



Nonnative plants reduce population growth of an insectivorous bird

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Human-dominated landscapes represent one of the most rapidly expanding and least-understood ecosystems on earth. Yet, we know little about which features in these landscapes promote sustainable wildlife populations. Historically, in urban areas, landowners have converted native plant communities into habitats dominated by nonnative species that are not susceptible to pest damage and require little maintenance. However, nonnative plants are also poor at supporting insects that are critical food resources for higher order consumers. Despite the logical connection, no study has examined the impact of nonnative plants on subsequent population responses of vertebrate consumers. Here, we demonstrate that residential yards dominated by nonnative plants have lower arthropod abundance, forcing resident Carolina chickadees (*Poecile carolinensis*) to switch diets to less preferred prey and produce fewer young, or forgo reproduction in nonnative sites altogether. This leads to lower reproductive success and unsustainable population growth in these yards compared with those with >70% native plant biomass. Our results reveal that properties landscaped with nonnative plants function as population sinks for insectivorous birds. To promote sustainable food webs, urban planners and private landowners should prioritize native plant species.

conservation | urban ecology | food webs | plant–animal interactions | native plants

Wilson (1) has called insects “the little things that rule the world,” underscoring their contribution to the maintenance of ecosystem function. Unfortunately, recent studies have documented drastic declines in insect abundance following decades of human land use (2–4)—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 (5)—thus, ecosystems dominated by nonnative plants are characterized by reduced insect diversity, abundance, and biomass (6–9). Given that the majority of terrestrial birds rely on insects as a primary food source for reproduction and survival (10), 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 (11–13) and the decline of biodiversity (14) in built landscapes.

Because >80% of the conterminous United States is privately managed land, much of which has been converted from coevolved to novel ecosystems, the success of future conservation efforts may depend on identifying successful restoration strategies for private properties. 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 (15). 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 residential landscapes (12), it is imperative that we evaluate their contribution to ecosystems relative to the native species they displace (16).

Here, we measure how nonnative plants influence insectivorous birds by quantifying arthropod abundance, avian diet, reproductive success, and adult and juvenile survival of Carolina chickadees (*Poecile carolinensis*) in private yards across a metropolitan area that varied in proportion of nonnative plant biomass (SI Appendix, Fig. S1). We then incorporate our reproductive and survival confidence intervals (CIs) into an iterative population-growth equation to examine how population growth (r) varies with proportion of nonnative plant biomass.

Results

Arthropod Availability and Diet. Arthropod sampling showed that mean abundance of both caterpillars and spiders declined as nonnative plant biomass increased across sites [$n = 110$, generalized linear model (GLM) with quasi-Poisson regression: $\beta = -1.33 \pm 0.40$, $P = 0.001$, CI: $-2.11, -0.56$; Fig. 1]. Concurrently, $\delta^{15}\text{N}$ within chickadee blood plasma revealed that the proportion of predatory arthropods (e.g., spiders) in chickadee diets increased as nonnative plants became more dominant ($n = 60$, GLM: $\beta = 2.14 \pm 0.69$, $P = 0.002$, CI: $0.79, 3.49$; Fig. 1). There

Significance

Nonnative plants lack an evolutionary history with native fauna and support insect communities that are less abundant and diverse, and this may change food availability for vertebrate consumers. Most insectivorous birds are absent or declining in urban areas, yet no study has tested whether nonnative plants impact bird populations via food limitation. We monitored reproduction and survival of Carolina chickadees within residential yards and found that when nonnative plants increased, both insect availability and chickadee population growth declined. We also found that populations could only be sustained if nonnative plants constituted <30% of plant biomass. Our results demonstrate that nonnative plants reduce habitat quality for insectivorous birds and restoration of human-dominated areas should prioritize native plants to support local food webs.

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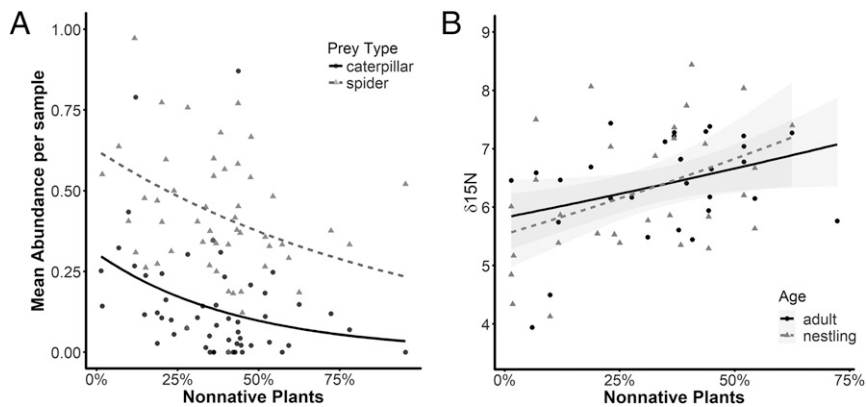


