

Native plants improve breeding and foraging habitat for an insectivorous bird



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ARTICLE INFO

Keywords:

Food webs
Lepidoptera
Urban landscapes
Breeding birds
Foraging
Chickadee

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.

1. 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 affect 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.

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Enemy Release Hypothesis; Keane and Crawley, 2002).

It is well documented that the biomass of arthropods, particularly Lepidoptera larvae, supports large and diverse trophic webs, and is 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, 2007). 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, 2013). 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.

2. Methods

2.1. 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.

2.2. 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: Supplementary Fig. 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 (Supplementary Fig. 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.

2.3. 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 25 m from the center of the yard in each cardinal direction and sampling the four plant species encountered (total: 16 plants per site). For 5 min 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 1.5 m × 1.5 m) up to 4 m high, and measured each caterpillar to the nearest 0.5 mm. 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).

2.4. 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 1 h per visit.

2.5. 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 50 m radius. The central point of the survey was located approximately 10 m 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 50 m-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.

2.6. 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 50 m-radius area (0.79 ha) using ArcGIS software. This area was chosen because other Paridae species respond strongest to local plant cues within 50 m of the nest (Hinks et al., 2015), and the 50 m-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 > 0.5 m 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, 1971, 1977). 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 7.854×10^{-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.

2.7. 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.

2.8. 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.

2.9. Chickadee occupancy, abundance, and breeding

To test what variables predict occupancy and abundance of chickadees, we used hierarchical models in package 'unmarked' (Fiske and Chandler, 2011) using Program R (R Core Team, 2017) to compare fit of nested models in an AIC framework (variables used, Supplementary Table 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.

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, 2016). All covariate models were also ranked against a ‘global’ and ‘null’ (no covariates) model.

3. Results

In 2014, chickadees were detected at least once in 69.07% of 97 sites. The number of chickadees observed ranged from 0 to 6 with an average 0.80 ± 1.04 SD chickadees per survey. Chickadee breeding evidence was confirmed within the 50 m point count radius in 33 sites (36.67%).

3.1. 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 $39.30\% \pm 23.56\%$ SD. Basal area varied from 1.12 m^2 to 160.98 m^2 with a mean of $22.09 \text{ m}^2 \pm 30.67$ 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: $\beta 0.43 \pm 0.05$ SE, $p < 0.001$, CI = 0.33, 0.53, Fig. 1), and negatively related to plant origin (non-native: $\beta -0.65 \pm 0.12$ SE, $p < 0.001$, CI = -0.88, -0.42, Fig. 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: $\beta -0.66 \pm 0.16$ 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: $v = 1218$, $p = 0.005$, Supplementary Fig. 3).

