking foraging substrates. Spiders are also high in protein and carotenoids, but they typically provide less biomass and fewer calories and nutrients per single unit than caterpillars because of their smaller size (Avery 1971). Thus, adults provisioning a primarily spider-based diet must visit more often in order to maintain optimal growth and condition in

nestlings. The modest differences we observed in both nestling growth and condition suggests that adult chickadees are able to partially compensate for reduced abundance of prey. This also suggests that adults may absorb negative effects of nonnative plants in part by increasing reproductive costs. These costs are known to manifest in increased stress (Partecke et al. 2006), slower feather molt (Hope et al. 2016), or even lower annual survival (Evans et al. 2015). For a small bird with a relatively short lifespan (average: 1.1 years, Brewer 1963), this gamble may result in a net positive fitness gain if even one nest during a lifetime is successful. Determining whether reproductive costs in habitats dominated by nonnative plants has carryover effects to subsequent stages of the avian annual cycle remains an area that is ripe for further study.

Our nestling measurements reveal that chickadees breeding in areas with high proportions of nonnative plants have reduced condition, slower feather growth, and increased time in the nest. Individual condition does not just affect survival in the nest; birds that fledge the nest in higher condition are known to have the highest survival during the post-fledging period (Hochachka and Smith 1991; Naef-Daenzer et al. 2001). Sexually selected plumage signals can also be condition- and nutrition-dependent (Hill and Montgomerie 1994; Johnsen et al. 2003), which can have substantial repercussions on lifetime fitness. Our hematocrit ratios complement our mass measurements; nestlings have lower quantities of red blood cells as nonnative plants increase. Red blood cells can be reduced during periods of high strenuous activity or reduced nutrition as shown in migrating birds (Jenni et al. 2006). Given that nestlings are stationary while in the nest, and proportions of high quality prey are reduced when the surrounding landscape is dominated by non-native plants, it is likely

that these nestlings are experiencing reduced nutrition compared to those raised in yards with high native plant biomass. Whether the reductions in condition observed in this study are functionally important should be investigated further by looking at other condition-dependent features such as immune function.

Our body growth measurements demonstrated that, for the most part, nestlings are maintaining consistent growth regardless of prey availability. During short periods of reduced food availability, nestlings experience fluctuations in mass and no differences in body growth, a likely adaptation to uncertain fluctuations in daily food supply (Negro et al. 1994). Moreover, some growth, like tarsal bone length, may be more limited by calcium availability then by overall nutritional condition *per se* (Tilgar et al. 2004), and calcium may not be limited for this bird species in these landscapes given the high amounts of calcium found in spiders (Razeng and Watson 2014). Of our four growth measurements, nonnative plants had the most pronounced negative impact on wing length which is a function of flight feather growth. At the same age, nestlings in yards with high nonnative plant biomass had significantly shorter wings. Because molt is energetically costly, the speed of feather growth can be positively related to food availability at the time of molt (Grubb and Cimprich 1990; Danner et al. 2015; Lodjak et al. 2015). We found no impact on the length of feather 'out of sheath', suggesting reduced feather growth was most evident on total feather length. Importantly, nestlings in nonnative yards also remained in the nest longer than nestlings in native yards. The amount of time spent in the nest increases the exposure of nestlings to predation, and thus, birds should maximize growth in favor of reducing exposure time (Ricklefs 1968). However, cavity-nesting birds may be buffered from this tradeoff, given high nestling survival and mobility of newly fledged young. In

chickadees, nestlings likely remain in the nest long enough to reach the feather length required to be able to fledge the nest with the ability to fly (Narango personal observation). Open-cup nesting birds do not have such flexibility in the timing of fledging and reduced feather growth during the nestling stage may drastically reduce the survival of young during and after fledging.

In previous work, we found that chickadees have a lower probability of nesting in yards with high nonnative plant biomass (Narango et al. in review). Our study of provisioning diets and nestling condition provides an explanation for this pattern; yards that are not able to provide the necessary nutrients needed to successfully raise nestlings will be less likely to have breeding individuals. The decision to postpone breeding when prey availability is low may reduce reproductive costs in favor of future reproduction or improvements in territory quality. Alternatively, females may be less likely to pair with males occupying territories that do not have sufficient prey for nesting. Although chickadees appear flexible enough to change both prey type and provisioning behavior, it may be that in areas with high nonnative plants, it is impossible to maintain optimal growth given energetic constraints of the adults. Modeling behavioral dynamics as habitat changes in both plant quality and quantity may tease out what degree of nonnative plants biomass is tolerable to provisioning birds.

Our results provide further evidence that the abundance of nonnative plants in urban areas is a feature that limits that ability of insectivorous birds to breed and successfully raise young. Future work should determine the specific identity of both the plants and arthropods that maximize the success of insectivorous birds in these landscapes. Providing homeowners with this information will assist in improving

habitat quality for biodiversity in urban areas through horticultural landscaping and provide a foundation for healthy food webs in general.

Figure 4.1 Examples of food items brought to chickadee nests. Caterpillars (top) and spiders (bottom) were the most commonly provisioned items.

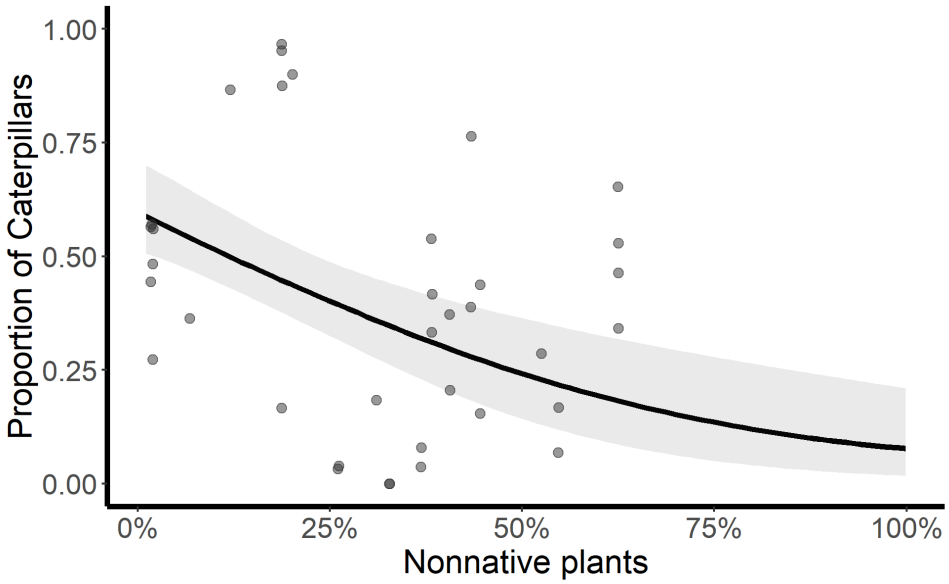


Figure 4.2 Proportion of caterpillars in nestling diet declined as nonnative plants increased when controlling for plant biomass. Graph shows mean predicted value (black line) and the 95% credible interval for the posterior distribution of the mean predictions (gray ribbon). Points are raw data.

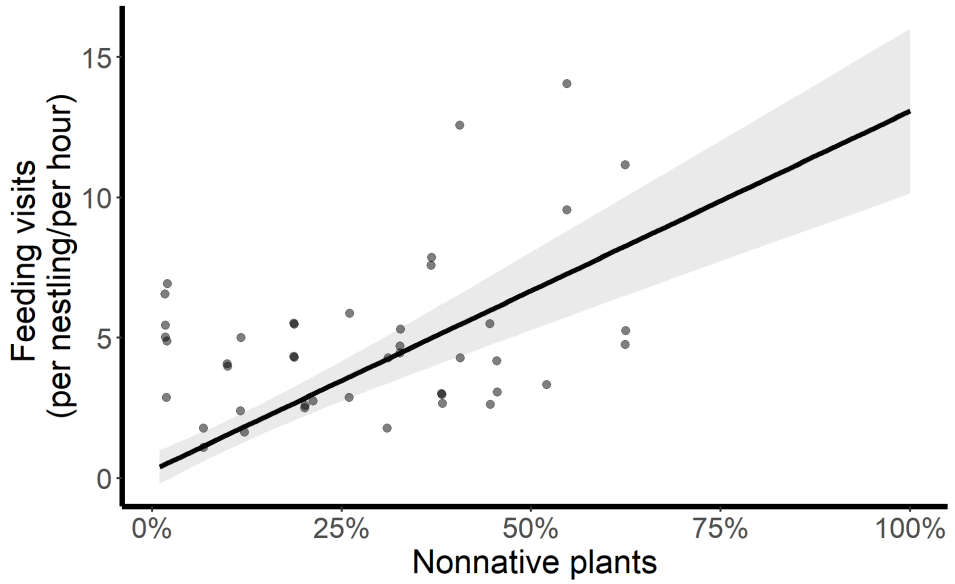


Figure 4.3 Feeding visit rates per increased as nonnative plants increased when controlling for plant biomass. Graph shows mean predicted value (black line) and the 95% credible interval for the posterior distribution of the mean predictions (gray ribbon). Points are raw data.

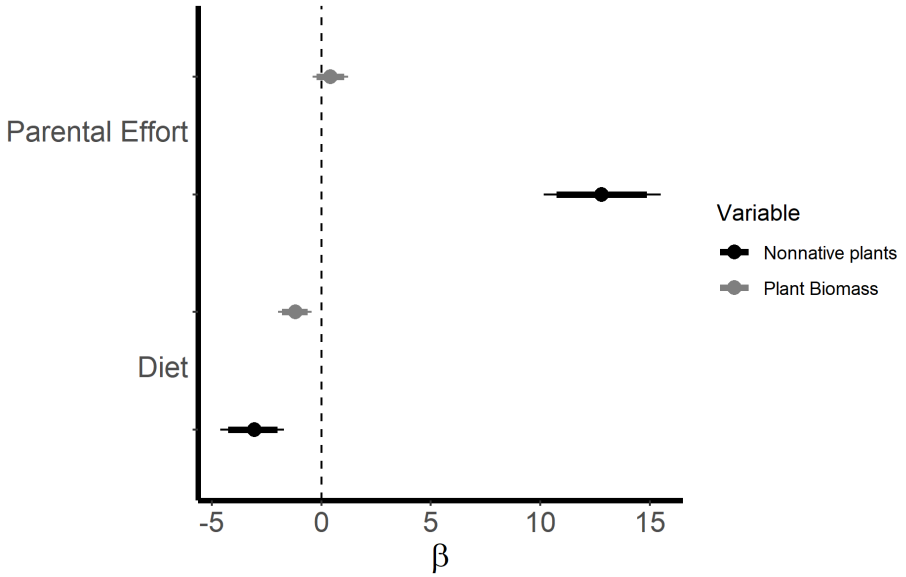


Figure 4.4 Mean β coefficient (circle), 90% (thick line) and 95% (thin line) credible intervals for the beta estimates for models of nestling diet and parental effort. Proportion of caterpillars declined as nonnative plants increased, while parental effort (visits per nestling per hour) increased.

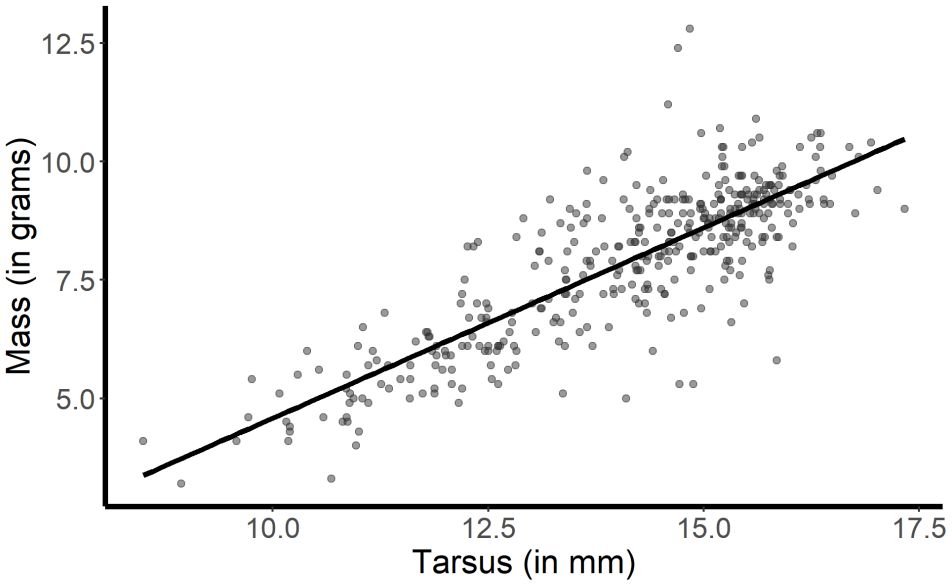


Figure 4.5 Nestling mass is strongly related to tarsal length. In our subsequent model, body condition is defined as the residual of each point to the linear mean.

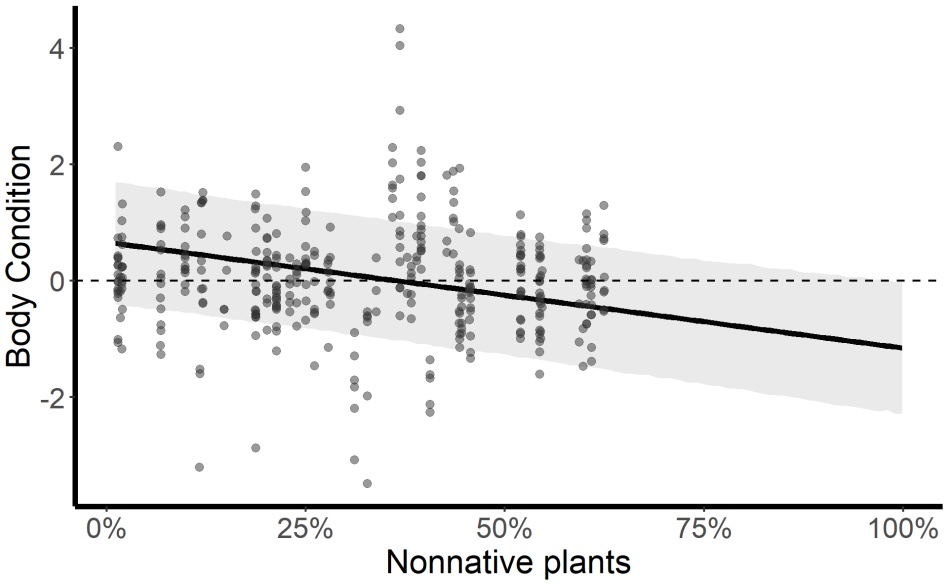


Figure 4.6 Controlling for total foliage volume, relative body condition (i.e. residual body size adjusted mass in grams) declines as nonnative plants biomass increases. Positive values indicate 'good' body condition relative to body size, while negative values indicate 'poor' body condition. Graph shows mean predicted value (black line) and the 95% credible interval for the posterior distribution of the mean predictions (gray ribbon). Points are raw data. No nestlings were available for measurement over 62% nonnative plants; however, our model predictions extend out to 100%.

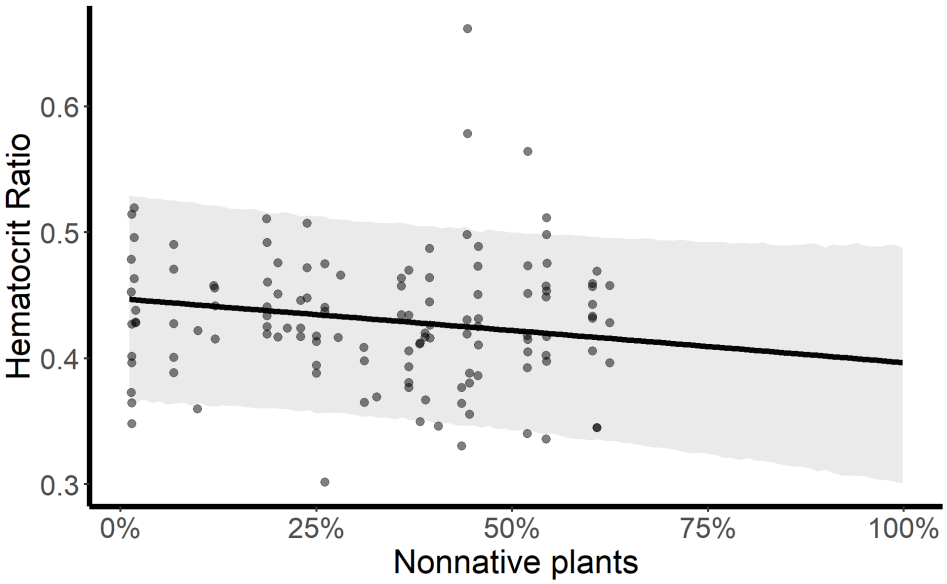


Figure 4.7 Hematocrit ratio (i.e. proportion of red blood cells to plasma) weakly declined as nonnative plants increased, when controlling for total plant biomass. Graph shows mean predicted value (black line) and the 95% credible interval for the posterior distribution of the mean predictions (gray ribbon). Points are raw data. No nestlings were available for measurement over 62% nonnative plants; however, our model predictions extend out to 100%.

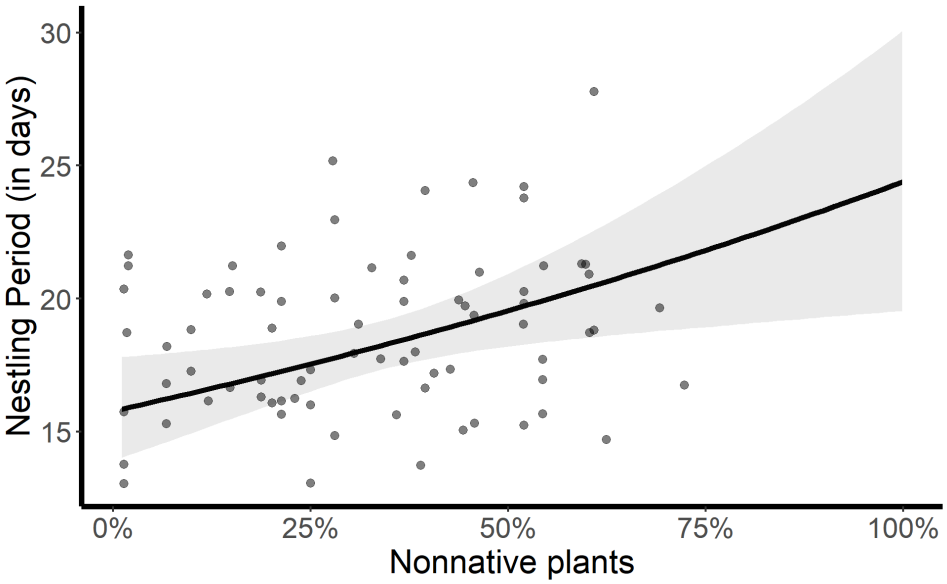


Figure 4.8 Nestling period (i.e. number of days young were in the nest) lengthened as nonnative plants increased, when controlling for total plant biomass. Graph shows mean predicted value (black line) and the 95% credible interval for the posterior distribution of the mean predictions (gray ribbon). Points are raw data. No nests were monitored over 72% nonnative plants; however, our model predictions extend out to 100%.