Fig. 1. Prey availability and chickadee diet across a gradient of nonnative plants. (A) Abundance of caterpillars and spiders declined as yards became more dominated by nonnative plants; spiders tended to be more abundant than caterpillars, irrespective of plant communities. (B) As nonnative plants increased within the territory, blood plasma $\delta^{15}\text{N}$ also increased, suggesting a decline in herbivorous arthropods and an increase in predatory arthropods within diet.

was no difference between adults and nestlings in $\delta^{15}\text{N}$ (GLM: $\beta = -0.02 \pm 0.25$, $P > 0.1$, CI: $-0.50, 0.47$) or between years in levels of $\delta^{15}\text{N}$ in blood plasma (GLM: $\beta = 0.10 \pm 0.25$, $P > 0.1$, CI: $-0.39, 0.58$). Our threshold models indicated that the slope of prey decline leveled off at 33.46% nonnative plants and that chickadees ate more predatory arthropods such as spiders when yards were composed of 37.61% or more nonnative plants.

Reproduction. We used life history aster models (AMs) (17) to simultaneously test the effect of nonnative plants on reproduction as a whole, as well as to 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

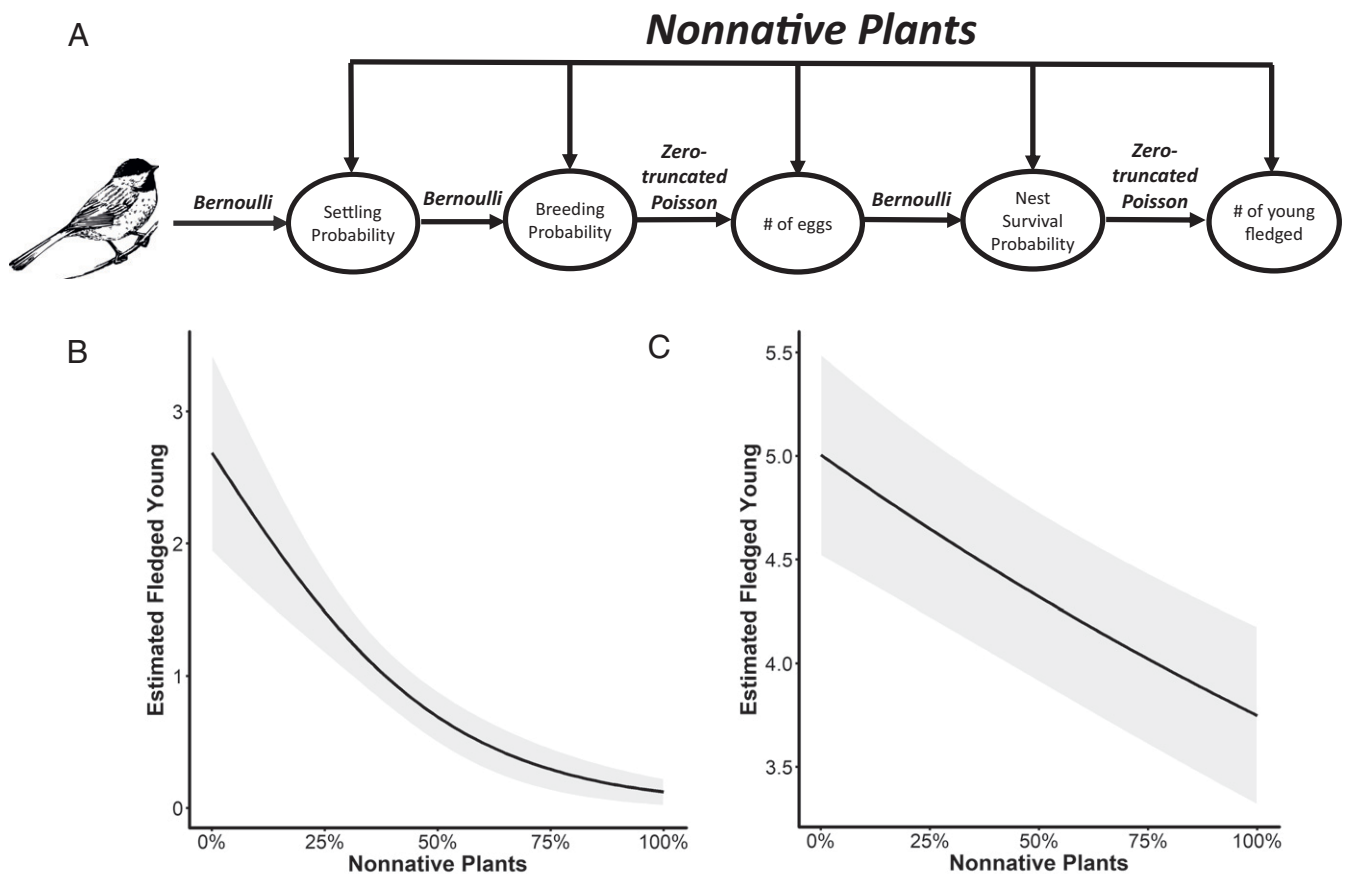


Fig. 2. Predicted chickadee reproduction produced by sites across a gradient of nonnative plants as predicted by our top AM. (A) Graphical depiction of the AM for reproduction. Our model included the reproductive components of settlement probability, breeding probability, number of eggs, nest survival 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 the proportion of nonnative plants increased (*SI Appendix, Figs. S2–S5*).

apply broadly to insectivorous birds and partially explain the local extinction of these species from human-dominated habitats. If 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 may represent a maximum limit for sustaining avian insectivores in these landscapes.

These results add to the growing body of evidence that native plants are essential for providing ecosystem services and resources for wildlife in human-modified landscapes (9, 24–26). Nevertheless, even within sites with predominately native plant communities, we found 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 (9, 27). 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 (28). 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 popular in horticulture and are able to provide some ecological services and resources for wildlife such as nest sites and fruit (29, 30); however, ecological benefits of introduced plants cannot be evaluated in isolation of their ecological costs. Our study suggests that, from an ecological perspective, nonnative plants should only be promoted when there is the net ecological benefit from the addition of these plants to the landscape. One of the major roles of plants is to harness the energy required to support complex consumer food webs. Here, we show that in highly managed, human-dominated environments, nonnative plant species are not ecologically equivalent to native plants in terms of meeting the nutritional needs of native fauna that rely on insect populations for food.