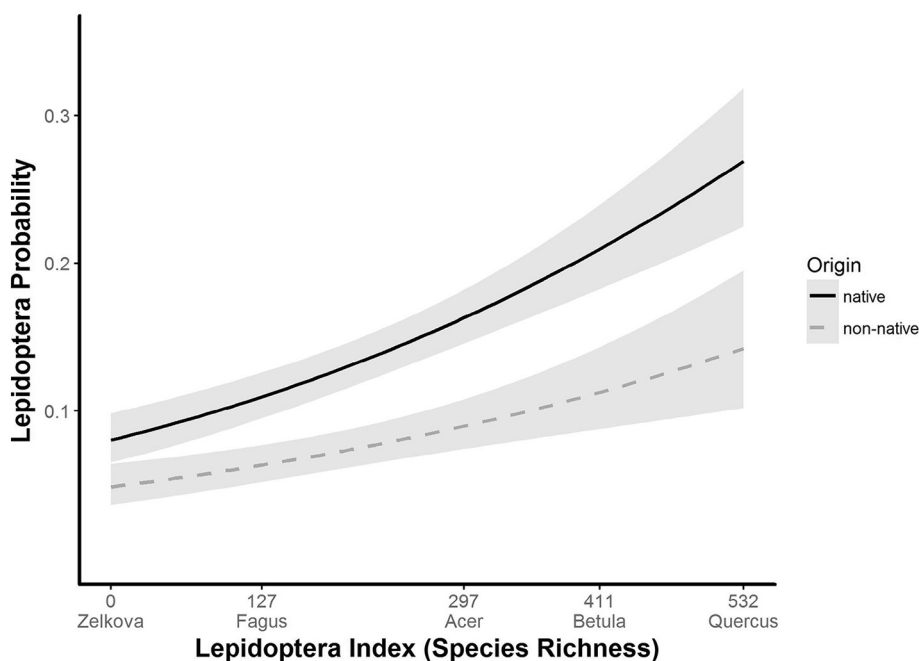


Fig. 1. A model of the probability of Lepidoptera being found on a 5-minute search period for native and non-native plant species. When controlling for the diversity of Lepidoptera found on a given genus, non-native species had a lower probability of having caterpillars than native species (non-native: $\beta -0.65 \pm 0.12$, $p < 0.001$, CI = -0.88, -0.42).

3.2. 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, 2398 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 $16.90 \text{ m} \pm 9.71$ SD (range: 0–40 m). 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, $p < 0.001$, Supplementary Fig. 4). Moreover, as the proportion of non-native plants increased, chickadees significantly increased their preference for native plants ($\beta -0.42 \pm 0.05$ SE, $p < 0.001$, $R^2: 0.68$, CI: -0.52, -0.31, Fig. 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 (Supplementary Table 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: $\beta 6.27 \pm 0.72$ SE, $p < 0.001$, Fig. 3), however preferences were lower (non-native: $\beta -3.53 \pm 1.47$ SE, $p = 0.02$, CI: -6.43, -0.63) and the relationship weaker for non-native plants (non-native: $\beta -5.17 \pm 1.42$ SE, $p < 0.001$, CI: -7.96, -2.38).

3.3. 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 ($\Delta\text{AIC} < 2$, Supplementary Table 3). Therefore, no variables were included in occupancy models to account for detection; however, detection was allowed to be imperfect.

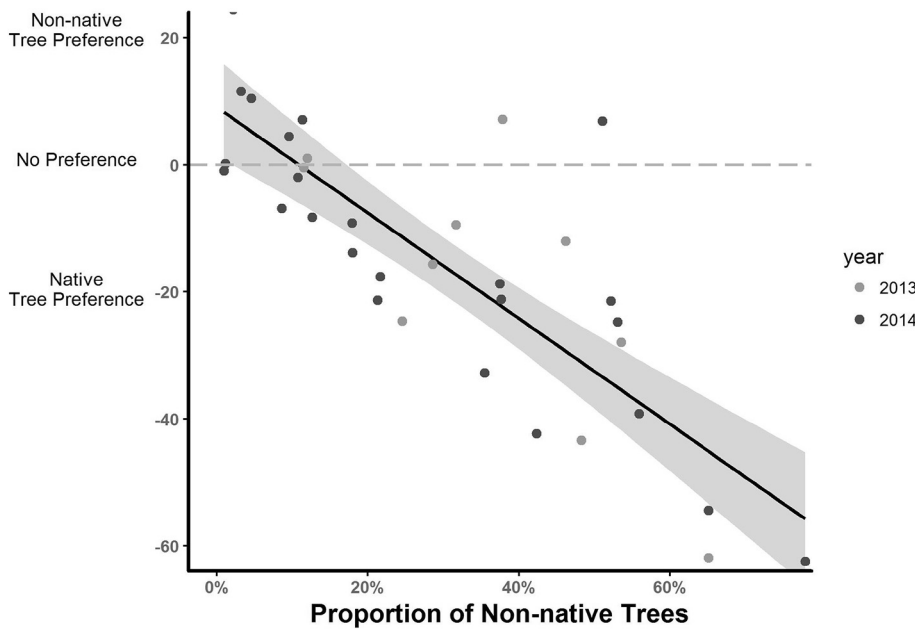


Fig. 2. Relationship between chickadee non-native plant aversion (negative values) and proportion of non-native plants within 50 m of the nest box (β : -0.42 ± 0.05 , $p < 0.001$, R^2 : 0.68, CI: $-0.52, -0.31$). Plant preferences at the same site in both years were highly correlated ($r > 0.8$); therefore, 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.

Chickadee detection probability of abundance was negatively related to BUILDING (model averaged: $\beta -0.39 \pm 0.14$, CI: $-0.67, -0.12$, Supplementary Table 3; Supplementary Fig. 5), and this variable was included in subsequent abundance models.