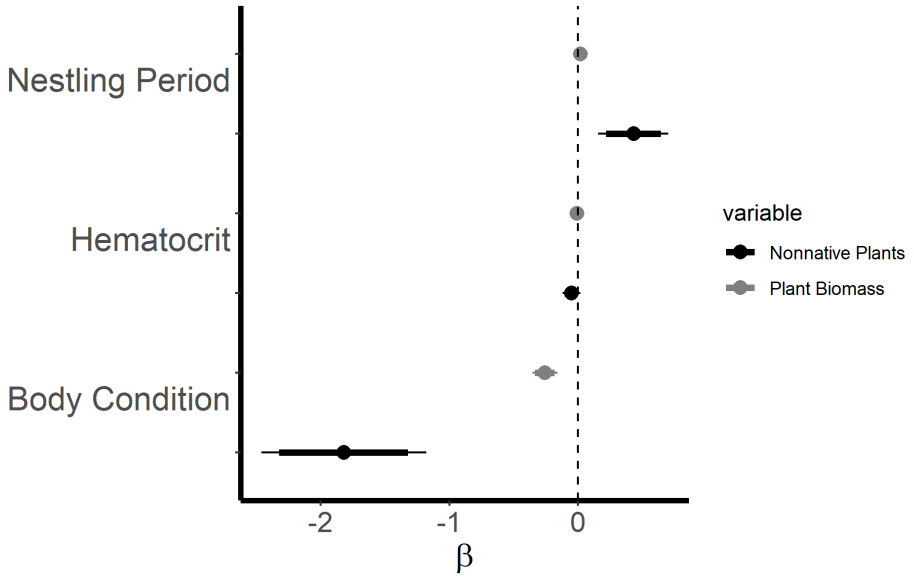
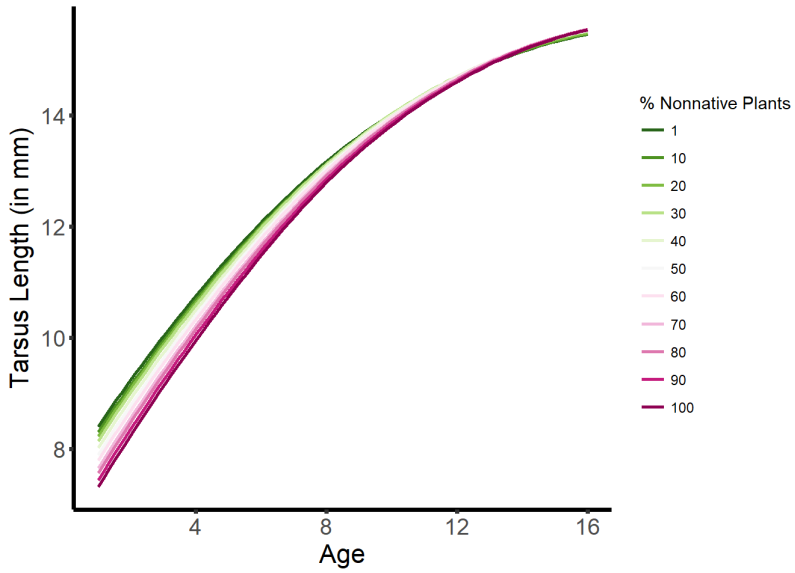
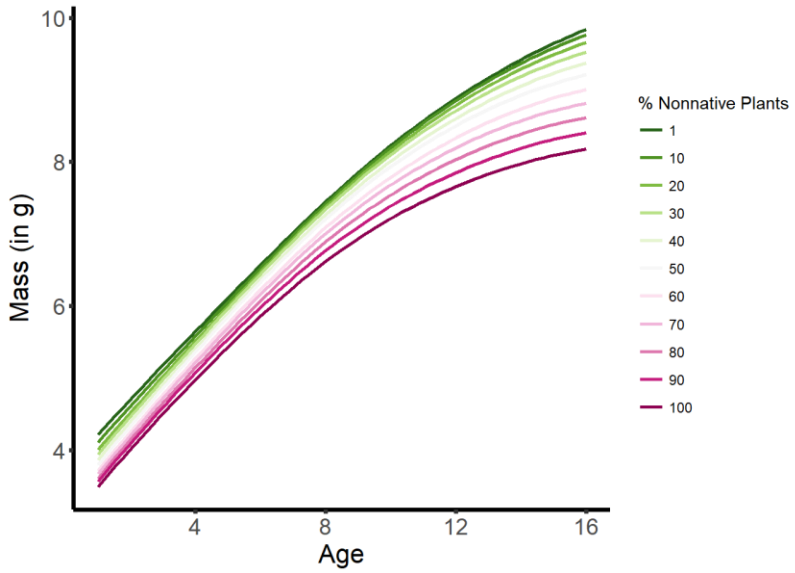


Figure 4.9 Mean β coefficient (circle), 90% (thick line) and 95% credible intervals for the beta estimates for each model of nestling condition. Nestling period increased, and body condition decreased as nonnative plant biomass increased. Hematocrit ratios tended to decrease; however, both the 90% and 95% credible intervals overlapped zero.

A)


Tarsus Length (in mm)
14
12
10
8
4
8
12
16
Age
% Nonnative Plants
1
10
20
30
40
50
60
70
80
90
100

B)


Mass (in g)
10
8
6
4
4
8
12
16
Age
% Nonnative Plants
1
10
20
30
40
50
60
70
80
90
100

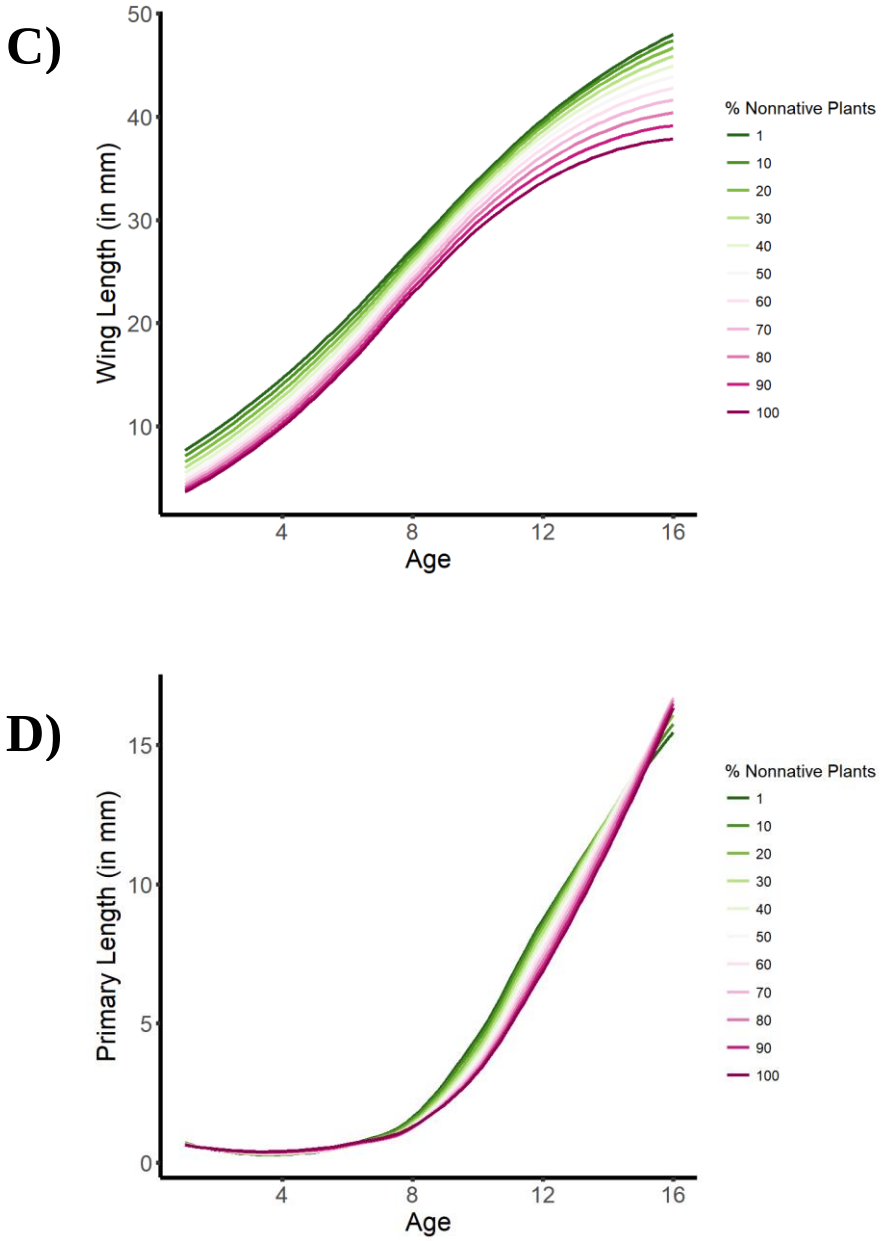


Figure 4.10 Nestling growth models for a) tarsus, b) mass, c) wing and d) exposed primary as yards increase from low proportion of nonnative plant biomass (green) to high proportions of nonnative plant biomass (pink). The only effect of nonnative plants was on the wing and mass variable. Nestling wings were shorter and mass lower but grew at faster rates in nonnative yards.

Table 4.1 Mean beta coefficients ± standard deviation for each growth parameter in the non-linear mixed effect model. Parameter 95% credible intervals are in the parentheses. 95% credible intervals that do not overlap zero are in bold and 90% credible intervals that do not overlap zero are in italics.

NONNATIVE PLANTS

Measurement Description	*Asymptote (A)*	*Inflection point (I)*	*Growth Rate (K)*
Tarsus	0.21 ± 0.68 (-1.12, 1.57)	1.34 ± 1.14 (-1.08, 3.34)	0.03 ±0.08 (-0.12, 0.18)
Mass	*-2.40 ± 1.37 (-4.90, 0.60)*	-1.07 ± 1.68 (-4.49, 2.18)	0.15 ± 0.13 (-0.13, 0.40)
Wing	**-15.08 ± 5.95 (-26.39, -3.14)**	-0.94 ± 1.21 (-3.35, 1.43)	**0.13 ± 0.05 (0.02, 0.24)**
Exposed primary	2.78 ± 5.25 (-4.05, 9.98)	*1.39 ± 0.96 (-0.48, 3.28)*	-0.19 ± 0.20 (-0.59, 0.20)

PLANT BIOMASS

Measurement Description	*Asymptote (A)*	*Inflection point (I)*	*Growth Rate (K)*
Tarsus	0.20 ± 0.16 (-0.12, 0.51)	0.00 ± 0.22 (-0.45, 0.41)	-0.01 ±0.01 (-0.03, 0.02)
Mass	-0.56 ± 0.36 (-1.02, 0.28)	-0.30 ± 0.41 (-1.15, 0.51)	0.03 ± 0.04 (-0.04, 0.10)
Wing	-1.05 ± 1.52 (-4.04, 1.88)	0.10 ± 0.29 (-0.46, 0.64)	0.00 ± 0.01 (-0.02, 0.03)
Exposed primary	*1.37 ± 0.85 (-0.24, 3.12)*	**0.52 ± 0.23 (0.06, 0.96)**	**-0.07 ± 0.03 (-0.12, -0.02)**

REFERENCES

1. Arnold, K. E., S. L. Ramsay, L. Henderson, and S. D. Larcombe. 2010. Seasonal variation in diet quality: antioxidants, invertebrates and blue tits *Cyanistes caeruleus*. Biological Journal of the Linnean Society 99:708–717.

2. Avery, R. A. 1971. Estimates of Food Consumption by the Lizard Lacerta vivipara Jacquin. Journal of Animal Ecology 40:351–365.

3. Avolio, M. L., D. E. Pataki, T. L. E. Trammell, and J. Endter-Wada. n.d. Biodiverse cities: the nursery industry, homeowners, and neighborhood differences drive urban tree composition. Ecological Monographs, in press.

4. Bańbura, J., J. Blondel, H. de Wilde-Lambrechts, M.-J. Galan, and M. Maistre. 1994. Nestling diet variation in an insular Mediterranean population of blue tits *Parus caeruleus*: effects of years, territories and individuals. Oecologia 100:413–420.

5. Bell, G. P. 1990. Birds and mammals on an insect diet: a primer on diet composition analysis in relation to ecological energetics. Studies in avian biology 13.

6. Bernays, E., and M. Graham. 1988. On the Evolution of Host Specificity in Phytophagous Arthropods. Ecology 69:886–892.

7. Blondel, J., A. Dervieux, M. Maistre, and P. Perret. 1991. Feeding ecology and life history variation of the blue tit in Mediterranean deciduous and sclerophyllous habitats. Oecologia 88:9–14.

8. Both, C., M. E. Visser, and N. Verboven. 1999. Density–dependent recruitment rates in great tits: the importance of being heavier. Proceedings of the Royal Society of London. Series B: Biological Sciences 266:465–469.

9. Brown, J. S., D. W. Stephens, and R. C. Ydenberg. 2007. Foraging: behavior and ecology. University of Chicago Press.

10. Burger, C., E. Belskii, T. Eeva, T. Laaksonen, M. Mägi, R. Mänd, A. Qvarnström, et al. 2012. Climate change, breeding date and nestling diet: how temperature differentially affects seasonal changes in pied flycatcher diet depending on habitat variation. Journal of Animal Ecology 81:926–936.

11. Burghardt, K. T., D. W. Tallamy, C. Philips, and K. J. Shropshire. 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. Ecosphere 1:art11.

12. Burnham, K.P. and Anderson, D.R., 2003. Model selection and multimodel inference: a practical information-theoretic approach. Springer Science & Business Media.

13. Chamberlain, D. E., A. R. Cannon, M. P. Toms, D. I. Leech, B. J. Hatchwell, and K. J. Gaston. 2009. Avian productivity in urban landscapes: a review and meta-analysis. Ibis 151:1–18.

14. Danner Raymond M., Greenberg Russell S., Danner Julie E., Walters Jeffrey R., and Piersma Theunis. 2015. Winter food limits timing of pre-alternate moult in a short-distance migratory bird. Functional Ecology 29:259–267.

15. Eeva, T., S. Helle, J.-P. Salminen, and H. Hakkarainen. 2010. Carotenoid Composition of Invertebrates Consumed by Two Insectivorous Bird Species. Journal of Chemical Ecology 36:608–613.

16. Evans, B. S., T. B. Ryder, R. Reitsma, A. H. Hurlbert, and P. P. Marra. 2015. Characterizing avian survival along a rural-to-urban land use gradient. Ecology 96:1631–1640.

17. Evans, C., E. Abrams, R. Reitsma, K. Roux, L. Salmonsen, and P. P. Marra. 2005. The Neighborhood Nestwatch Program: Participant Outcomes of a Citizen-Science Ecological Research Project. Conservation Biology 19:589–594.

18. Forister, M. L., V. Novotny, A. K. Panorska, L. Baje, Y. Basset, P. T. Butterill, L. Cizek, et al. 2015. The global distribution of diet breadth in insect herbivores. Proceedings of the National Academy of Sciences 112:442–447.

19. García-Navas, V., and J. J. Sanz. 2011. The importance of a main dish: nestling diet and foraging behaviour in Mediterranean blue tits in relation to prey phenology. Oecologia 165:639–649.

20. Grubb, T. C., and D. A. Cimprich. 1990. Supplementary Food Improves the Nutritional Condition of Wintering Woodland Birds: Evidence from Ptilochronology. Ornis Scandinavica (Scandinavian Journal of Ornithology) 21:277–281.

21. Hildebrandt, B., and M. Schaub. 2018. The effects of hatching asynchrony on growth and mortality patterns in Eurasian Hoopoe *Upupa epops* nestlings. Ibis 160:145–157.

22. Hill, G. E., and R. Montgomerie. 1994. Plumage colour signals nutritional condition in the house finch. Proc. R. Soc. Lond. B 258:47–52.

23. Hinsley, S. A., R. A. Hill, P. E. Bellamy, N. M. Harrison, J. R. Speakman, A. K. Wilson, and P. N. Ferns. 2008. Effects of structural and functional habitat gaps on breeding woodland birds: working harder for less. Landscape Ecology 23:615–626.

24. Hochachka, W., and J. N. M. Smith. 1991. Determinants and Consequences of Nestling Condition in Song Sparrows. Journal of Animal Ecology 60:995–1008.

25. Holmes, R. T., and S. K. Robinson. 1981. Tree Species Preferences of Foraging Insectivorous Birds in a Northern Hardwoods Forest. Oecologia 48:31–35.

26. Hope, S. F., F. A. Stabile, and L. K. Butler. 2016. Urban living alters moult dynamics in a passerine. Journal of Avian Biology 47:304–311.

27. Isaksson, C., and S. Andersson. 2007. Carotenoid diet and nestling provisioning in urban and rural great tits Parus major. Journal of Avian Biology 38:564–572.

28. Jenni, L., S. Müller, F. Spina, A. Kvist, and Å. Lindström. 2006. Effect of endurance flight on haematocrit in migrating birds. Journal of Ornithology 147:531.

29. Johnsen, A., K. Delhey, S. Andersson, and B. Kempenaers. 2003. Plumage colour in nestling blue tits: sexual dichromatism, condition dependence and genetic effects. Proceedings of the Royal Society of London B: Biological Sciences 270:1263–1270.

30. Lerman, S. B., K. H. Nislow, D. J. Nowak, S. DeStefano, D. I. King, and D. T. Jones-Farrand. 2014. Using urban forest assessment tools to model bird habitat potential. Landscape and Urban Planning 122:29–40.

31. Litt, A. R., E. E. Cord, T. E. Fulbright, and G. L. Schuster. 2014. Effects of Invasive Plants on Arthropods. Conservation Biology 28:1532–1549.

32. Lodjak, J., M. Mägi, U. Rooni, and V. Tilgar. 2015. Context-dependent effects of feather corticosterone on growth rate and fledging success of wild passerine nestlings in heterogeneous habitat. Oecologia 179:937–946.

33. Mägi, M., R. Mänd, H. Tamm, E. Sisask, P. Kilgas, and V. Tilgar. 2009. Low reproductive success of great tits in the preferred habitat: a role of food availability. Ecoscience 16:145–157.

34. Martin, A. C. 1951. American wildlife & plants, a guide to wildlife food habits; the use of trees, shrubs, weeds, and herbs by birds and mammals of the United States. McGraw-Hill, New York.

35. Martin, T. E. 1987. Food as a limit on breeding birds: a life-history perspective. Annual review of ecology and systematics 453–487.

36. Mostrom, A. M., R. L. Curry, and B. S. Lohr. 2002. Carolina Chickadee: *Poecile Carolinensis*. Birds of North America.

37. Naef-Daenzer, B., F. Widmer, and M. Nuber. 2001. Differential post-fledging survival of great and coal tits in relation to their condition and fledging date. Journal of Animal ecology 70:730–738.

38. Narango, D. L., D. W. Tallamy, and P. P. Marra. 2017. Native plants improve breeding and foraging habitat for an insectivorous bird. Biological Conservation 213:42–50.

39. Negro, J. J., A. Chastin, and D. M. Bird. 1994. Effects of Short-Term Food Deprivation on Growth of Hand-Reared American Kestrels. The Condor 96:749–760.

40. Newhouse, M. J., P. P. Marra, and L. S. Johnson. 2008. Reproductive success of House Wrens in suburban and rural landscapes. The Wilson Journal of Ornithology 120:99–104.

41. Partecke, J., I. Schwabl, and E. Gwinner. 2006. Stress and the city: urbanization and its effects on the stress physiology in European blackbirds. Ecology 87:1945–1952.

42. Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar. 2014. R Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1-117. Available at h ttp://CRAN. R-project. org/package= nlme.

43. Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

44. Razeng, E., and D. M. Watson. 2014. Nutritional composition of the preferred prey of insectivorous birds: popularity reflects quality. Journal of Avian Biology

45. Ricklefs, R. E. 1968. Patterns of growth in birds. Ibis 110:419–451.

46. Ricklefs, R. E. 1974. Energetics of reproduction in birds. Pages 152–292 *in* Avian energetics (Vol. 15). Nuttall Ornithological Club Cambridge, MA.

47. Rosenberg, K. V., and R. J. Cooper. 1990. Approaches to avian diet analysis. Studies in avian biology 13:80–90.

48. Sauter, A., R. Bowman, S. J. Schoech, and G. Pasinelli. 2006. Does optimal foraging theory explain why suburban Florida scrub-jays (*Aphelocoma coerulescens*) feed their young human-provided food? Behavioral Ecology and Sociobiology 60:465–474.

49. Schroeder, L. 1977. Distribution of caloric densities among larvae feeding on black cherry tree leaves. Oecologia 29:219–222.

50. Schulte-Hostedde, A. I., B. Zinner, J. S. Millar, and G. J. Hickling. 2005. Restitution of Mass–Size Residuals: Validating Body Condition Indices. Ecology 86:155–163.

51. Scriber, J. M., and F. Slansky Jr. 1981. The nutritional ecology of immature insects. Annual review of entomology 26:183–211.

52. Sofaer, H. R., P. L. Chapman, T. S. Sillett, and C. K. Ghalambor. 2013. Advantages of nonlinear mixed models for fitting avian growth curves. Journal of Avian Biology 44:469–478.

53. Thorne, M. S., Q. D. Skinner, M. A. Smith, J. D. Rodgers, W. A. Laycock, and S. A. Cerekci. 2002. Evaluation of a Technique for Measuring Canopy Volume of Shrubs. Journal of Range Management 55:235–241.

54. Tilgar, V., R. Mänd, I. Ots, M. Mägi, P. Kilgas, and S. J. Reynolds. 2004. Calcium availability affects bone growth in nestlings of free-living great tits (*Parus major*), as detected by plasma alkaline phosphatase. Journal of Zoology 263:269–274.

55. Wilkin, T. A., L. E. King, and B. C. Sheldon. 2009. Habitat quality, nestling diet, and provisioning behaviour in great tits *Parus major*. Journal of Avian Biology 40:135–145.