Moreover, the negative effects of nonnative plants on insect availability are compounded onto higher trophic levels. Therefore, our study suggests that nonnative plants do not provide enough arthropod prey during reproduction to sustain bird populations, making any postreproductive benefits from the production of fruit or seed irrelevant. Going forward, 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 whenever possible.

Methods

Study Sites and Species. Carolina chickadees (*P. carolinensis*) were studied within Neighborhood Nestwatch, a citizen science program that monitors breeding birds in residential yards across the Washington, DC, metropolitan area (ref. 31 and *SI Appendix*, Fig. S1). Because birds operate at a patch rather than a yard scale (20), 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 (32). Sites were separated by at least 1 km, located within a residential landscape, and no sites were located within publicly owned parkland.

We chose chickadees as a study species because of their common presence in urban and suburban environments of the Southeast United States and predominantly insectivorous diet throughout most of the year, such that caterpillars and spiders are disproportionately important prey relative to other invertebrate taxa (10, 33). 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 $^{15}\text{N}/^{14}\text{N}$ in blood plasma

($\delta^{15}\text{N}$). We also used a 17-y 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. Here, we summarize our field and statistical methods, but additional information on all aspects of data collection can be found in *SI Appendix*.

Field Methods. In 2013–2014, we quantified arthropod abundance using a timed-search approach on 16 woody plants per site. In each cardinal direction, we randomly chose four plant species 25 m from the center of the yard and conducted three 5-min visual searches per plant for all arthropods within an $\sim 2.25\text{-m}^2$ foliage area (total of 48 samples per site). Our searches were restricted to areas of woody plant foliage that could be reached with a standard ladder ($\sim 4\text{--}5$ m high). All arthropod searches were conducted between mid-May and early June to reduce variation in phenology and to ensure arthropod counts would be relevant to the breeding period of chickadees. 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.

Within those years, we also determined the trophic level of individual adult and nestling chickadees using stable isotope ratios of $\delta^{15}\text{N}$ found in the blood plasma of captured birds. We used values of $\delta^{15}\text{N}$ to assign trophic position of individual birds, where lower values indicated a higher consumption of herbivorous arthropods (such as caterpillars) and higher values indicated higher consumption of predatory arthropods (such as spiders) (34). 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°C . Before isotopic analysis, we freeze-dried samples for at least 24 h and weighed 0.5–0.7 mg into tin capsules. For nestlings, individuals within a nest are nonindependent; 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 $^{15}\text{N}/^{14}\text{N}$ based on international standards of atmospheric nitrogen.