3.4. Chickadee occupancy and abundance

For chickadee occupancy, all top models included the variable BASAL ($\Delta AIC < 4$, $w = 0.76$, Supplementary Table 4). The relative importance of BASAL accounted for the majority of the weight across models ($w = 0.87$, Supplementary Table 5). BASAL was significantly positively related to occupancy ($\beta 1.47 \pm 0.64$, CI: 0.21, 2.73, Fig. 4a). Chickadee occupancy was also negatively related to NON-NATIVE TREE ($\beta -0.80 \pm 0.44$) 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 ($\Delta AIC < 4$, $w = 0.74$, Supplementary

Table 4). The relative importance of IMPERVIOUS accounted for 0.75 of the weight and BASAL accounted for 0.72 (Supplementary Table 5). Chickadee abundance was negatively related to IMPERVIOUS ($\beta -0.32 \pm 0.12$, CI: $-0.55, -0.08$, Fig. 4b), and positively related to BASAL ($\beta 0.34 \pm 0.10$, 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 NON-NATIVE TREE ($\Delta AIC < 4$, $w = 0.94$, Supplementary Table 4). The probability of nesting chickadees was negatively related to NON-NATIVE TREE ($\beta -1.49 \pm 0.3$, CI: $-1.49, -0.3$, Fig. 4c). Overall, the relative importance of NON-NATIVE TREE accounted for 0.95 of the weight (Supplementary Table 5).

4. Discussion

Urbanization drastically alters the abiotic and biotic properties of the landscape including large conversions of regional floristics due to

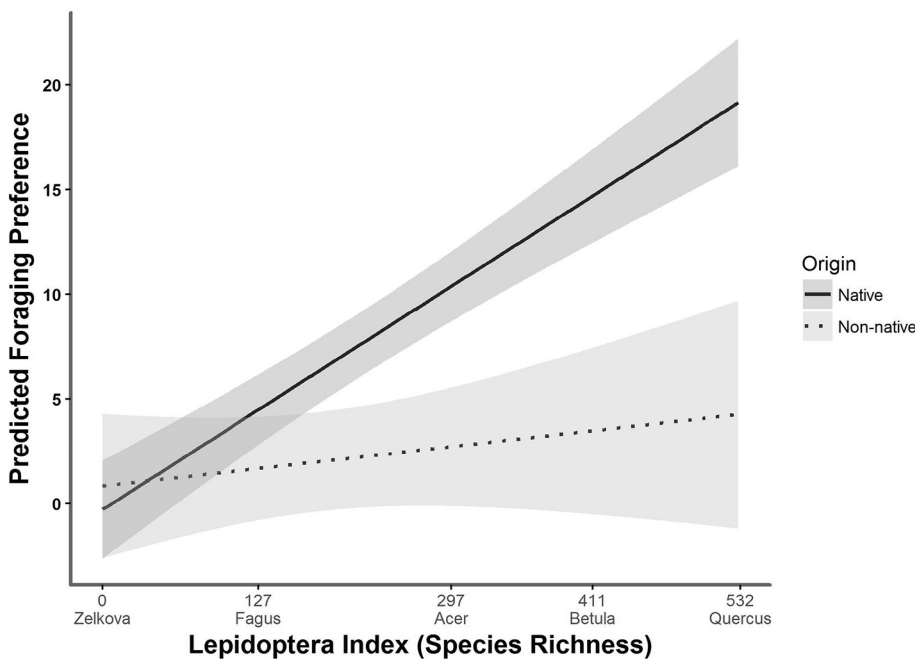


Fig. 3. Relationship between the Lepidoptera Index and predicted foraging preference of chickadees in Washington, D.C. residential yards. Relative to the plant availability at the yard level (random effect), foraging preferences are positively related to the Lepidoptera Index (β : 6.27 ± 0.72 , $p < 0.001$, 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: $-6.43, -0.63$).