Chapter 5

MAPPING VERTICAL ENERGY FLOW OF NATIVE VS. NONNATIVE PLANTS TO FOOD WEBS USING A STABLE ISOTOPE TRACER

Abstract

Empirical work suggests that nonnative plants can limit food availability for breeding birds by reducing important arthropod prey biomass; however, no study has directly compared the contributions of native and nonnative trees to diets of consumers at a community level. To test whether more energy is transferred to an urban, terrestrial plant-insect-bird food web from native trees, we used a foliar-applied ^{15}N isotope tracer to enrich leaves on either native (12 sites) or nonnative ornamental trees (12 sites) within residential yards. We found that, following treatment, the proportion of ^{15}N in leaves, caterpillars and spiders increased dramatically (up to 116% higher) and was not significantly different between native and nonnative treatments. However, both caterpillar and spider biomass was lower on nonnative trees across the season which ultimately limits the availability of nitrogen-enriched prey for consumers. Consequently, we found higher proportions of ^{15}N in blood samples from breeding birds occupying yards where native trees were treated for 5 out of 6 focal species. This study provides direct evidence that native trees supply disproportionately more nitrogen to bird diets via arthropod prey items for both obligate and facultative

insectivores. These results unequivocally show that homeowners can increase the food resources for breeding birds, and create foundations for local food webs, by prioritizing native plant biomass in residential landscapes.

Introduction

Historically, landscaping plants have been chosen primarily for aesthetics and ease of care rather than the ecological services they provide [1]. In urban areas, nonnative plants typically dominate residential plant assemblages, yet may not provide the same quality of habitat and food resources to local biodiversity as native flora [2]. Insects are a primary mechanism by which energy is transferred between plants and consumers because plants support a diverse and abundant suite of phytophagous species that are essential prey for predatory arthropods, birds and mammals. Most herbivorous insects are specialized toward one or a few plant lineages [3, 4]; thus, evolutionarily novel nonnative plant species tend to support a lower abundance and diversity of prey required by higher trophic levels [5, 6]. Although these patterns suggest that consumers may receive fewer resources from nonnative plants, some studies have concluded that nonnative plants provide useable habitat for wildlife from evidence of consumer presence in areas dominated by nonnative plants [7–10]. However, a critical limitation in our understanding of the impacts of nonnative plants is a lack of direct comparisons between the energy transfer of nonnative plant communities and native plant communities that were displaced.

The most direct way to compare the relative contribution of individual plant species to local food webs is to track resources that are provided to other organisms in the ecosystem over space and time. However, evaluating plant-animal interactions

simultaneously in the field is challenging because standard observations can be time-consuming, expensive or subject to detection biases. For example, our ability to collect accurate data on the distribution of prey is constrained because the individuals available to sample represent the 'residue' of predation itself [11]. Moreover, the scope of most studies of nonnative plants has been limited to just a few highly abundant invasive species or the responses of one trophic level to those species [12].

Elemental isotopic signatures have been widely used in ecological research to provide a snapshot of the interrelatedness of organisms and the ecosystems in which they reside. Because isotopic signatures are assimilated into the inert tissues of an organism, this molecular tool can be used as a non-invasive method to identify trophic relationships among organisms [13], track pathways of nutrients and contaminants through food webs [14,15], and understand habitat relationships [16]. One way to track the flow of a resource across space and time is to deliberately introduce an isotope signature to 'trace' the pathway from origin to assimilation [17, 18]. For example, by labeling a parent tree with a unique isotopic signature, energy that is provided by that tree to the local food web can be tracked through time and space by comparing ratios of the unique isotope in herbivores and their predators to the abundance of the atmospheric element. This method has been used for years by biogeochemists [15, 19] and plant ecologists [20] to follow the cycling of nitrogen through aquatic and terrestrial systems as well as by biologists to track metabolic rates in vertebrates [21]. Rarely have unique isotopic tracers been used to track energy transfer through multiple trophic levels despite that consumers incorporate natural isotopic signatures into their tissues through their diet [but see 19].

The phylogenetically and functionally diverse plant communities in suburban landscapes provided a unique opportunity to measure whether nonnative plants provide equivalent energy to local fauna as native plants. In this study, we hypothesized that the relative trophic contributions to higher-order consumers is higher for native plants compared to nonnative plants. To test our hypothesis, we used a foliar-applied ^{15}N isotope tracer to label either native or nonnative plants in residential yards with similar local features. We then tracked the upward energy transfer from plant leaves to herbivorous caterpillars, predatory spiders and insectivorous birds in order to compare the degree of enrichment between plants of different origin.

Methods

Site Selection

This study was conducted over two years from 2015-2016 within the Smithsonian Migratory Bird Center's Neighborhood Nestwatch program [23], in yards of private homeowners in the Washington D.C. metropolitan area. From a larger pool of yards, twenty-four (12 native-treated and 12 nonnative-treated) were chosen for inclusion in the experimental application and all were separated by at least 1km. Sites were chosen so that each had similar biotic and abiotic conditions, surrounding landscapes that did not border a forest or park, and a similar mix of native and nonnative plant biomass (appendix figure C.13). We designated the 'site' as the central yard owned by the Neighborhood Nestwatch participant, as well as a 50m radius around the center of the property. Most plants that received the nitrogen

application were within the focal yard, however, neighboring yards were used for bird capture, nest searching, territory monitoring, and plant community surveys when property access was granted. Prior to the breeding season, all sites also received artificial nest boxes to encourage breeding activity of cavity nesting birds.

To confirm that our sites had similar local attributes, we identified the following features: 1) the proportion of nonnative woody plant biomass (trees and shrubs), 2) the total volume of woody plant biomass (in m^3), 3) housing density, 4) tree canopy cover, and 5) impervious surface. Nonnative plant biomass and total plant biomass was quantified using methods from [6]. For housing density, tree canopy and impervious surface we used a 1m-resolution land cover data layer (via Chesapeake Conservancy) and calculated the surface area of buildings, tree canopy and impervious surface in m^2 within a 50-m radius. All spatial features were calculated using packages 'raster', 'sp' and 'rgeos' in program R.

^{15}N Isotope Application

To evaluate the vertical flow of energy in a native versus nonnative plant community, we applied a ^{15}N isotope tracer using foliar spray as in methods from Carlo et al. 2009 [17]. Prior to application, we identified 4-6 individual trees and large shrubs per site that were suitable for nitrogen application. Sites were chosen for spraying native or nonnative plants based on the availability and accessibility of sufficient foliage for spraying within the central yard. No coniferous or unidentified trees were considered and all species considered for spraying were popular ornamental trees used in suburban landscaping and commercially available (appendix table C.2).

In 2015 we began spraying on April 28th and in 2016 we began spraying on May 4th and in both years it took approximately 2 weeks to complete all sites.

To label our experimental trees, we sprayed foliage with an enriched ^{15}N solution so that trees would incorporate nitrogen through leaf stomata and distribute it throughout the foliage. We mixed 0.25g/L 99.5% ^{15}N Ammonium Nitrate (Icon Isotope Services Inc.) with reverse osmosis/deionized water and added at least 3ml/L of surfactant to increase surface tension between the solution and the leaf surface and maximize nitrogen absorption. We sprayed 30-40L of nitrogen mixture to the focal trees using a handheld fertilizer sprayer attempting to saturate all accessible foliage below ~7m high. We applied the nitrogen mixture to all leaves that were not directly adjacent to plant species of opposite origin; for example, branches of native trees that were next to nonnative trees were avoided so as to not contaminate non-focal plants. As needed, plants below the trees of opposite origin were covered with a tarpaulin to avoid unintentional application. The nitrogen mixture was applied on days of low wind and no precipitation immediately before, after or during application. We applied the mixture on two consecutive occasions, once in the morning, and once in the afternoon, or vice versa, to ensure that trees were adequately saturated.

Post-Application Sampling

Two weeks following application, sites were visited approximately every four days from May to July to collect blood samples from birds (when possible) and resight previously captured birds. We also collected arthropod and plant material from the focal trees approximately every two weeks for a total of four sampling periods; one pre-treatment (the 'control' sampling period) and three post-treatment (the 'enriched'

sampling periods). We collected leaves from each side of our focal plant to ensure that our treatment was successful. We sampled arthropods by conducting three, 5-minute searches on each focal plant within non-overlapping 2.25m^2 areas. We used aspirators (foliage arthropods) or hand collection (caterpillars) to collect arthropods for identification and isotopic analysis. All samples were stored in a -80˚C freezer and weighed to the nearest milligram prior to identification and analysis.

Our aim was to collect blood samples from eight breeding passerines during the course of the experiment. Four obligate insectivores: Carolina chickadee (*Poecile carolinensis*), House Wren (*Troglodytes aedon*), Carolina Wren (*Thryothorus ludovicianus*), and Tufted Titmouse (*Baeolophus bicolor*); and four facultative insectivores: Song Sparrow (*Melospiza melodia*), Northern Cardinal (*Cardinalis cardinalis*), Gray Catbird (*Dumetella carolinensis*), and American Robin (*Turdus migratorious*). These species were chosen because they are common in urban landscapes and vary in the proportion of insect material within adult diets (appendix figure C.14). Each visit, we attempted to capture territorial birds of our focal species to collect blood samples. Adult birds were sampled by capturing with mist-nets and bled using brachial vein puncture. For nests within the site area, we monitored every four days and collected nestling blood on days 8-9 for open cup nesters and days 10-14 for cavity nesters.

After collection, blood samples were stored in a cooler until they could be spun in a centrifuge to separate red blood cells from plasma. They were then frozen for storage before being processed for ^{15}N. Next, samples were freeze-dried to remove water and prepared in tin capsules for isotopic analysis. Because we were primarily interested in focal tree use over the season and we suspected that isotope dilution from

non-enriched trees would be high, we only used red blood cells for this analysis because the half-life of blood cells (~15 days) is significantly longer than plasma (~6 days) [24] which would increase the probability that we would capture enrichment. Our goal was to determine the proportion of ^{15}N from birds that were actively territorial on the site to increase the probability that their diet derived from trees within our study area. Therefore, we only processed blood samples from individuals that had been resighted at least once within our 50m-radius buffer during the course of the season.

We analyzed plant, insect and bird material for the amount of ^{15}N using the mass spectrometry at the Smithsonian Isotope lab in Suitland MD. We processed leaf samples and bird blood from both years and insect samples from 2015. Our insect samples were processed as batch samples of all individuals collected during each sampling period for each focal tree. For leaves, spiders and caterpillars, we used four standards: acetanilide, keratin, urea and an additional urea standard with enriched ^{15}N. For bird blood, we used only acetanilide, keratin and urea. For all statistical analyses, we used the linear corrected ratio of ^{15}N:^{14}N ($\delta^{15}N$).

Statistical Analysis

We first tested whether our sites differed in local scale attributes using a Welch's t-test for unequal variance. For these tests we used site as our sample unit and compared the means between native- and nonnative-treated sites. We conducted a separate test on each variable (nonnative plants, plant biomass, housing density, tree canopy and impervious surface).

For plants, caterpillars, spiders and birds, we used linear mixed models with site as a random effect. Our primary interest was to test whether 1) plants and caterpillars were enriched by our treatment and 2) whether the degree of enrichment (i.e. slope) differed between native and nonnative sites. In each model we included the $\delta^{15}N$ of each sample as our response variable and fixed effects of sample visit (control | enriched) to test for successful enrichment, and the interaction between site type and sample visit to test for differences in slope. We also tested for the significance of our interaction term by comparing the full model with a reduced model without interaction with a likelihood ratio test (LRT).

For our consumer samples (spiders and birds), we also analyzed the proportion of diet derived from control vs. enriched plant sources using the package 'mixSIAR' [25]. This package uses an extension of the traditional mixing model approach while incorporating both fixed and random effects in a Bayesian analysis. We included a fixed effect of site type (native or nonnative) and a continuous effect of days since first enrichment. We included two potential sources, control plant samples or enriched plant samples from native and nonnative sites separately and two isotopic sources, $\delta^{15}N$ and $\delta^{13}C$. We ran each analysis with 50,000 iterations, an initial burn-in of 25,000 iterations, a thinning rate of 25 and 3 chains. We assessed convergence ensuring that each R-hat value was <1.1. For birds, we ran separate analyses for each species, as well as a pooled sample of all species. Because we were interested in the relative difference between our treatments and not exact diet proportions *per se*, we used a discrimination factor of 1 for both treatments.

Because we suspected that the nitrogen contributions of our labeled trees to individual diet would be very low, we used an informative prior in our mixing model.

Individual birds have territories that encompass many more unlabeled trees relative to the ones included in this study. Moreover, the dilution would be high given that our ^{15}N label needed to be detected over multiple trophic levels. We included alpha priors in our mixing model such that the distribution of predicted probability of proportion values of source 1 (controls) was highest at 1 and gradually declined up to 0.6 and our predicted probability of proportion of source 2 (enriched) was highest at 0 and gradually declined up to 0.4. Including this prior constrained our values of diet proportions from enriched plants to low values and increased the precision in our estimated diet proportions.

Our biomass weight data were composed of continuous positive responses but many zeros resulted in over dispersion. To test whether arthropod biomass was different between native and nonnative plants across sampling periods, we used a two-step hurdle model where zeros were modeled with a binomial distribution and non-zeros were modeled with a gamma distribution [26]. We included the total biomass of prey collected from each plant at each sampling period as a response, and plant type (native | nonnative) and sampling period, as well as the interaction between plant type and sampling period. If the interaction term was nonsignificant, we reran a reduced model without interaction. We report our estimates ± standard error, as well as the overall significance of the term with a chi-square test.

Results

Summary Data

In 2015, we applied our isotopic tracer to treatment plants at 16 sites. In 2016 we included 8 additional sites for a total of 12 native and 12 nonnative treatment sites across the two years. The mean proportion of nonnative plant biomass was 41.78% ± 12.36 across all the sites. There was no difference among sites in the mean proportion of nonnative plant biomass (t=-1.69, p=0.11, 95% confidence interval [95% CI]: -0.18, 0.02), plant biomass (t=-1.97, p=0.07, 95% CI: -13,479, 559), housing density (t=-0.38, p=0.71, 95% CI: -464.65, 322.45), mature canopy cover (t=-1.28, p=0.22, 95% CI: -1658.71, 420.71), or impervious cover (t=-0.85, p=0.41, 95% CI: -447.23, 190.23, table 5.1).

Enrichment at Each Trophic Level

Plants

Following our application of foliar ^{15}N, trees were significantly enriched with higher ratios of ^{15}N to ^{14}N (Sampling period [enriched]: β 389.41 ± 1.48, CI: 386.51, 392.32, figure 5.1). Controlling for sampling occasion (control vs. enriched), there was no difference between native and nonnative plants (Plant origin [nonnative]: β: -19.36 ± 22.40, CI: -63.23, 24.14), nor was there a significant interaction between sampling occasion or plant origin (Sampling period [enriched] * Plant origin [nonnative]: β: -19.48 ± 22.40, CI: -63.11, 24.30); thus, native and nonnative trees did not differ in the magnitude of enrichment following the nitrogen application.

Caterpillars

Our isotopic label also enriched the next trophic level of sessile herbivorous insects. Caterpillars were significantly enriched with higher ratios of ^{15}N to ^{14}N (Sampling period [enriched]: β 352.26 ± 2.87, CI: 346.66, 357.87, figure 5.2). Controlling for date of sampling, there was no significant interaction between sampling period and plant origin (Sampling period [enriched] * Plant origin [nonnative]: β: -0.04 ± 10.10, CI: -19.77, 19.75) indicating that caterpillars found on native and nonnative trees did not differ in the magnitude of enrichment following the nitrogen application.

Spiders

At the next trophic level, spiders were also significantly enriched with higher ratios of ^{15}N to ^{14}N but at a much lower degree compared to herbivores (Sampling occasion [enriched]: β 24.04 ± 10.35, CI: 3.19, 43.94, figure 5.3). There was no significant interaction between sampling occasion and treatment (Sampling occasion [enriched] * Plant origin [nonnative]: β: 7.56 ± 11.34, CI: -14.58, 29.29, figure 5.3) indicating that enrichment in spiders values was not different between native- and nonnative-treated sites.

Controlling for sampling period, the proportion of spider diet attributed to enriched sources was similar between native-treated sites compared to nonnative (Native: mean enriched=0.06 ± 0.02, CI=0.03, 0.12; Nonnative: mean enriched=0.05 ± 0.02, CI=0.02, 0.10, figure 5.4a). The distribution of predicted differences between native and nonnative-treated sites also overlapped zero (figure 5.4b).

Birds

In total we made 467 captures of the eight focal species across the 24 sites. From those captures, 282 blood samples were successfully collected after the isotope treatment and from individuals who were confirmed to be territorial adults at the site. These samples were processed for stable isotope analysis and used in subsequent analyses. For Tufted titmouse and Carolina wren, we did not collect enough samples to have sufficient power to detect differences (Tufted Titmouse: 19, Carolina Wren: 10); therefore these species were excluded from further analysis. Our final sample size included samples from 253 birds; 91 pre-treatment, and 162 post-treatment.

Birds were significantly enriched with ^{15}N following our treatment (β 1.19 ± 0.28, t=4.24, p<0.001). In nonnative-treated yards, the slope of enrichment was weaker than in native-treated yards, indicating that birds in nonnative yards received less nitrogen-enriched prey from enriched trees (β -0.61 ± 0.23, t=-2.69, p=0.007, figure 5.5).

Our mixing model showed that native-treated yards supplied a higher proportion of diet to birds compared to nonnative-treated yards (Native: mean enriched=0.011 ± 0.003, CI=0.007, 0.015; Nonnative: mean enriched=0.003 ± 0.002, CI=0.000, 0.007, figure 5.6a). The 95% confidence interval of the predicted differences between native- and nonnative-treated yards was positive and did not include zero (figure 5.6b).

For our individual species models, we found that the slope of ^{15}N enrichment, indicated by a β coefficient of our interaction term that does not overlap zero, was higher in four of the six species: Carolina chickadee, House wren, Northern cardinal and Song sparrow (supplemental results). Proportion of diet predicted by our mixing model was higher for five of six species (Carolina chickadee, House wren, American

robin, Northern cardinal and Song sparrow). There was no difference in the degree of post-treatment enrichment, nor diet proportions in gray catbirds. For this species, the predicted difference in the proportion of enriched diet between native- and nonnative-treated sites had 95% confidence intervals that overlapped zero.

Caterpillar and Spider Biomass

The probability of finding caterpillars on our focal plants was modestly higher on native plants (β 0.56 ± 0.29, $p=0.05$), and significantly declined over the season (β -0.46 ± 0.14, $p<0.001$, figure 5.7). When caterpillars were present, biomass was similar on native and nonnative plants (β -0.80 ± 0.61, $p=0.19$) and declined over the season (β -0.69 ± 0.24, $p=0.006$). The highest peak of caterpillar biomass occurred during the first sampling period (figure 5.7), when native plants had substantially higher biomass than nonnative plants.

The probability of finding a spider on our focal plants was higher on native plants (β 0.96 ± 0.24, $p<0.001$) and increased over the season (β 0.36 ± 0.11, $p<0.001$, figure 5.8). When present, spider biomass was also higher on native plants (β 0.63 ± 0.23, $p=0.006$) and modestly increased over the season (β 0.19 ± 0.11, $p=0.08$) such that the highest biomass was found during the third and fourth sampling periods (figure 5.8).

Discussion

Using a unique application of the isotope tracer technique on woody plants within private properties, we provide experimental evidence that nonnative species do not provide the same quantity of energetic contributions as native plants in human-

dominated landscapes. We also show that an isotope tracer can be successfully tracked over subsequent trophic levels and multiple consumers that vary in foraging behavior over time and space.

As expected given their limited range of movement and strong host specificity, we found no difference in the nitrogen enrichment of caterpillars. Similarly, we found no difference in predatory spider enrichment, likely due to their range of trophic positions and generalist foraging tactics within this predatory guild [27]. Our spider samples were composed of both free-hunting (Salticidae & Thomsidae) as well as web-building (Araneidae, Tetragnathidae) and sheetweb spiders (Linyphiidae) whose diets are composed of flying insects, primarily flies, leafhoppers, and moths, that may have developed on living or dead plant material other than our enriched plants. The variation in enrichment we found in our spider samples points to an important limitation in comparisons of arthropod communities on native and nonnative plants; generalist arthropods may not derive energy from the plant they are found on. Yet both caterpillar and spider biomass was significantly lower on nonnative plants compared to natives, suggesting that the amount of enriched resources available for birds was due to reduced prey abundance rather than prey choice of particular arthropod consumers.