From 2013 to 2016, we collected data on chickadee occupancy and reproduction by conducting monthly 10-min point count surveys and monitoring nest boxes during the chickadee breeding season [March–June; for more details see Narango et al. (9)]. Nest-box monitoring was completed by both technicians and volunteer homeowners trained in monitoring protocol. 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 one young fledged), and total number of young produced. Nests were not considered active until at least one egg was laid.

We quantified annual survival using a 17-y 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 and August to color-band chickadees and resight returning individuals [for more details, see Evans et al. (35)]. Our dataset included birds captured from 2000 to 2016; however, 2006 and 2011 were not included because no data were collected in these years.

We determined juvenile survival by following family groups with radio telemetry and monitoring the daily survival of 88 fledglings after leaving the nest. Radio-telemetry tags were applied to adults ($n = 20$) just prior to or immediately after fledging. Approximately every 2 d, an observer located the family group and identified how many fledglings remained alive until individuals reached 21 d (the approximate time juveniles reach independence).

We determined proportion of nonnative plant biomass at the site level, using a modified i-Tree protocol for assessing wildlife habitat (36). We surveyed five nonoverlapping 0.04-Ha circular plots, including one centered on the nest box and four 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 [for more details, see Narango et al. (9) and *SI Appendix*, *SI Methods*]. “Importance value” is a forestry metric for how dominant a species is at a site by summing the relative density and relative dominance for each plant species.

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 modified basic ellipsoid volume formula from Thorne et al. (37). For shrubs, we used the height and width of the full shrub. For trees, we used the height and width of the canopy.

We determined plant origin using US Geological Survey (38, 39) and US Department of Agriculture (40) range maps and information from the Missouri Botanical Garden (41). 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). This definition includes species both related (i.e., nonnative congeners) and unrelated to locally native flora. 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. 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 ($n = 110$), and our error distribution was quasi-Poisson. Our diet model included nonnative plants, age (i.e., adult or nestling), year ($n = 60$), and a Gaussian error distribution. Chickadees with diets composed of herbivorous consumers (e.g., caterpillars) occupy a lower trophic level and, thus, have low $\delta^{15}\text{N}$; therefore, chickadees in areas dominated by nonnative vegetation were predicted to have higher values of $\delta^{15}\text{N}$ 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: $-b/2 \times a$, where a represents the coefficient of our linear term, and b represents the coefficient of our quadratic term.

We used life-history AMs (17, 42) to test whether nonnative plants influence several related and conditional levels of reproductive success ($n = 411$ sites per year combinations). The benefit of using AMs is that these models allow one to test for the effect of a 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 and number of fledglings; Fig. 1). In our model, we tested three variables in which we were primarily interested and that 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 by using LRTs. 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 to 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 pseudocovariate for each stage and then used LRTs 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 with 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.

To estimate apparent adult survival, we fit our capture-resight data using a CJS model to determine the relationship between our covariate of interest (nonnative plants) and chickadee apparent survivorship, as well as to account for detection probability (18). Because transient individuals are not breeding and may not be relevant to the local plant community, 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).

To estimate apparent juvenile survival, we used CJS models that allowed daily survival to change across time (1–21 d) to determine mean daily survival of fledglings. Because fledglings in each family group are nonindependent, 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 in which we assessed plant communities. Therefore, we determined mean daily survival across all sites and did not allow survival to vary with nonnative plants.

We fit both 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 (43) called by package “jagsUI” (44) in program R (45). 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^{\wedge} was <1.1 for all parameters estimated.

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

$$r = \ln(N_{t+1}) = \ln \left(\frac{(N_{t0} * \frac{1}{2} * R_s) * N_p * N_s * J_s}{N_{t0}} + N_{t0} * A_s \right)$$

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 CIs calculated from the models between 0 and 100% nonnative plants. From the AM, 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 1,000 individuals after $t + 1$. To obtain a CI around our growth estimates, we ran 10,000 iterations. We plotted the mean population growth and CIs across the nonnative plant gradient and determined where in the gradient the population becomes unsustainable by the point at which CIs do not overlap replacement ($r = 0$).

Data and Materials Availability. All data are available at the Smithsonian Migratory Bird Center Data repository (<https://nationalzoo.si.edu/migratory-birds/data>).

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