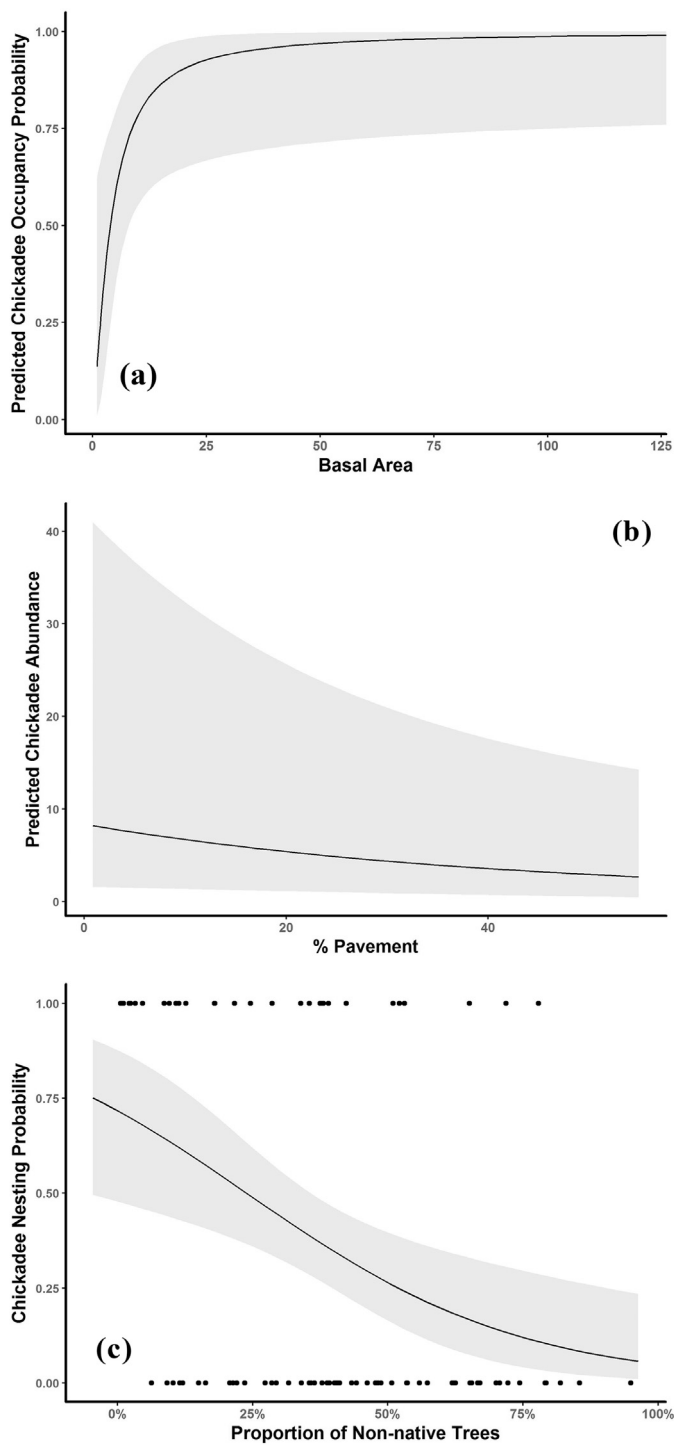


Fig. 4. Relationships between local variables and chickadee occupancy, abundance and breeding activity. Estimates shown are model-averaged. (a) The probability of chickadee occupancy is positively related to the basal area of trees at the 50 m-radius site (BASAL: β 1.47 ± 0.64 , CI: 0.21, 2.73). (b) The abundance of chickadees is negatively related to the average % impervious surface at the 50 m-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 (NON-NATIVE TREE: β -0.90 ± 0.30 , CI: -1.49 , -0.30).

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 *Acer platanoides* and *Quercus acutissima*. 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, > 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 m. 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.

5. 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) 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.

Acknowledgements

Foremost we thank the numerous Neighborhood Nestwatch volunteers and their friendly and accommodating neighbors for help monitoring nest boxes and for allowing us to conduct this study on their properties. None of this work could be possible without their help, support and occasional coffee. We also thank C. Crank, T. Guida, J. Herbert, S. Kay, K. Oswald, J. Rajbhandary, K. Shropshire, K. Snyder, A. Studd-Sojka, and several undergraduate and high school volunteers for their assistance in collecting and entering data as well as B. Reitsma for help with lab work and equipment. We appreciate statistical advice from J. Buler, G. Shriver and M. Hallworth. We appreciate suggestions by four anonymous reviewers that greatly improved this manuscript. This work was supported by the National Science Foundation [award #DEB-1257526 to D. Tallamy and P. Marra]. The authors declare that they have no conflict of interest.

Appendix A. Supplementary Information

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.biocon.2017.06.029>.

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