The degree of ^{15}N enrichment was higher in native-treated yards for five of the six bird species, including both facultative and obligate insectivores. Our previous work found that chickadees, which have breeding season diets composed of almost entirely of arthropods [28], strongly prefer foraging in native plants [6] and individuals that breed in nonnative-dominated yards experience conditional- (chapter 4) and reproductive- declines that can reduce the sustainability of the population as a whole

(chapter 3) . Accordingly, differences between native- and nonnative-treated yards were most pronounced for our obligate insectivores. This study expands on our previous results by demonstrating that nonnative plants supply less nitrogen for generalist omnivores as well despite diet flexibility. Arthropods are key sources for calcium for bone health [29], carotenoids for immune function & pigments [30], and protein & lipids for energy metabolism [31]. Thus, widespread conversion of native flora to nonnative plant communities in residential landscapes can reduce arthropod resources such that even species that do not rely solely on animal-based food throughout the year could experience negative consequences.

The species that did not show a clear difference in enrichment was Gray catbird, a generalist omnivore that also feeds heavily on fruit when available [32]. None of the treated trees in this study produced any fruit during the sampling periods, but suburban areas in general produce abundant ornamental fruit during the breeding season (personal observation) which may have diluted our ability to detect any differences due to arthropod consumption. Catbirds are also ground foragers that prey on diverse arthropod taxa, such as earthworms and beetles. The prolific success of catbirds in urban areas is likely due to the diet flexibility this species exhibits. Future work should assess whether shifts to alternative diets resulting from changes in plant communities has cascading impacts on nutrition and fitness for generalist omnivores.

The stronger increases in nitrogen enrichment in native-treated yards provides compelling support that increasing native plant biomass in suburban yards would have positive impacts on food availability for insectivorous birds across foraging guilds. This effect was independent of plant biomass as well as plant identity. Increasing food availability has the potential to increase reproductive fitness of urban birds [6, 33],

thereby improving the ability of urban landscapes to function as population sources for insectivores [33]. The pervasive scale of global land conversion to urban development, and the widespread preference for nonnative plants in horticultural, suggests that shifting landscaping priorities to local flora that maximize resources for biodiversity could have profound effects on food web stability. Needed are quantitative studies that scale up from individual yards to determine at what scale changes in homeowner landscaping preferences can make lasting positive impacts to biodiverse populations.

Table 5.1 Summary of mean ± standard deviation for land cover variables within a 50m-radius area around the site. Data from the same land cover classes and resolution was not available for Virginia sites (n=2) and were not included in this comparison.

Treatment	*Proportion nonnative biomass*[*]	*Plant Biomass* (m^3)[*]	*Building densities* (m^2)[†]	*Canopy Cover* (m^2)[*‡]	*Impervious Cover* (m^2)[†‡]
Native plants	37.69% ± 0.12	7521 ± 4218	9.58% ± 3.95	57.90% ± 17.19	8.27% ± 3.88
Nonnative plants	45.88% ± 0.12	13981 ± 10556	10.49% ± 6.31	65.78% ± 9.19	9.91% ± 4.69

[*] These features are measured using five i-Tree vegetation plot surveys within a 50-m radius area

[†] These features are measured using 1m-resolution land cover data (Chesapeake Conservancy) within a 50-m radius buffer

[‡] Canopy cover features include tree canopy + canopy over roads, structure and impervious surface. Impervious cover includes roads and impervious surface.

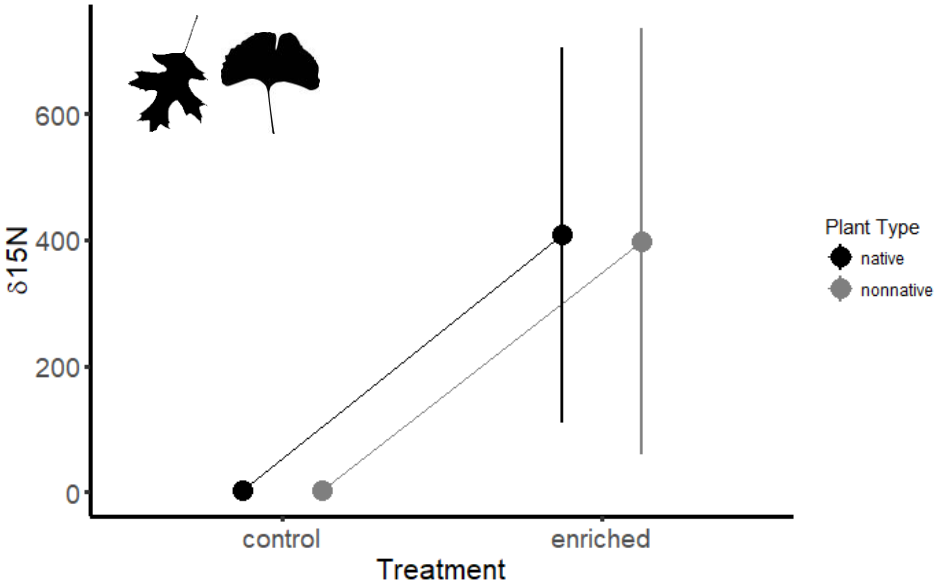


Figure 5.1 Mean ± SD of native (black) and nonnative (gray) plants before (control) and after (enriched) application of foliar ^{15}N. Leaves were significantly higher in nitrogen-15 after application, but there was no difference between $\delta^{15}N$ of native and nonnative leaves before, nor after, application.

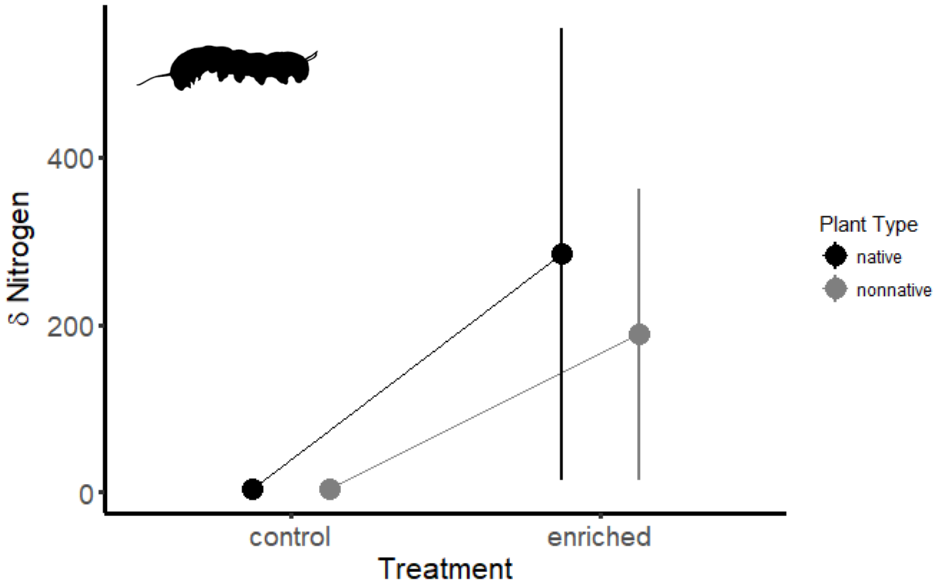


Figure 5.2 Mean ± SD of native (black) and nonnative (gray) caterpillars before (control) and after (enriched) application of foliar nitrogen-15. Caterpillars were significantly higher in $\delta^{15}N$ after application, but there was no difference between native and nonnative sites before nor after application. One caterpillar outlier collected on a nonnative plant with an unusually high value ($\delta^{15}N$=3856) is not included.

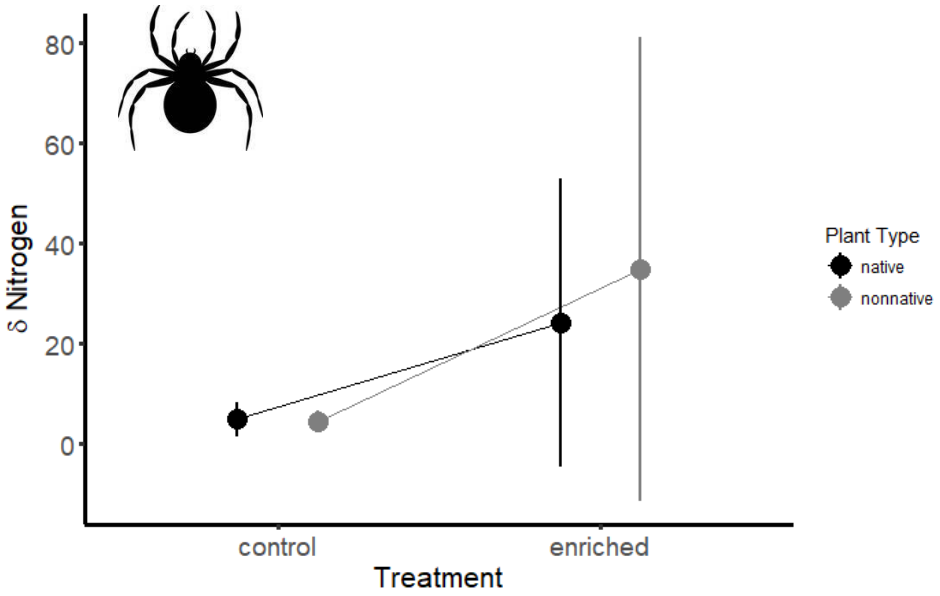


Figure 5.3 Mean ± SD of native (black) and nonnative (gray) spiders before (control) and after (enriched) application of foliar ^{15}N. Spiders were significantly higher in $\delta^{15}N$ after application, but there was no difference between native and nonnative leaves before nor after application.

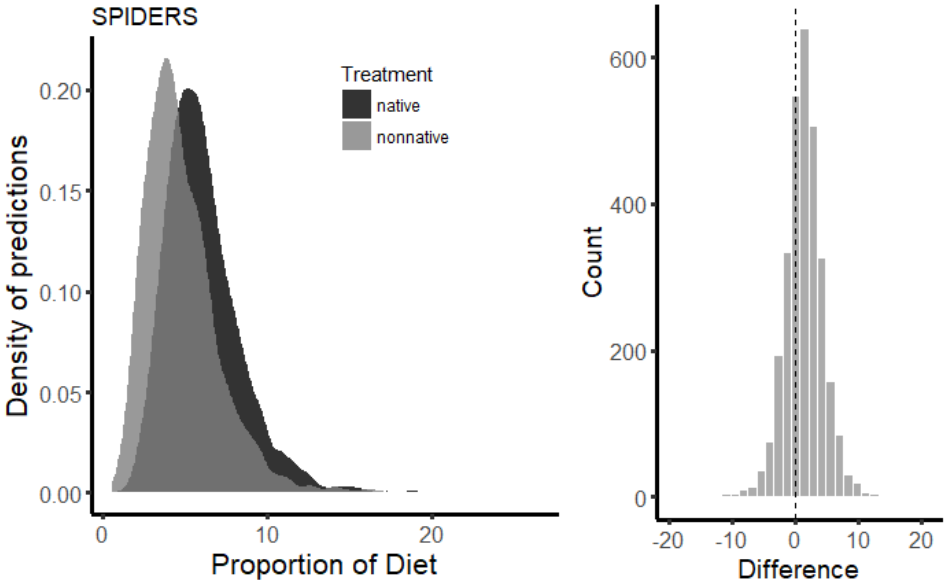


Figure 5.4 (A) Posterior probability density of predicted proportion of enriched diet in spiders between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

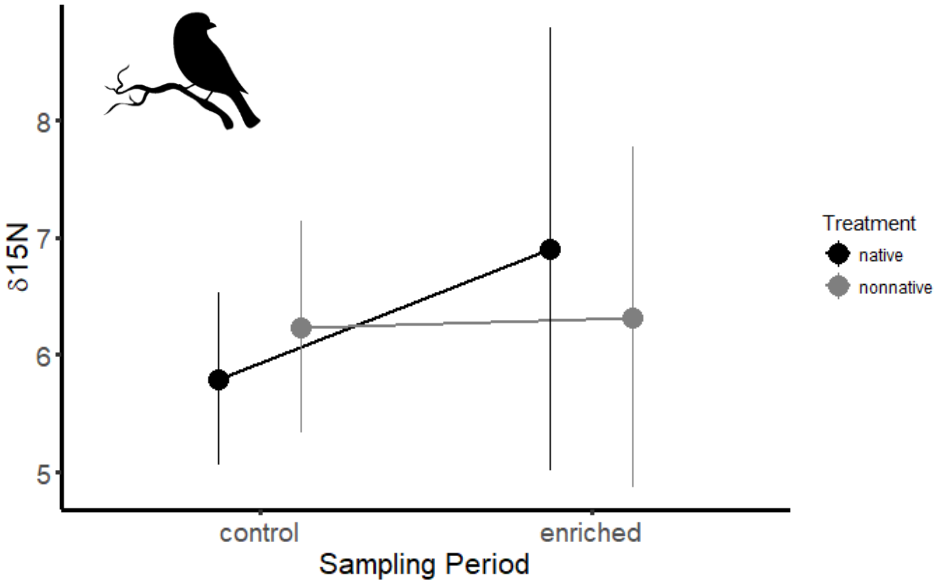


Figure 5.5 Mean (± SD) blood ^{15}N in birds from native-treated (black) and nonnative-treated (gray) yards before (control) and after (enriched) application of the foliar isotope tracer. Bird blood was significantly higher in ^{15}N after application, and in native compared to nonnative-treated yards.

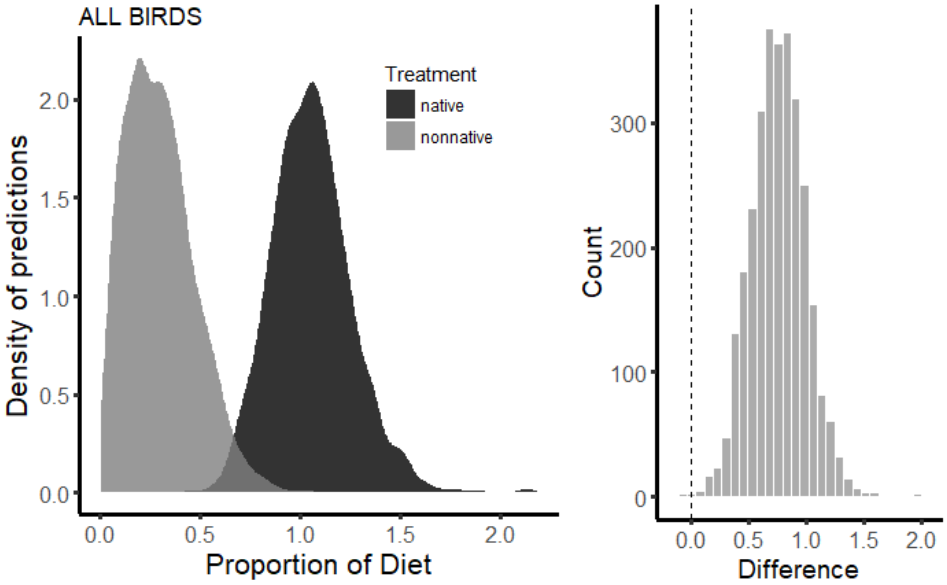


Figure 5.6 (A) Posterior probability density of predicted proportion of enriched diet in bird blood between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

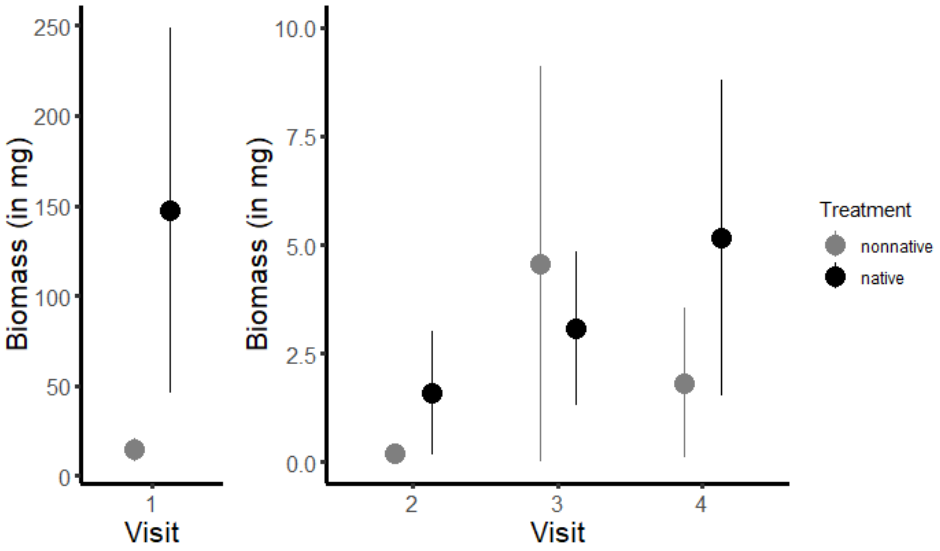


Figure 5.7 Predicted mean caterpillar biomass ± SE over the 4 visits. Note the different y-axes between the 1st visit and succeeding visits due to the first peak of caterpillars producing large biomass early in the season.

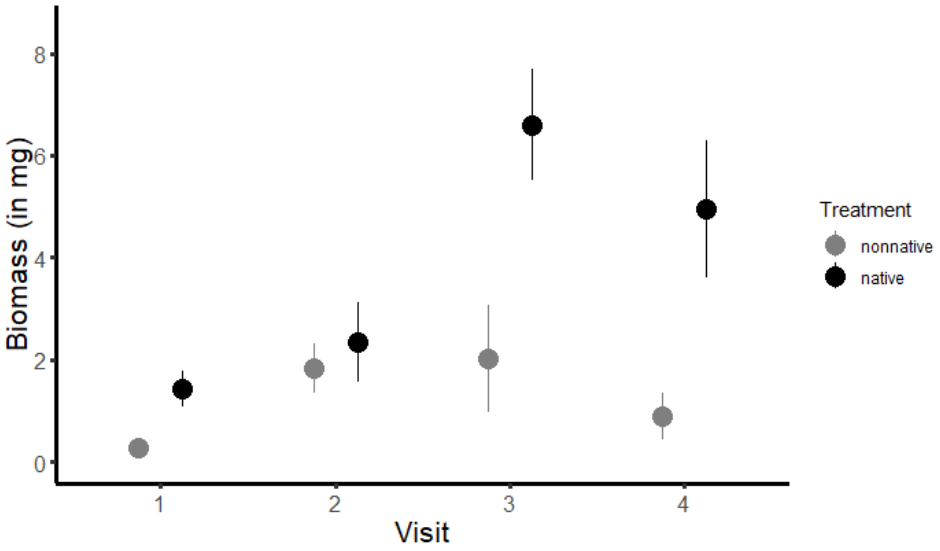


Figure 5.8 Predicted mean spider biomass ± SE over the 4 visits. Mean spider biomass was higher on native trees in all visits and increased over the season.

REFERENCES

1. Avolio ML, Pataki DE, Trammell TLE, Endter-Wada J. In press. Biodiverse cities: the nursery industry, homeowners, and neighborhood differences drive urban tree composition. Ecol Monogr (doi:10.1002/ecm.1290)

2. Lerman SB, Warren PS. 2011 The conservation value of residential yards: linking birds and people. Ecological Applications 21, 1327–1339. (doi:10.1890/10-0423.1)

3. Bernays E, Graham M. 1988 On the Evolution of Host Specificity in Phytophagous Arthropods. Ecology 69, 886–892. (doi:10.2307/1941237)

4. Forister ML et al. 2015 The global distribution of diet breadth in insect herbivores. Proceedings of the National Academy of Sciences 112, 442–447.

5. Burghardt KT, Tallamy DW, Shriver WG 2009 Impact of native plants on bird and butterfly biodiversity in suburban landscapes. Conservation Biology 23, 219–224.

6. Narango DL, Tallamy DW, Marra PP. 2017 Native plants improve breeding and foraging habitat for an insectivorous bird. Biological Conservation 213, 42–50.

7. Gleditsch JM, Carlo TA. 2011 Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. Diversity and Distributions 17, 244–253. (doi:10.1111/j.1472-4642.2010.00733.x)

8. Davis MA. 2011 Do native birds care whether their berries are native or exotic? No. BioScience 61, 501–502.

9. Schlaepfer MA, Sax DF, Olden JD. 2011 The potential conservation value of non-native species. Conservation Biology 25, 428–437.

10. Dickie IA et al. 2014 Conflicting values: ecosystem services and invasive tree management. Biological invasions 16, 705–719.

11. Smith KG, Rotenberry JT. 1990 Quantifying food resources in avian studies: present problems and future needs. Studies in Avian Biology 13, 3–5.

12. Hulme PE, Pyšek P, Jarošík V, Pergl J, Schaffner U, Vilà M. 2013 Bias and error in understanding plant invasion impacts. Trends in Ecology & Evolution 28, 212–218. (doi:10.1016/j.tree.2012.10.010)

13. Layman CA et al. 2012 Applying stable isotopes to examine food-web structure: an overview of analytical tools. Biological Reviews 87, 545–562.

14. Nisbet I, Montoya J, Burger J, Hatch J. 2002 Use of stable isotopes to investigate individual differences in diets and mercury exposures among common terns *Sterna hirundo* in breeding and wintering grounds. Marine Ecology Progress Series 242, 267–274. (doi:10.3354/meps242267)

15. Stürup S, Hansen HR, Gammelgaard B. 2008 Application of enriched stable isotopes as tracers in biological systems: a critical review. Anal Bioanal Chem 390, 541–554. (doi:10.1007/s00216-007-1638-8)

16. Marra PP, Hobson KA, Holmes RT. 1998 Linking winter and summer events in a migratory bird by using stable-carbon isotopes. Science 282, 1884–1886.

17. Carlo TA, Tewksbury JJ, del Río CM. 2009 A new method to track seed dispersal and recruitment using ^{15}N isotope enrichment. Ecology 90, 3516–3525. (doi:10.1890/08-1313.1)

18. Carlo TA, García D, Martínez D, Gleditsch JM, Morales JM. 2012 Where do seeds go when they go far? Distance and directionality of avian seed dispersal in heterogeneous landscapes. Ecology 94, 301–307. (doi:10.1890/12-0913.1)

19. Elskens M, Baeyens W, Brion N, De Galan S, Goeyens L, de Brauwere A. 2005 Reliability of N flux rates estimated from ^{15}N enrichment and dilution experiments in aquatic systems. Global biogeochemical cycles 19.

20. Deng X, Weinbaum SA, DeJong TM, Muraoka TT. 1989 Utilization of nitrogen from storage and current-year uptake in walnut spurs during the spring flush of growth. Physiologia Plantarum 75, 492–498.

21. Nagy KA. 1987 Field Metabolic Rate and Food Requirement Scaling in Mammals and Birds. Ecological Monographs 57, 111–128. (doi:10.2307/1942620)

22. Lescano MN, Farji-Brener AG, Gianoli E, Carlo TA. 2012 Bottom-up effects may not reach the top: the influence of ant–aphid interactions on the spread of soil disturbances through trophic chains. Proc. R. Soc. B 279, 3779–3787. (doi:10.1098/rspb.2012.1066)

23. Evans C, Abrams E, Reitsma R, Roux K, Salmonsen L, Marra PP. 2005 The Neighborhood Nestwatch Program: Participant Outcomes of a Citizen-Science Ecological Research Project. Conservation Biology 19, 589–594.

24. Klaassen Marcel, Piersma Theunis, Korthals Harry, Dekinga Anne, Dietz Maurine W. 2010 Single-point isotope measurements in blood cells and plasma to estimate the time since diet switches. Functional Ecology 24, 796–804. (doi:10.1111/j.1365-2435.2010.01689.x)

25. Semmens B, Stock B, Ward E, Moore JW, Parnell A, Jackson AL, Phillips DL, Bearhop S, Inger R. 2013 MixSIAR: A Bayesian stable isotope mixing model for characterizing intrapopulation niche variation. Ecological Society of America, Minneapolis, MN , 04–09.

26. Martin Tara G., Wintle Brendan A., Rhodes Jonathan R., Kuhnert Petra M., Field Scott A., Low-Choy Samantha J., Tyre Andrew J., Possingham Hugh P. 2005 Zero tolerance ecology: improving ecological inference by modelling the source of zero observations. Ecology Letters 8, 1235–1246. (doi:10.1111/j.1461-0248.2005.00826.x)

27. Sanders Dirk, Vogel Esther, Knop Eva, Woodcock Ben. 2014 Individual and species-specific traits explain niche size and functional role in spiders as generalist predators. Journal of Animal Ecology 84, 134–142. (doi:10.1111/1365-2656.12271)

28. Cooper RJ. 1988 Dietary relationships among insectivorous birds of an eastern deciduous forest. Dissertation, West Virginia University.

29. Ladin ZS, D'Amico V, Jaisi DP, Shriver WG. 2015 Is brood parasitism related to host nestling diet and nutrition? The Auk 132, 717–734.

30. Eeva T, Helle S, Salminen J-P, Hakkarainen H. 2010 Carotenoid Composition of Invertebrates Consumed by Two Insectivorous Bird Species. J Chem Ecol 36, 608–613. (doi:10.1007/s10886-010-9796-0)

31. Razeng E, Watson DM. 2014 Nutritional composition of the preferred prey of insectivorous birds: popularity reflects quality. Journal of Avian Biology (doi:10.1111/jav.00475)

32. Oguchi Y, Pohlen Z, Smith RJ, Owen JC. 2017 Exotic- and native-dominated shrubland habitat use by fall migrating Swainson's Thrushes and Gray Catbirds in Michigan, USA. The Condor , 81–93. (doi:10.1650/CONDOR-17-27.1)

33. Martin TE. 1987 Food as a limit on breeding birds: a life-history perspective. Annual review of ecology and systematics, 453–487.

34. Lepczyk CA, Aronson MFJ, Evans KL, Goddard MA, Lerman SB, MacIvor JS. In press. Biodiversity in the City: Fundamental Questions for Understanding the Ecology of Urban Green Spaces for Biodiversity Conservation. BioScience (doi:10.1093/biosci/bix079).

Appendix A

SUPPLEMENTARY MATERIALS FOR CHAPTER 2

TABLES

Table A.1 Variables used in hierarchical models for chickadee occupancy, abundance and logistic models of breeding activity.

Variable	Description
Site Variables	
IMPERVIOUS	Average % pavement on plots
BASAL	Total basal area of all trees
EXOTIC TREE‡	Importance value of all non-native trees
SHRUBS	Total sum of all shrubs
VOLUME	Total volume of all shrubs $\left[\frac{2\pi height\left(\frac{width}{2} * \frac{depth}{2}\right)}{3}\right]$†
EXOTIC SHRUB‡	Importance value of all non-native shrubs
PRODUCTIVITY	$\sum(Plant^{Basal\ area} * Plant^{Lepidoptera\ Index})$
STEMS	Total sum of tree stems
Detection Variables	
Date	Julian date
Time	Time of day the bird survey was conducted
Building	Average proportion of plot that was occupied by buildings
Trees	Number of trees at 1.4m

†: Thorne, M.S., Skinner, Q.D., Smith, M.A., Rodgers, J.D., Laycock, W.A., Cerekci, S.A., 2002. Evaluation of a Technique for Measuring Canopy Volume of Shrubs. Journal of Range Management 55, 235–241.

‡We designated trees and shrubs using the following criteria: trees were plants that were >1.4 m high (height at which dbh is taken). Shrubs were plants that were < 1.4m high OR contained more than 10 stems that

were <2cm in diameter. The later designation was used in order to accurately measure large ornamental hedges (e.g. privacy hedges such as *Buxus* sp., *Ilex crenata*, etc.) that are pruned for tall heights and dense stem densities but do not retain the same structure as trees.

Table A.2 Most preferred plant group by foraging chickadees at each site. Native tree groups were preferred in all but one site and nearly all native tree groups were highly productive according to the Tallamy and Shropshire (2009) index.

Site Name	Tree Group	Preference Value	Lepidoptera Index
badmd1	*Quercus* – native	0.65	532
bekva1	*Quercus* – native	0.29	532
blmmd1	*Acer* – native	0.24	297
bunva1	*Quercus* – native	0.34	532
budva1	*Carya* – native	0.18	235
cagmd1	*Quercus* – native	0.11	532
cokmd1	*Acer* – native	0.15	297
crcva2	*Quercus* – native	0.19	532
dekva1	*Quercus* – native	0.24	532
edeva1	*Acer* – native	0.09	297
eglva1	*Acer* – native	0.46	297
evmmd1	*Quercus* – native	0.68	532
fifva1	*Prunus* – native	0.75	456
gecva1	*Acer* – unknown	0.13	297
hujva1	*Quercus* – native	0.31	532
kakdc1	*Metasequoia* – nonnative	0.30	0
lihmd1	*Quercus* – native	0.40	532
owdva1	*Quercus* – native	0.21	532
piedc1	*Quercus* – native	0.78	532
raamd1	*Quercus* – native	0.30	532
raemd2	*Acer* – native	0.27	297
rucmd1	*Quercus* – native	0.48	532
sammd1	*Quercus* – native	0.33	532
scmmd1	*Quercus* – native	0.13	532
stbmd1	*Pinus* – native	0.08	201
stcmd1	*Quercus* – native	0.20	532
taldc1	*Ulmus* – native	0.23	215
vojmd1	*Quercus* – native	0.26	532
wismd1	*Platanus* – native	0.15	45
wicmd1	*Quercus* – native	0.22	532
yokva1	*Quercus* – native	0.36	532

Table A.3 Top ranked models (ΔAIC<2) of local variables that predict Carolina chickadee detection during point counts in residential backyards in the Washington, D.C. area. Detection of nesting is assumed to be 1.

Analysis	Model	K	AIC	ΔAIC	Weight	Cumulative Weight
Chickadee Occupancy	psi(.), p(.)	3	234.73	0.00	0.26	0.26
	psi(.), p(BUILDING)	2	235.24	0.51	0.20	0.45
	psi(.), p(DATE)	4	235.44	0.86	0.18	0.63
	psi(.), p(BUILDING + DATE)	3	236.04	1.14	0.13	0.77
	psi(.), p(TIME)	4	236.73	1.99	0.09	0.86
Chickadee Abundance	psi(.), p(BUILDING)	3	419.44	0.00	0.43	0.43
	psi(.), p(BUILDING +TIME)	4	419.91	0.47	0.34	0.76
	psi(.), p(BUILDING + DATE)	4	421.04	1.60	0.19	0.95

Table A.4 Top ranked models (ΔAICc<4) of local variables that predict Carolina chickadee occupancy, abundance and breeding activity in residential backyards in the Washington, D.C. area.

Analysis	Model	K	AIC	ΔAIC	Weight	Cumulative Weight
Chickadee Occupancy	psi(.), p(BASAL + PAVEMENT)	4	219.39	0.00	0.28	0.28
	psi(.), p(BASAL + EXOTIC TREE)	4	219.47	0.07	0.27	0.56
	psi(.), p(BASAL)	3	221.80	2.41	0.09	0.64
	psi(.), p(BASAL+STEMS)	4	222.09	2.70	0.07	0.72
	psi(.), p(BASAL+VOLUME)	4	223.22	3.82	0.04	0.76
Chickadee Abundance	psi(BUILDING), p(IMPERVIOUS + BASAL)	5	394.62	0.00	0.49	0.49
	psi(BUILDING), p(IMPERVIOUS + STEMS)	5	396.73	2.11	0.17	0.66
	psi(BUILDING), p(BASAL + EXOTIC TREE)	5	398.34	3.72	0.08	0.74
Chickadee Breeding Activity	EXOTIC TREE + SHRUBS	3	109.62	0.00	0.31	0.31
	EXOTIC TREE + EXOTIC SHRUB	3	111.01	1.39	0.15	0.46
	EXOTIC TREE	2	111.08	1.46	0.15	0.60
	EXOTIC TREE + IMPERVIOUS	3	112.08	2.46	0.09	0.69
	EXOTIC TREE + VOLUME	3	112.53	2.91	0.07	0.77
	EXOTIC TREE + PRODUCTIVITY	3	112.63	3.01	0.07	0.83
	EXOTIC TREE + STEMS	3	112.96	3.34	0.06	0.89
	EXOTIC TREE + BASAL	3	113.19	3.57	0.05	0.94

Table A.5 Relative importance for variables used in AIC model selection for each model type. ***** indicates the variable with the most weight across all ranked models. Model averaged estimate of the highest weighted variable across all models <4 ΔAIC.

Model	BASAL	EXOTIC SHRUB	EXOTIC TREE	IMPERVIOUS	PRODUCTIVITY	SHRUB	VOLUME	STEMS
Occupancy	0.87*	0.04	0.32	0.35	0.08	0.06	0.06	0.10
Abundance	0.72	0.04	0.10	0.75*	0.09	0.02	0.02	0.21
Breeding	0.07	0.20	0.95*	0.10	0.08	0.32	0.08	0.07

Model	Top Variable	β (± SE)	95% Confidence Interval
Occupancy	BASAL	1.47 (± 0.64)	0.21, 2.73
Abundance	IMPERVIOUS	-0.32 (± 0.12)	-0.55, -0.08
	BASAL	0.34 (± 0.10)	0.14, 0.53
Breeding	EXOTIC TREE	-0.90 (± 0.30)	-1.49, -0.30

FIGURES

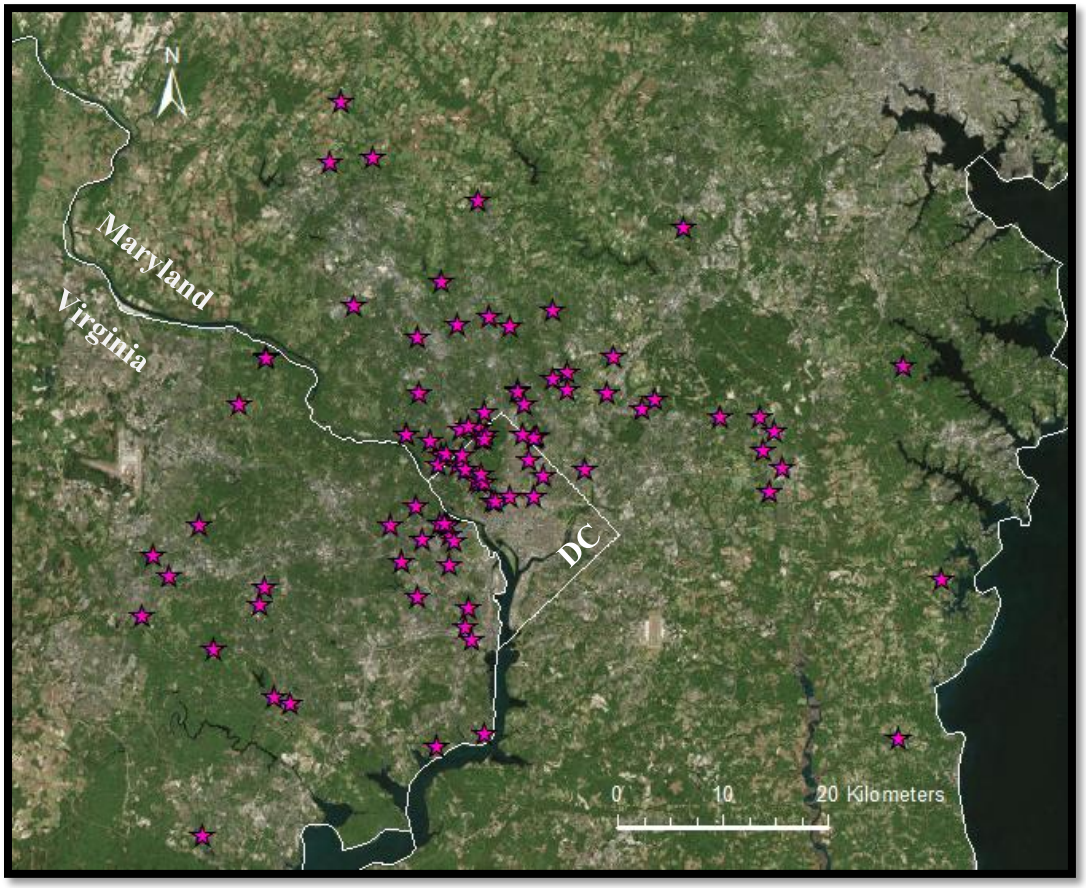


Figure A.1 A map of locations of study sites in and around the DC metropolitan area. Focal sites for bird surveys included the focal yard, and residential areas within a 50m-radius of the bird survey point.

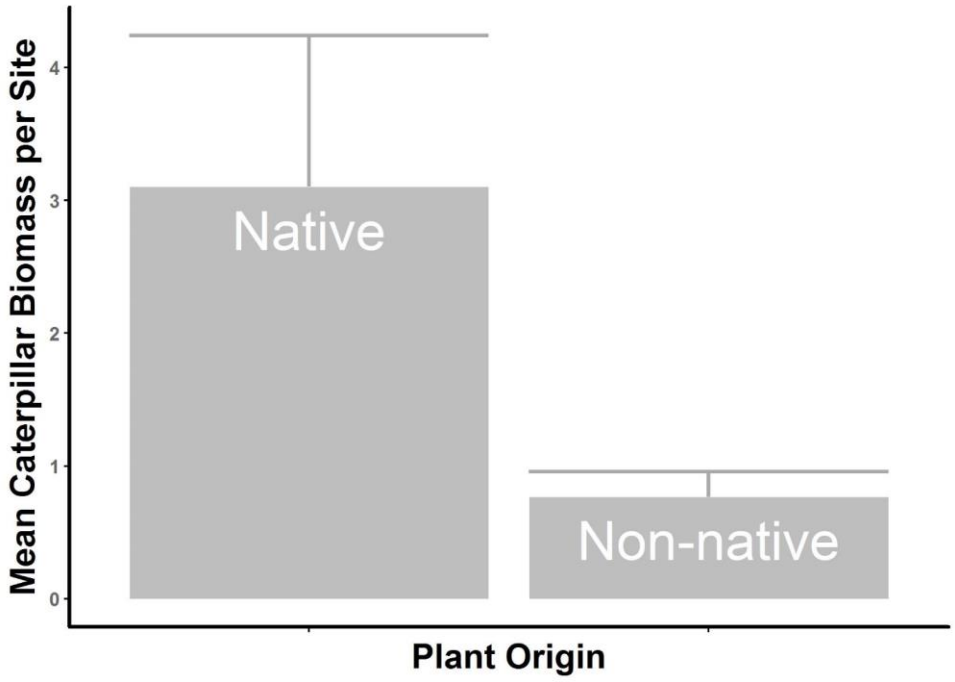


Figure A.2 Comparison between mean (± SE) biomass of caterpillars (grams) of native and non-native trees at 53 sites (Wilcoxon signed rank test: v=1218, p=0.005.

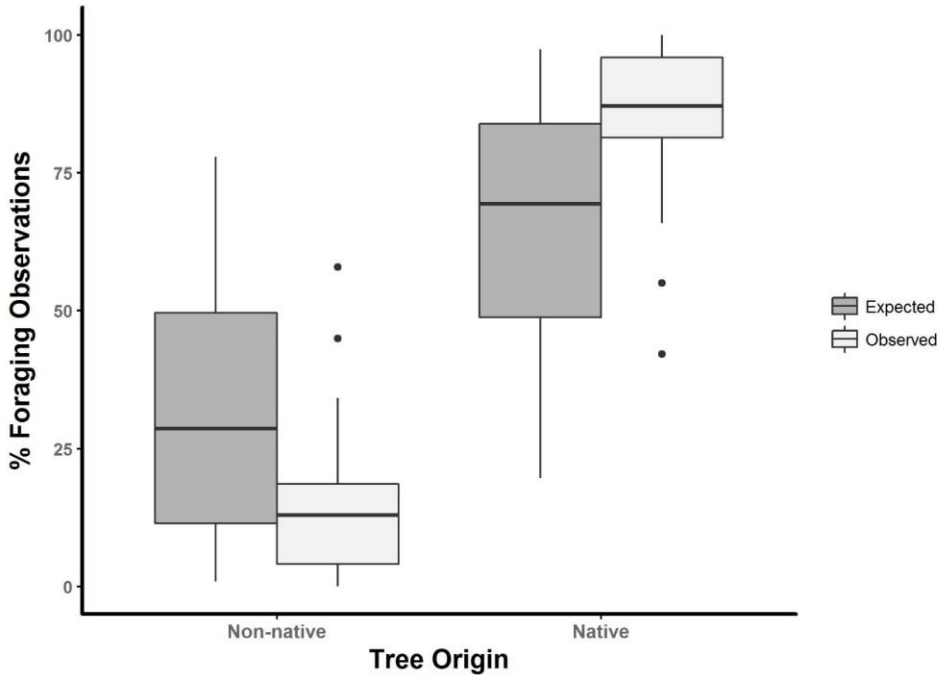


Figure A.3 Comparison between expected and observed mean (± SD) chickadee foraging observations for native and non-native plants (Fisher's Test: chi-square = 1636.08, $p<0.001$).

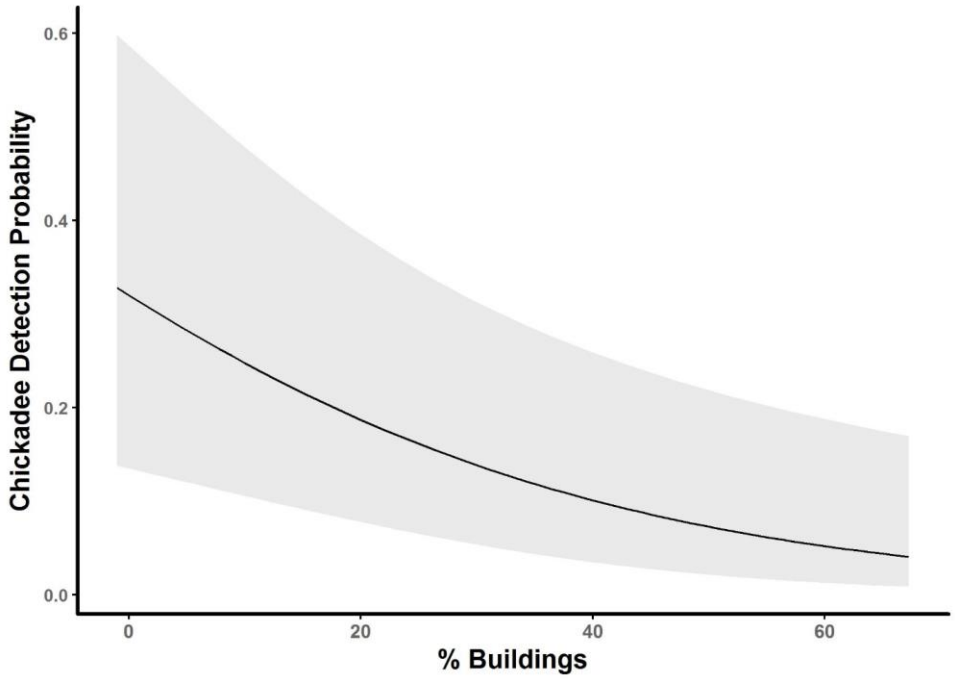


Figure A.4 Relationship between detection of abundance and average percent building. Detection strongly declines as percent building at a local scale increases (β -0.39 ± 0.14, CI: -0.67,-0.12).

Figure A.5 Diagram of plant, caterpillar and bird data collected at one site in Washington D.C. Study site included the focal yard that hosted the chickadee nesting tube (bird icon), the center of the point count survey (star), as well as a 50-m radius area (0.79 Ha) that encompassed neighboring yards (white circle). During bird surveys, all birds within 50m were counted. The caterpillar icons represent locations where plant species were chosen for caterpillar sampling. Green circles represent randomly selected woody plant community plots. Areas in purple represent foraging locations of the pair of chickadees breeding in the nesting tube.

Appendix B

SUPPLEMENTARY MATERIALS FOR CHAPTER 3

TABLES

Table B.1 Statistics for each component in the best fit aster model that included the nonnative plant term. Effects for each node are independent of the effects of earlier nodes. β coefficients, standard error of coefficients and z-values for the predictors are from the aster model (values for nonnative plants are from the final aster model). Deviance, degrees of freedom and p-values are from the likelihood ratio test. Models in italics represent the full aster model including all reproductive components.

Factor	Aster model components	β ± SE	z	deviance	df	p-value
Nonnative Plants	*Reproduction Success*	*-0.31 ± 0.06*	*-5.55*	*25.44*	*10*	*p<0.001*
	Settlement	-3.31 ± 0.64	5.19	30.19	6	p<0.001
	Breeding	-2.50 ± 0.77	-3.24	10.93	7	p<0.001
	Number of eggs	-0.09 ± 0.21	-0.43	0.18	7	p>0.1
	Nest survival	-1.70 ± 0.97	-1.76	3.88	7	p=0.07
	# of fledglings	-0.28 ± 0.29	-0.95	0.90	7	p>0.1
Foliage Biomass	*Reproductive Success*	*0.00* ± 0.01	*-0.08*	*0.01*	*1*	*p>0.1*
Year	*Reproductive Success*	-	-	*6.42*	*10*	*p=0.09*
	2014	-0.04 ± 0.03	-1.27			p>0.1
	2015	-0.06 ± 0.03	-2.32			p=0.02
	2016	-0.06 ± 0.03	-2.16			p=0.03

FIGURES

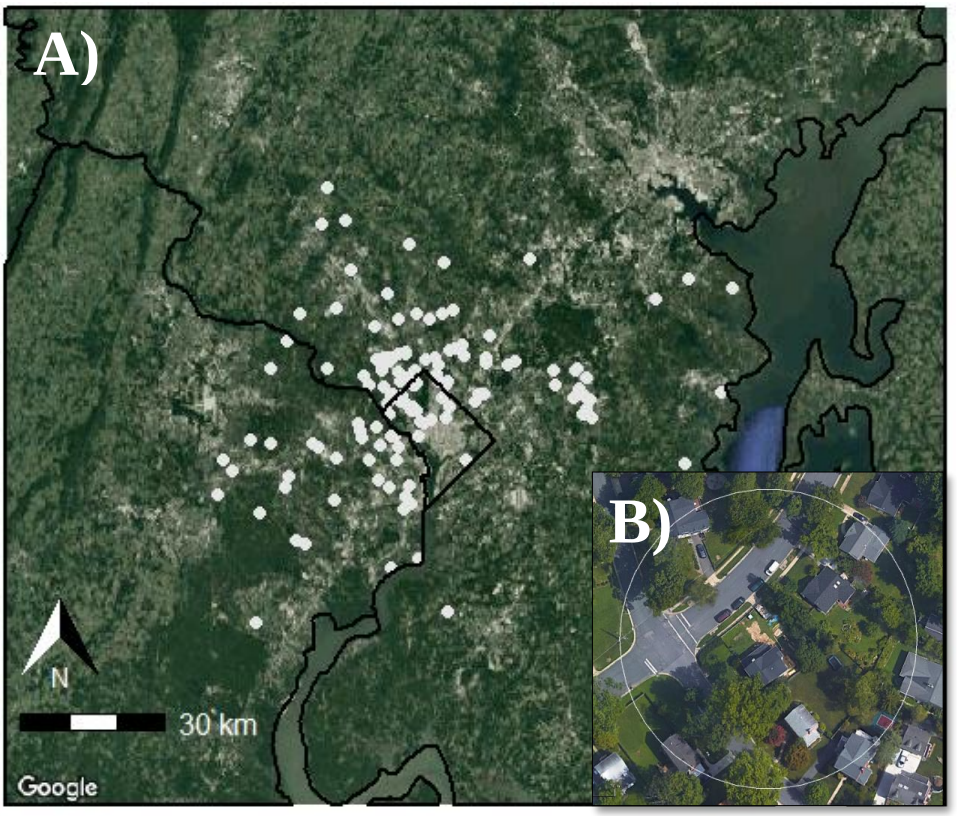


Figure B.1 Map of the entire study area and detailed location of one study site. (A) Chickadees were monitored at 159 sites over the Washington D.C. metropolitan area which included the District of Columbia, Maryland and Northern Virginia. (B) Each site consisted of the volunteering homeowner's property and a 50-m radius area around the house (white circle). A 50-m radius was chosen because this area is approximately the territory size of breeding chickadees (*28*).

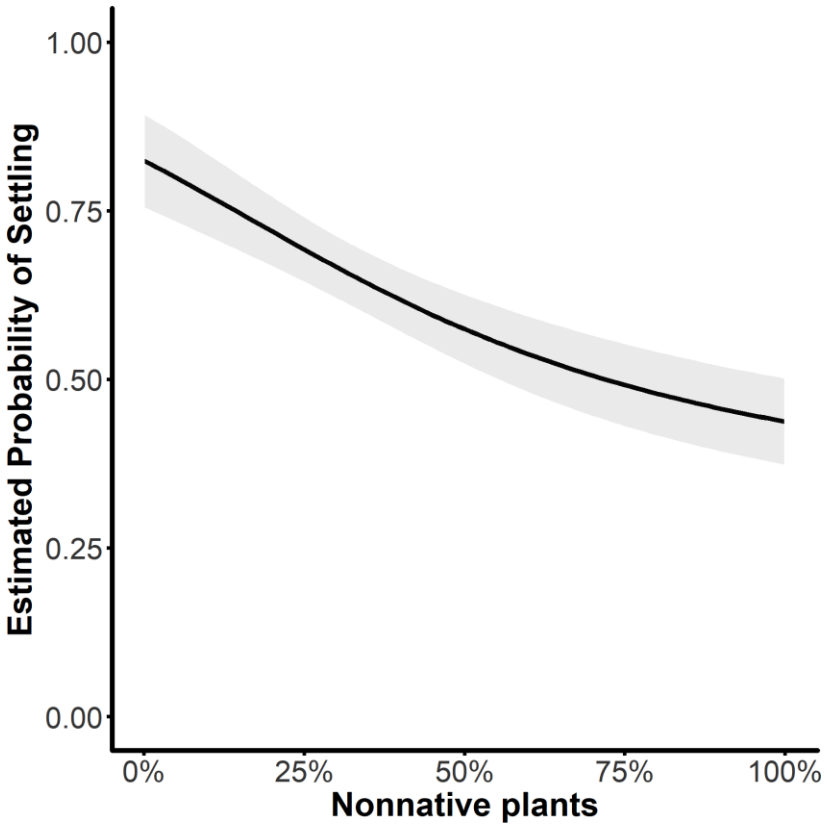


Figure B.2 Predicted probability of settling (i.e. site occupancy during the breeding season) declined across a gradient of nonnative plants.

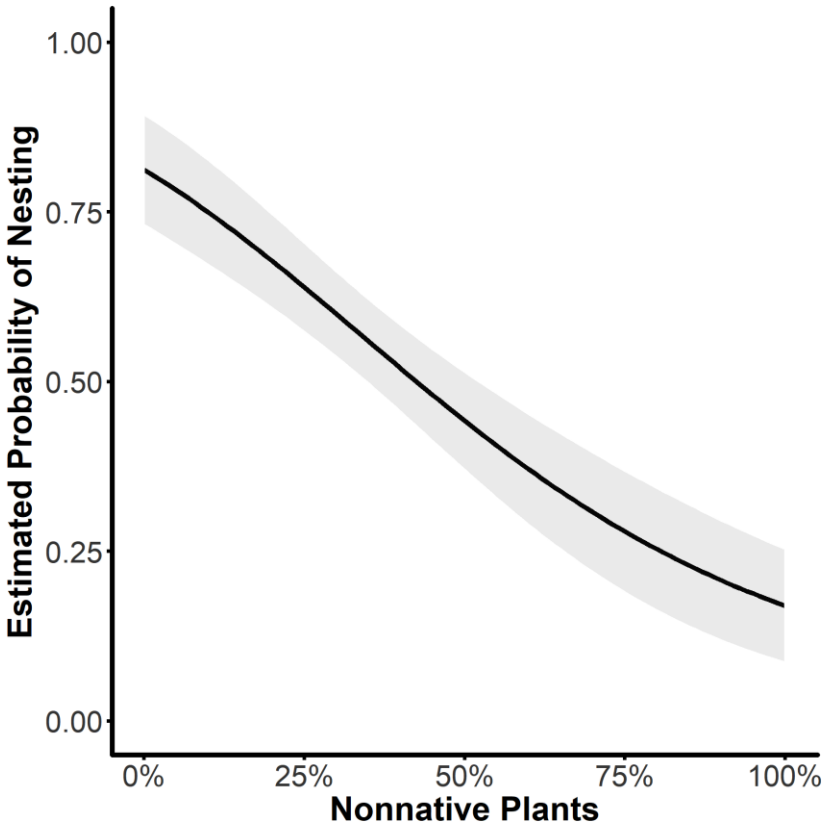


Figure B.3 Predicted probability of nesting (conditional on chickadees being occupying the site) declined across a gradient of nonnative plants.

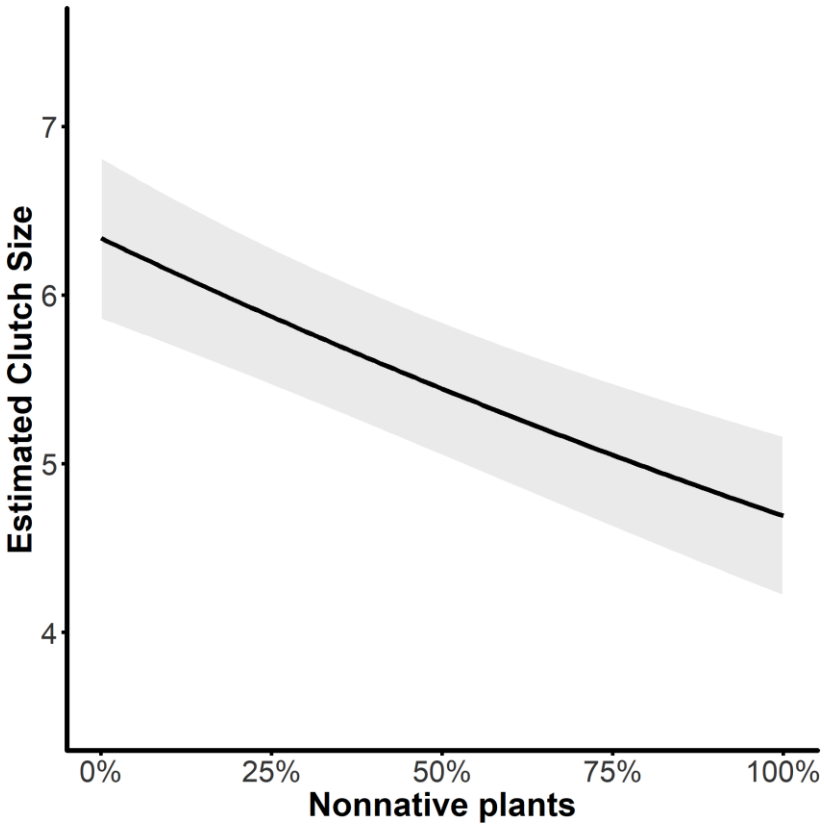


Figure B.4 Predicted clutch size (conditional on nesting) declined across a gradient of nonnative plants.

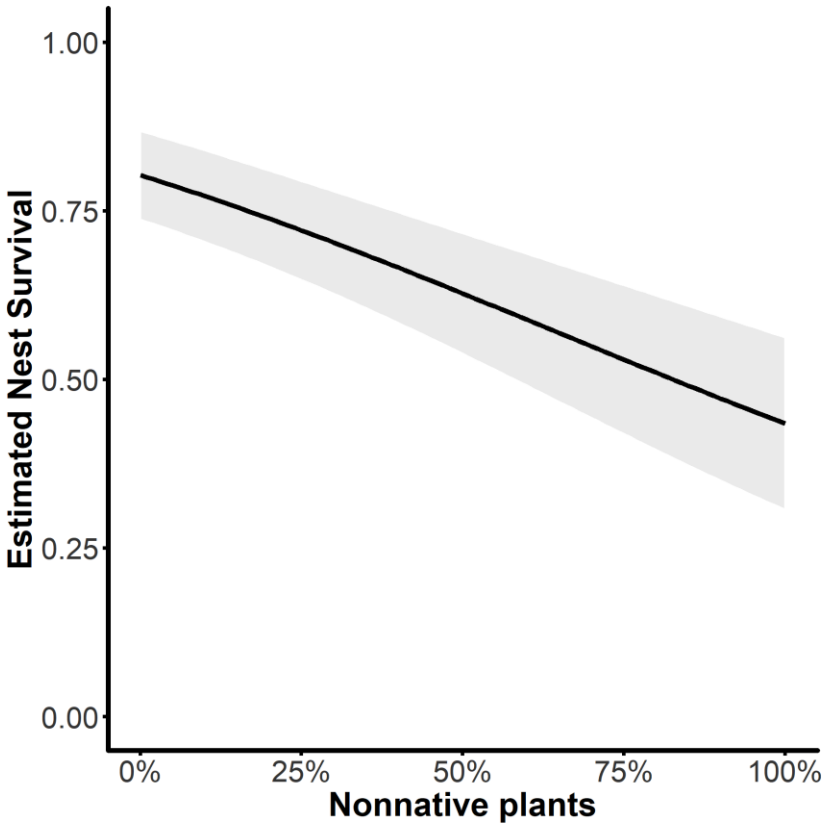


Figure B.5 Predicted probability of nest survival (conditional on chickadees laying eggs) declined across a gradient of nonnative plants.

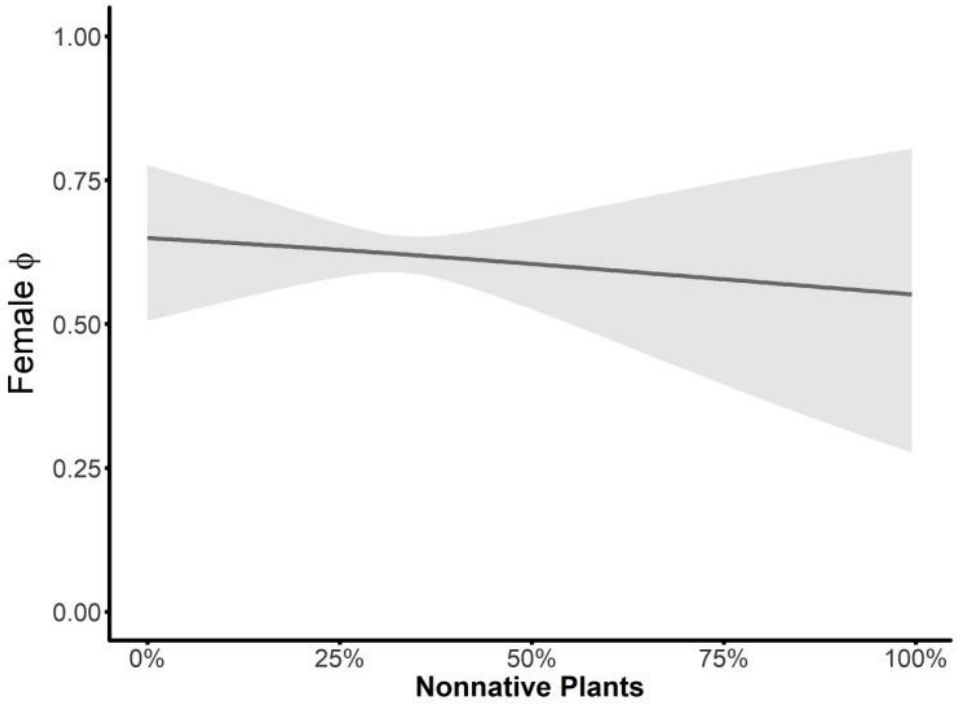


Figure B.6 Predicted apparent annual survival (φ) of female chickadees across a gradient of nonnative plants from a CJS model of survival accounting for detection. The dark line represents mean survival and gray shading shows 95% credible interval. Large uncertainty at high proportions of nonnative plants is due to low sample sizes of individuals occupying these sites.

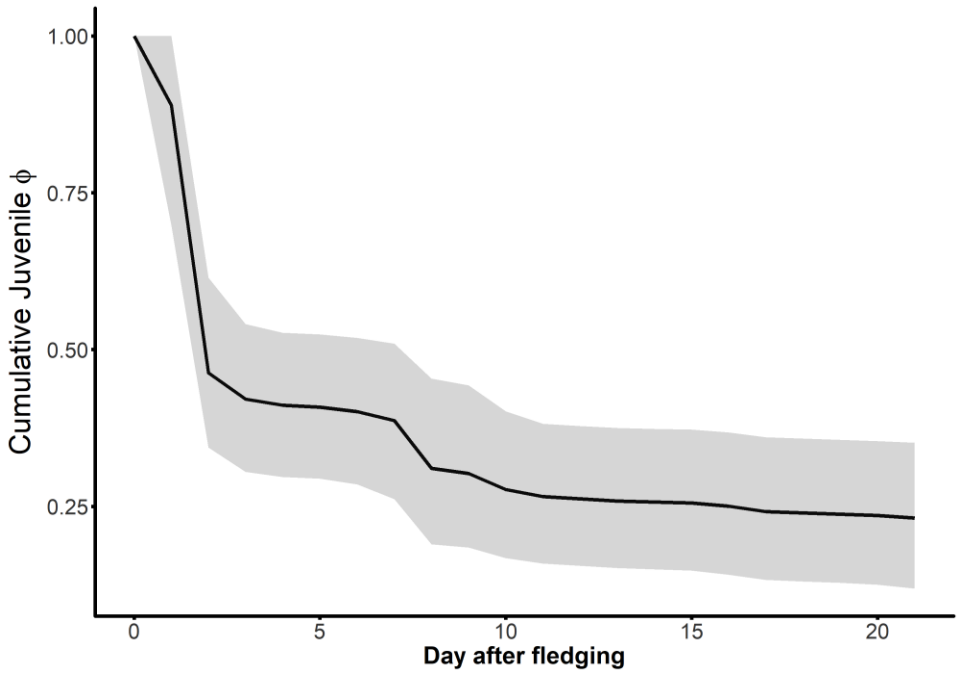


Figure B.7 Cumulative chickadee juvenile survival during the length of the fledgling period prior to independence (21 days). Line represents mean survival and the gray shading shows the 95% credible interval. The majority of mortality happened within the first three days of fledgling with modest declines occurring from day 4 to 21. For the population growth simulation we used the confidence interval of cumulative juvenile survival at day 21 (range: φ 0.13-0.35).

Appendix C

SUPPLEMENTARY MATERIALS FOR CHAPTER 5

INDIVIDUAL BIRD SPECIES ANALYSIS

Carolina Chickadee

For chickadees, we sampled 51 individuals; 20 before the nitrogen treatment and 30 following treatment. Accounting for site, there was a significant interaction between treatment and sampling period, such that chickadees had higher ^{15}N values after treatment, but only at the native treated sites (β -0.77 ± 0.26, LRT: p=0.009, appendix figure C.1).

Our diet mixing model revealed that chickadees in native-treated yards incorporated higher proportions of nitrogen from treated trees compared to nonnative treated yards. (Native treatment: 0.010 ± 0.002, CI: 0.006, 0.014; Nonnative treatment: 0.002 ± 0.001, CI: 0.000, 0.005, appendix figure C.2a). The distribution of differences between native and nonnative-treated yards was positive and did not overlap zero (appendix figure C.2b).

House Wren

We sampled 51 house wren individuals; 12 before the nitrogen treatment and 39 following treatment. The $\delta^{15}N$ of house wrens increased in both treatments (β 2.10

± 1.07, t=1.96, p=0.05, appendix figure C.3). There was a weak, but non-significant decline in enrichment in the nonnative-treated yards (β -1.09 ± 0.73, LRT: p=0.39).

Our mixing model showed that wrens in native-treated yards had higher proportions of enriched nitrogen compared to nonnative treated yards. (Native treatment: 0.015 ± 0.003, CI: 0.009, 0.023; Nonnative treatment: 0.006 ± 0.002, CI: 0.002, 0.011, appendix figure C.4a). The distribution of differences between native and nonnative-treated yards was positive and the 95% confidence interval did not overlap zero (appendix figure C.4b).

American Robin

We sampled 35 robins; 11 before the nitrogen treatment and 24 following treatment. Although many more robins were captured and bled, high turnover and low site fidelity prevented more samples from being processed. There was a significant increase in $\delta^{15}N$ of robins in both treatments (β 1.22 ± 0.54, t=2.26, p=0.03, appendix figure C.5), however there was no difference in the slopes between treatments (β -0.30± 0.34, LRT: p=0.39).

Our mixing model showed that robins in native-treated yards had higher proportions of enriched nitrogen compared to nonnative treated yards. (Native treatment: 0.012 ± 0.003, CI: 0.008, 0.019; Nonnative treatment: 0.004 ± 0.002, CI: 0.000, 0.009, appendix figure C.6a). The distribution of differences between native and nonnative-treated yards was positive and the 95% confidence interval did not overlap zero (appendix figure C.6b).

Gray Catbird

We sampled 32 gray catbirds; 16 before the nitrogen treatment and 21 following treatment. There was no change in $\delta^{15}N$ of catbirds (β 0.77 ± 0.69, t=1.11, p=0.27, appendix figure C.7), nor a difference in the slopes between treatments (β -0.10± 0.46, LRT: p=0.83).

Our mixing model showed that catbirds in native-treated yards tended to have higher proportions of enriched nitrogen compared to nonnative treated yards (Native treatment: 0.012 ± 0.003, CI: 0.008, 0.019; Nonnative treatment: 0.006 ± 0.002, CI: 0.000, 0.011, appendix figure C.8a). However, the 95% confidence interval of distribution of predicted differences between native and nonnative-treated yards overlapped zero (appendix figure C.8b).

Northern Cardinal

We processed samples from 30 cardinals; 13 prior to treatment and 17 after treatment. In both treatments, the $\delta^{15}N$ of cardinals significantly increased (β 1.29 ± 0.51, t=2.54, p=0.02, appendix figure C.9). There was a weak, but nonsignificant decline in the slope of enrichment in nonnative-treated yards (β -0.79 ± 0.52, LRT: p=0.14).

Our mixing model showed that cardinals in native-treated yards tended to have higher proportions of enriched nitrogen compared to nonnative treated yards (Native treatment: 0.012 ± 0.003, CI: 0.008, 0.017; Nonnative treatment: 0.006 ± 0.002, CI: 0.002, 0.010, appendix figure C.10a). The 95% confidence interval of distribution of predicted differences between native and nonnative-treated yards did not overlap zero (appendix figure C.10b).

Song Sparrow

We processed 30 samples of song sparrows; 14 pre-treatment, and 16 post-treatment. Following the treatment, $\delta^{15}N$ of sparrow blood was significantly higher (β 0.74 ± 0.32, t=2.29, p=0.03, appendix figure C.11). Sparrows were significantly more enriched in native-treated compared to nonnative-treated sites (β 0.65 ± 0.29, t=2.25, p=0.03).

The proportion of diet derived from enriched plants was higher in native-treated yards compared to nonnative-treated yards (Native treatment: 0.012 ± 0.002, CI: 0.008, 0.017; Nonnative treatment: 0.006 ± 0.002, CI: 0.002, 0.011, appendix figure C.12a). The 95% confidence interval of distribution of predicted differences between native and nonnative-treated yards did not overlap zero (appendix figure C.12b).

TABLES

Table C.1 Sample sizes for each bird species across the 24 experimental sites.

		Species (control samples/enriched samples)							
Site	**Treatment**	**Carolina chickadee**	**Tufted Titmouse**	**House wren**	**Carolina wren**	**American robin**	**Northern cardinal**	**Gray catbird**	**Song sparrow**
Diamd1	Native	1/3	0/1	0/3	0/0	1/0	2/3	1/2	0/1
Docmd1	Native	3/0	0/0	2/4	1/0	2/1	1/0	2/2	1/4
Fimmd1	Native	2/1	0/0	0/3	0/0	1/6	1/0	0/0	0/0
Fifva1	Nonnative	0/3	0/0	1/1	0/0	0/0	0/1	0/1	0/0
Fodmd1	Nonnative	1/2	0/1	1/2	0/0	3/0	1/2	3/0	1/0
Galmd1	Nonnative	2/0	0/0	0/0	0/0	2/4	0/0	1/2	1/1
Gunmd1	Nonnative	1/1	1/3	1/2	0/0	0/0	1/2	4/4	1/0
Jelmd1	Nonnative	0/1	0/1	0/1	0/0	0/0	0/0	0/1	1/0
Kosmd1	Nonnative	0/3	0/0	0/1	0/0	0/2	1/0	0/0	2/3
Malmd1	Nonnative	0/1	0/0	0/1	0/2	0/1	1/2	2/2	0/1
Mapmd2	Nonnative	1/0	0/0	2/2	0/3	1/1	0/1	2/2	0/0
Mijmd1	Nonnative	0/4	1 /2	0/2	0/1	0/3	0/1	0/0	0/0
Napmd1	Native	0/5	1/ 2	0/0	0/0	0/0	3/4	0/0	0/0
Opjmd1	Native	0/1	0/0	0/1	0/0	0/0	0/1	0/3	0/0
Ribmd1	Native	1/1	0/0	0/2	0/0	0/0	0/0	0/0	1/0
Rojmd1	Native	0/0	0/0	0/2	0/0	0/0	1/0	0/1	1/0
Salmd1	Nonnative	0/1	0/1	1/0	0/2	0/0	0/0	0/0	0/0
Shemd1	Native	3/0	0/1	1/0	0/0	0/0	0/0	0/1	1/2
Sismd1	Native	0/0	0/0	2/1	0/0	0/1	0/0	0/0	1/0
Sidmd1	Native	1/0	1/0	1/1	0/0	0/0	1/1	0/0	0/0
Spmmd1	Native	2/0	0/0	0/0	0/0	0/0	0/0	0/0	0/1
Stbmd1	Nonnative	1/2	0/0	0/4	0/0	0/1	0/0	0/0	2/1
Thbmd1	Native	0/0	0/0	0/2	0/0	0/0	0/0	0/0	0/1
Wicmd1	Nonnative	1/1	0/0	0/2	0/0	2/3	0/1	1/0	0/1

Table C.2 List of plant species used for ^{15}N enrichment at the native and nonnative treated sites.

Native Plants		**Nonnative Plants**	
Common name	Scientific name	Common name	Scientific name
American Beech	*Fagus grandifolia*	Autumn Olive	*Elaeagnus umbellata*
Black Cherry	*Prunus serotine*	Bamboo	*Phyllostachys sp.*
Black Gum	*Nyssa sylvatica*	Bradford Pear	*Pyrus calleryena*
Carolina Snowbell	*Halesia Carolina*	Burning Bush	*Euonymus alatus*
Flowering Dogwood	*Cornus florida*	Bush Honeysuckle	*Lonicera maackii*
Fringetree	*Chionanthus virginicus*	Cherry Plum	*Prunus cerasifera*
Gray birch	*Betula populifolia*	Chinese Chestnut	*Castanea mollissima*
Honey Locust	*Gleditsia triacanthos*	Chinese Elm	*Ulmus parvifolia*
Ironwood	*Carpinus caroliniana*	Chinese Witchhazel	*Hamamelis mollis*
Northern Red Oak	*Quercus rubra*	Crape Myrtle	*Lagerstroemia sp.*
Pin Oak	*Quercus palustris*	Forthysia	*Forthysia sp.*
Red Maple	*Acer rubrum*	Fragrant Snowbell	*Styrax obassia*
Redbud	*Cercis Canadensis*	Japanese Cherry	*Prunus serrulata*
River Birch	*Betula Nigra*	Japanese Cherry	*Prunus x yedoensis*
Serviceberry	*Amelanchier sp.*	Japanese Maple	*Acer palmatum*
Silver Maple	*Acer saccharinum*	Japanese Silverbell	*Styrax japonicus*
Spicebush	*Lindera benzoin*	Japanese snowball	*Viburnum plicatum*
Sugar Maple	*Acer saccharum*	Katsura Tree	*Cercidiphyllum japonicum*
Sweetgum	*Liquidambar styraciflua*	Kousa Dogwood	*Cornus kousa*
Tulip poplar	*Liriodendron tulipifera*	Norway Maple	*Acer platanoides*
Southern Arrowwood	*Viburnum dentatum*	Persian Ironwood	*Parrotia persica*
Swamp White Oak	*Quercus bicolor*	Saucercup Magnolia	*Magnolia x soulangeana*
White Oak	*Quercus alba*	Star magnolia	*Magnolia stellata*
Willow Oak	*Quercus phellos*	Weeping Cherry	*Prunus pendula*
		White Mulberry	*Morus alba*
		Zelkova	*Zelkova serrata*

FIGURES

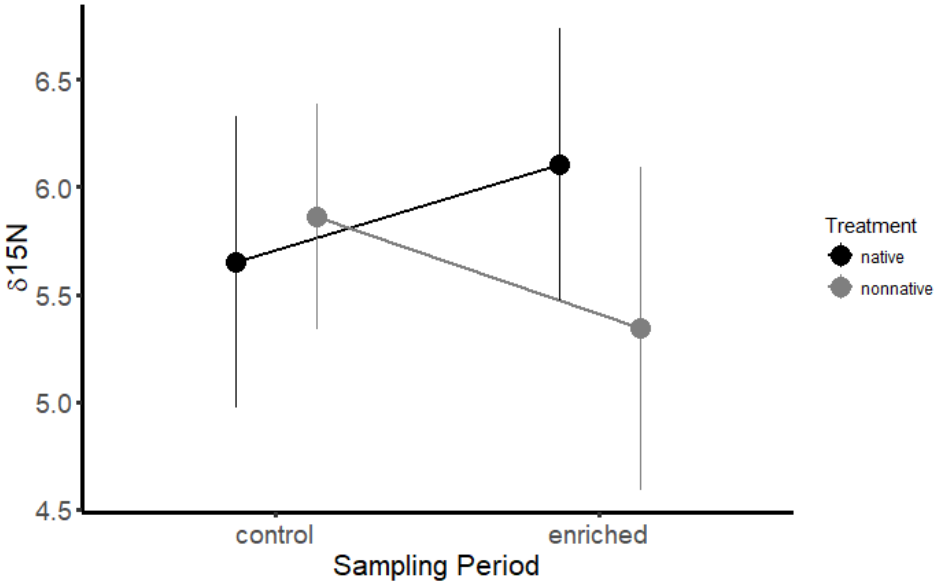


Figure C.1 Mean (± SD) blood ^{15}N in chickadees from native-treated (black) and nonnative-treated (gray) yards before (control) and after (enriched) application of the foliar isotope tracer.

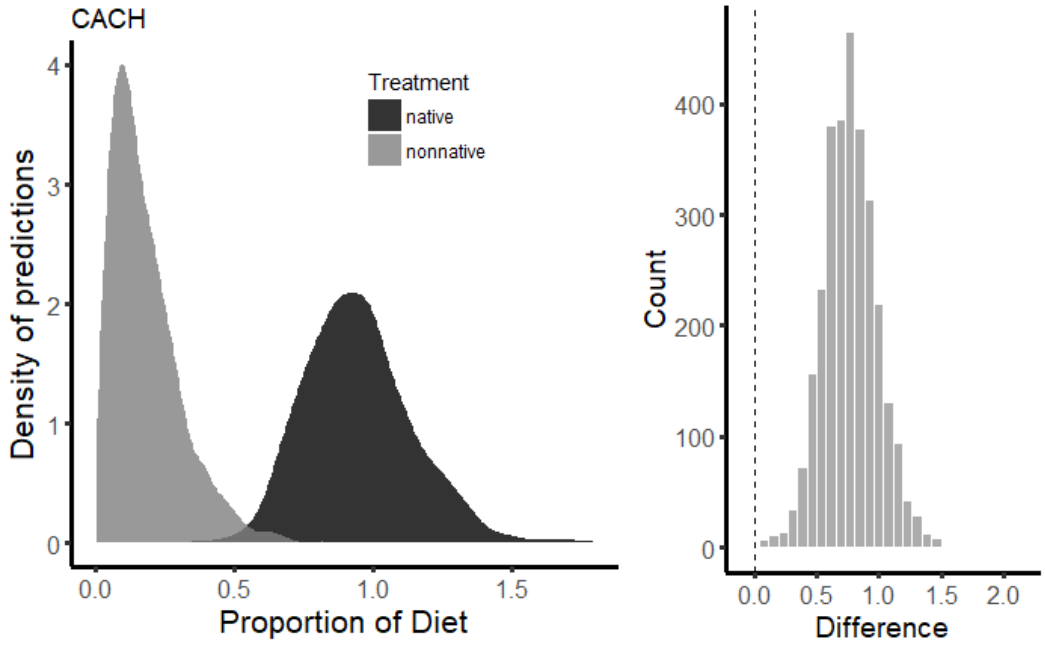


Figure C.2 (A) Posterior probability density of predicted proportion of enriched diet in chickadee blood between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

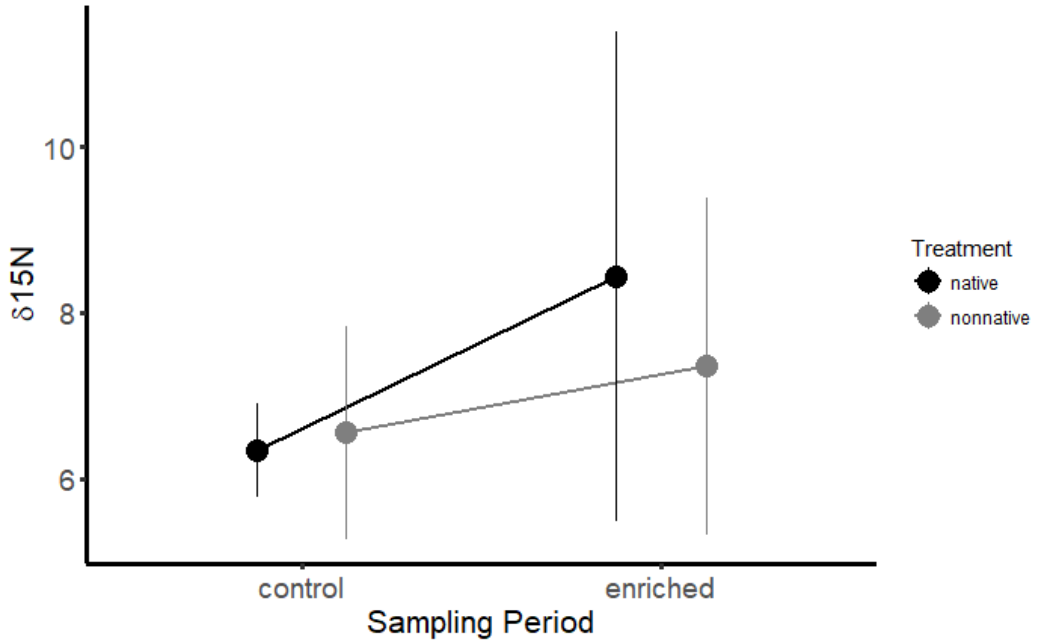


Figure C.3 Mean (± SD) blood ^{15}N in wrens from native-treated (black) and nonnative-treated (gray) yards before (control) and after (enriched) application of the foliar isotope tracer.

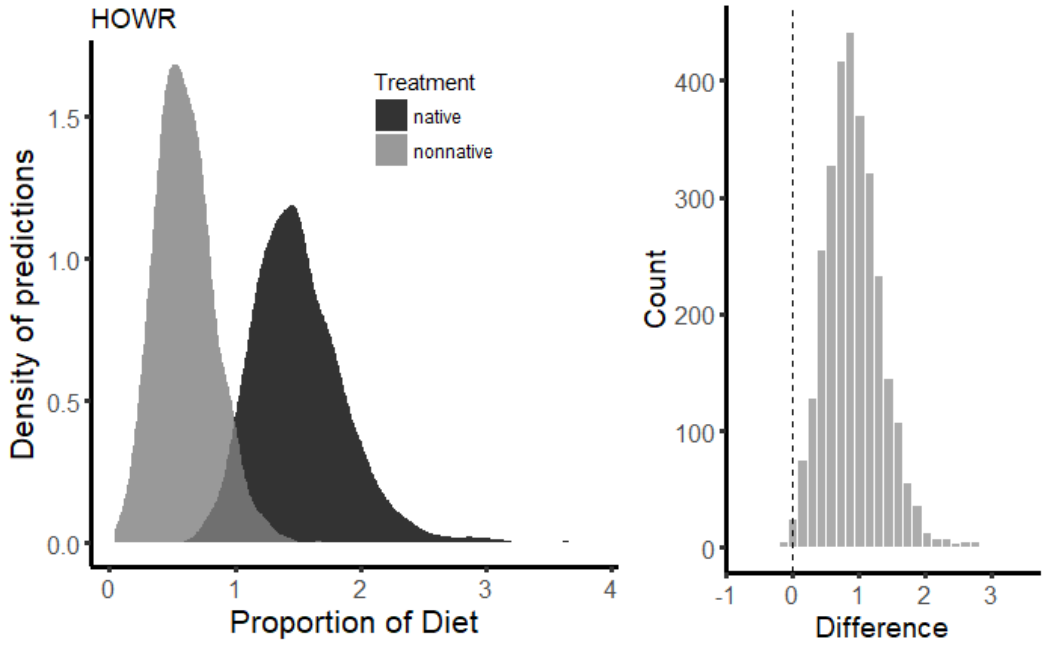


Figure C.4 (A) Posterior probability density of predicted proportion of enriched diet in wren blood between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

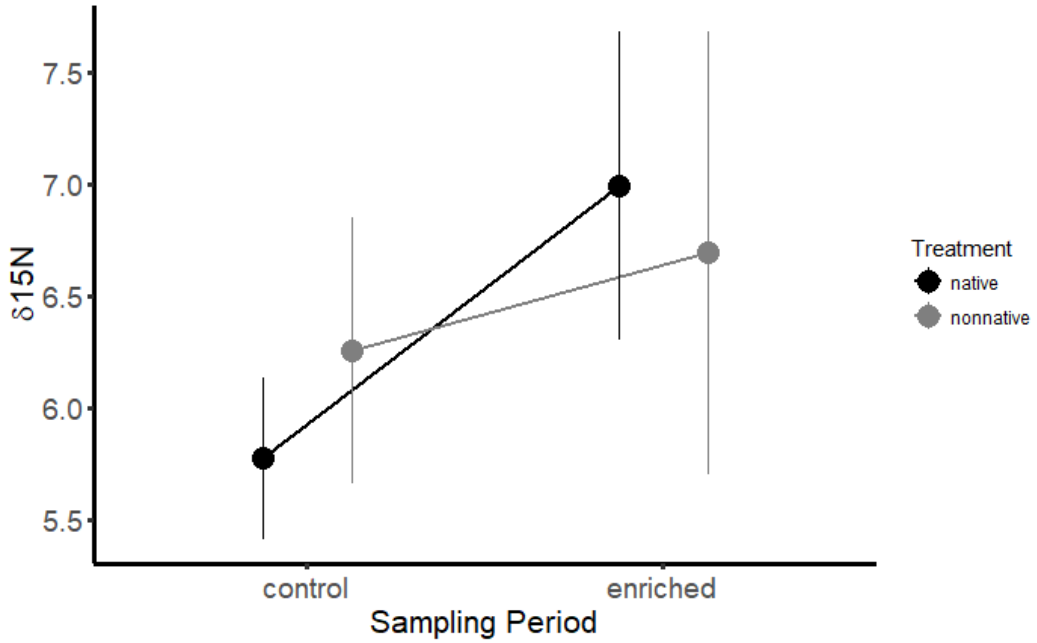


Figure C.5 Mean (± SD) blood ^{15}N in robins from native-treated (black) and nonnative-treated (gray) yards before (control) and after (enriched) application of the foliar isotope tracer.

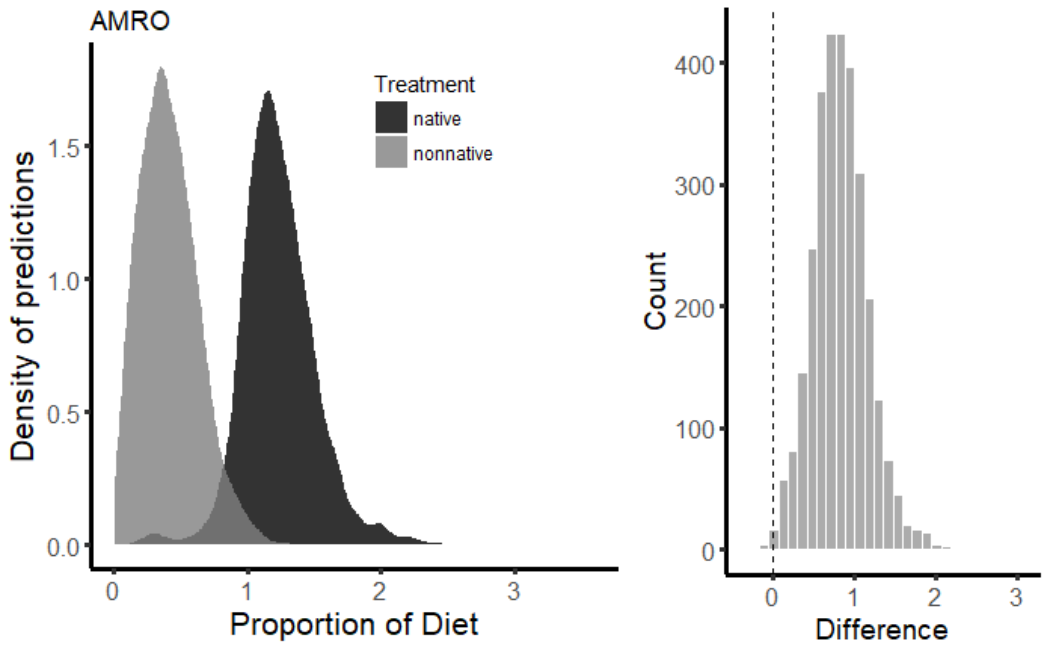


Figure C.6 (A) Posterior probability density of predicted proportion of enriched diet in robin blood between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

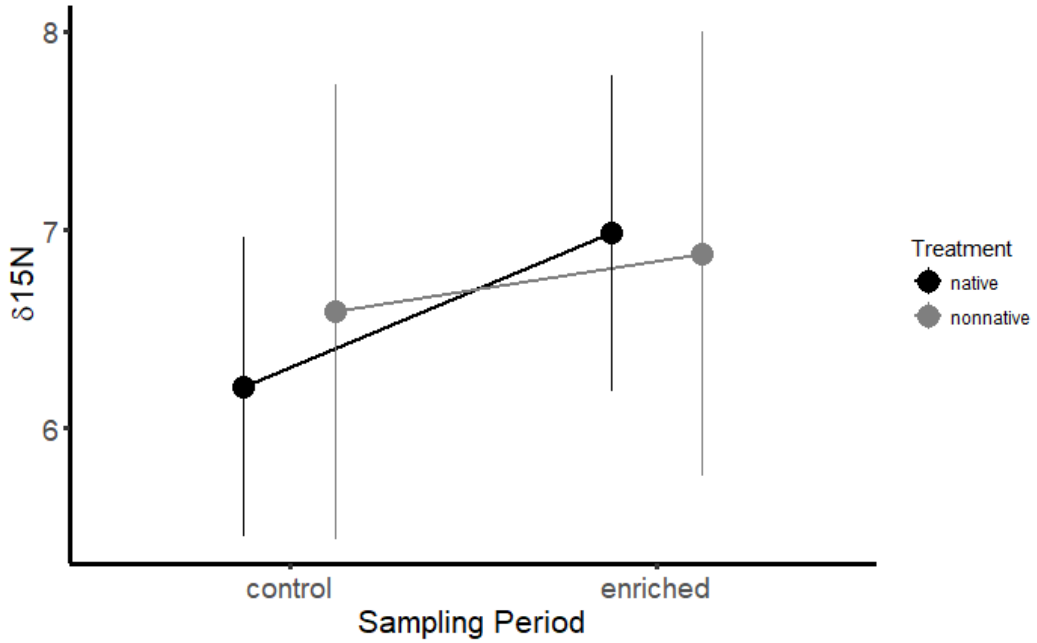


Figure C.7 Mean (± SD) blood ^{15}N in catbirds from native-treated (black) and nonnative-treated (gray) yards before (control) and after (enriched) application of the foliar isotope tracer.

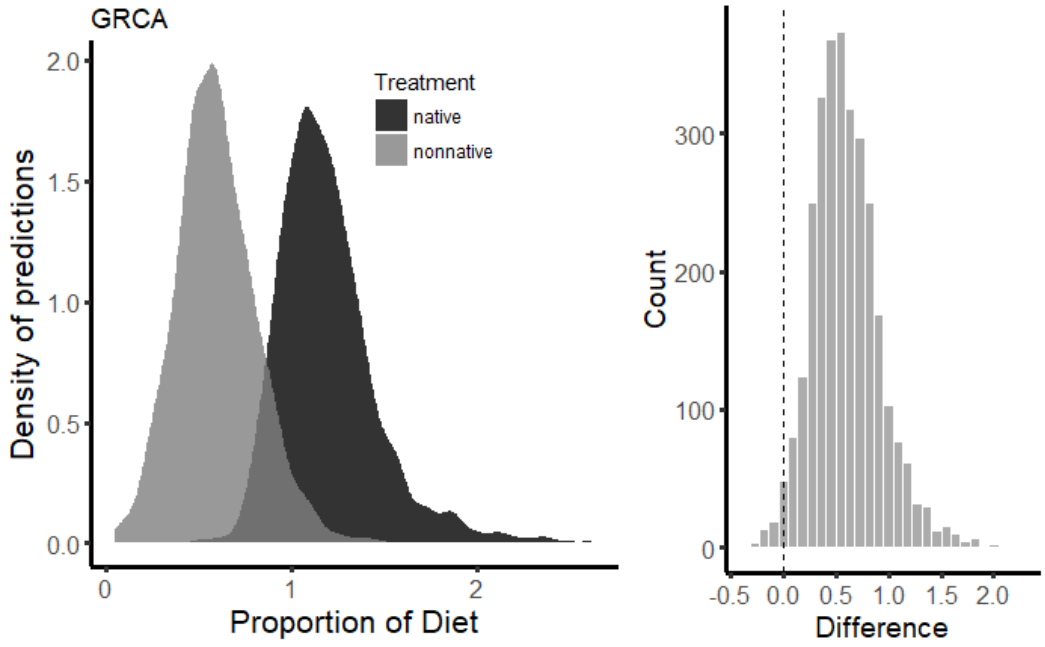


Figure C.8 (A) Posterior probability density of predicted proportion of enriched diet in catbird blood between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

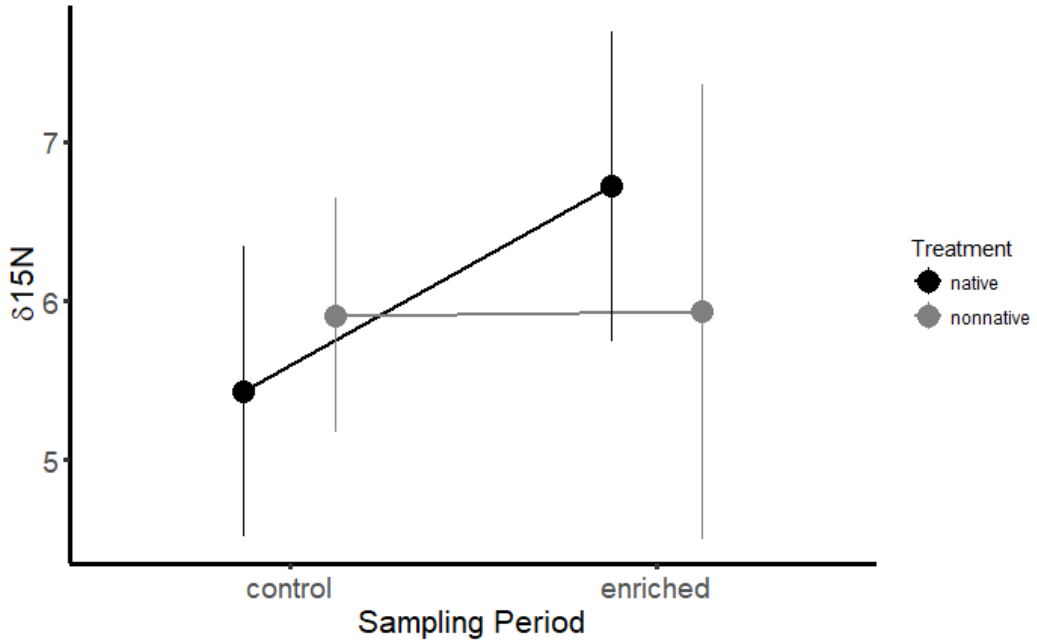


Figure C.9 Mean (± SD) blood ^{15}N in cardinals from native-treated (black) and nonnative-treated (gray) yards before (control) and after (enriched) application of the foliar isotope tracer.

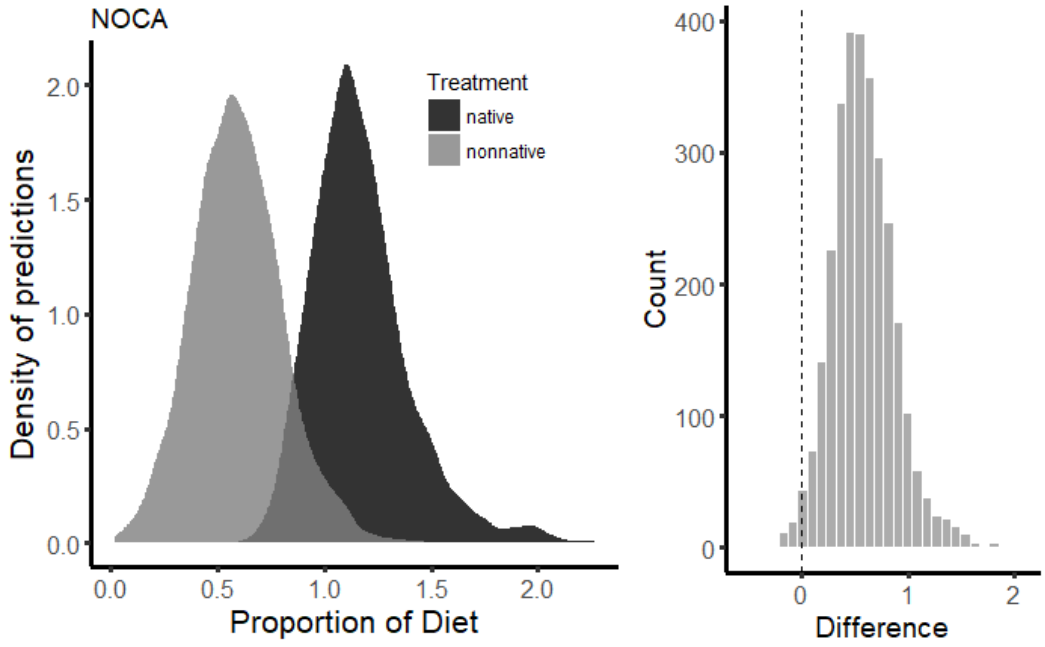


Figure C.10 (A) Posterior probability density of predicted proportion of enriched diet in cardinal blood between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

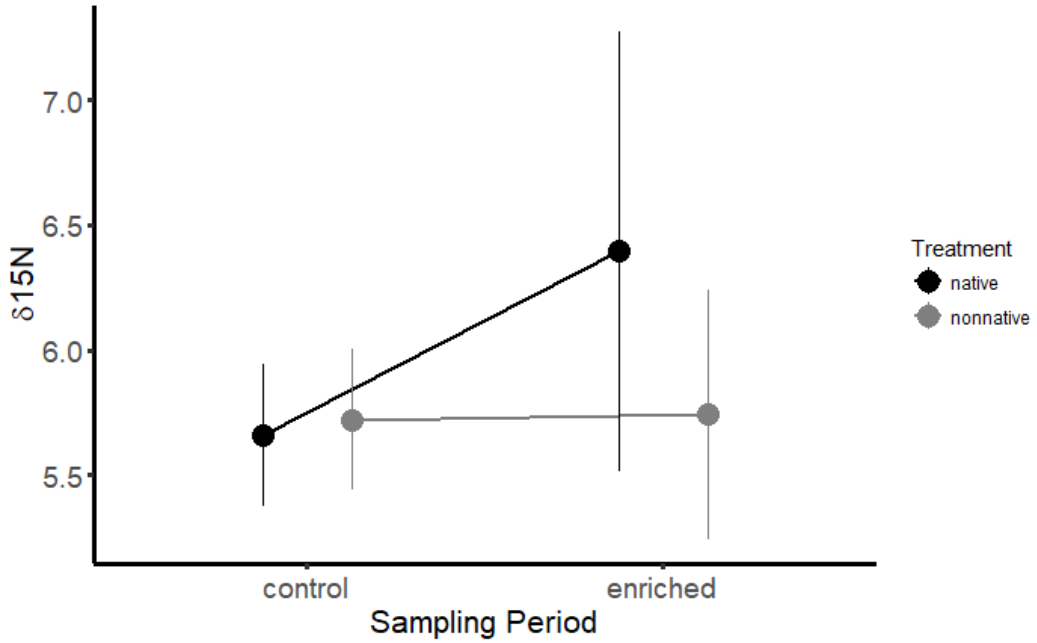


Figure C.11 Mean (± SD) blood ^{15}N in sparrows from native-treated (black) and nonnative-treated (gray) yards before (control) and after (enriched) application of the foliar isotope tracer.

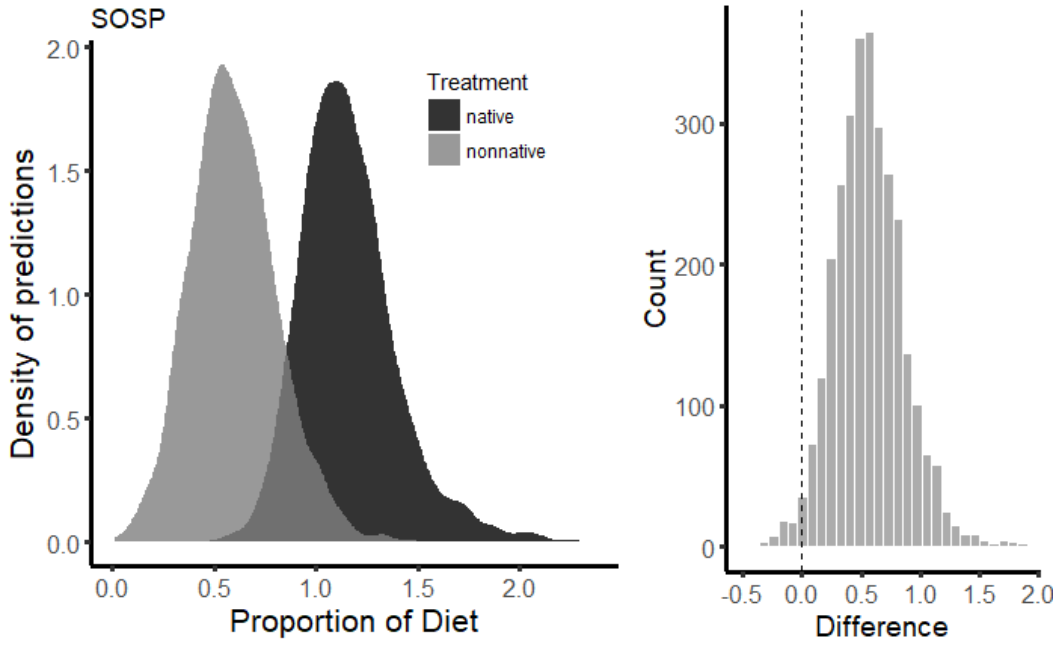


Figure C.12 (A) Posterior probability density of predicted proportion of enriched diet in sparrow blood between native- (black) and nonnative-treated (gray) sites accounting for days since first enrichment. (B) Posterior probability distribution of predicted differences in the proportion of diet between native-treated and nonnative-treated sites.

Figure C.13 A sample native (top) and nonnative (bottom) yard with 30 and 50m radius circles around the focal property. Yards did not differ in the proportion of nonnative biomass, total plant biomass, mature tree canopy, housing density or impervious surface.

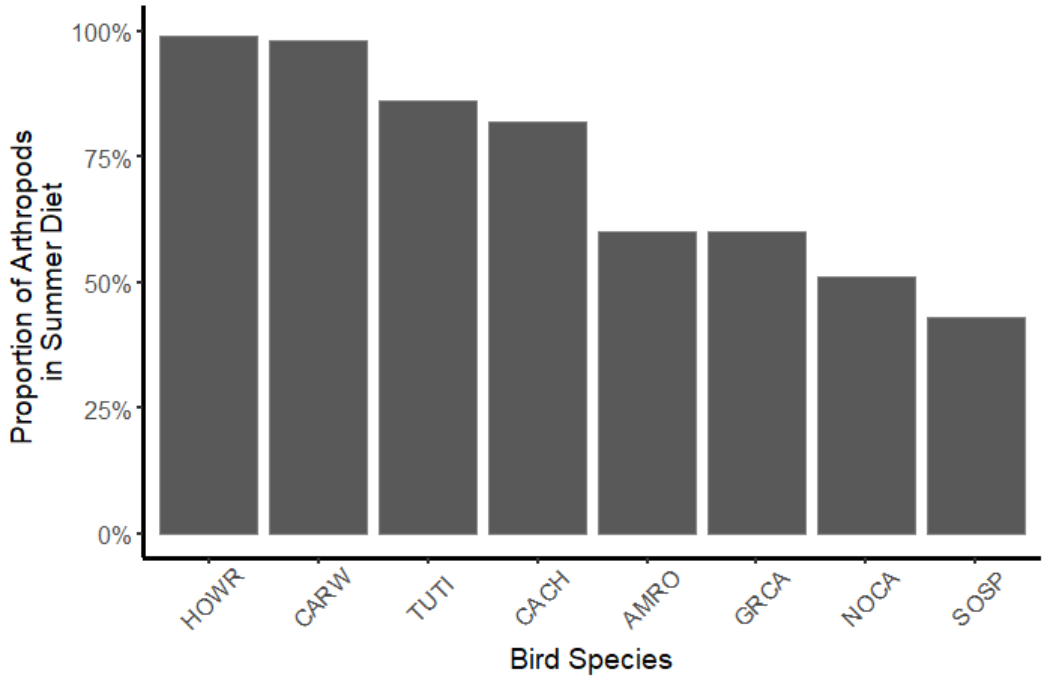


Figure C.14 Percent arthropods in spring and summer diet of the eight focal species. Diets were gleaned from Martin et al. (1951) which is based on hundreds of stomach dissections of birds by USGS Biological Survey in the early 20th century.

Appendix A

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