



Invasive plants as a foraging resource for insectivorous birds in a Connecticut, USA forest: insights from a community-level bird-exclusion experiment

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Abstract Biological invasions can threaten biodiversity by outcompeting native species and disrupting food webs. Invasive species are now a leading driver of biodiversity and imperiled species declines worldwide. In temperate forests of eastern North America, understory plant communities are frequently dominated by invasive woody shrubs and trees. For many species of insectivorous birds and mammals, these invasive plants may threaten populations by providing less and/or lower quality food. Conservation practitioners expend significant resources to remove invasive plants, but evidence that such practices improve food abundance or quality to wildlife is surprisingly limited. Using a bird exclusion experiment, we compared arthropod abundance, biomass, and quality (protein content), and bird foraging intensity

among four invasive and six native woody plant species in a Connecticut, USA forest. Analysis revealed instances where native trees were actually poorer foraging resources for songbirds than certain species of invasive shrubs. Some invasive species, such as honeysuckle (*Lonicera morrowii*), supported higher arthropod biomass and protein content than the native plants. Conversely, Japanese barberry (*Berberis thunbergii*) had fewer arthropods overall and arthropods of lower protein content compared to native shrubs. Contrary to predictions from other food web experiments, bird predation effects were of similar magnitude on native and invasive plants, demonstrating that insectivorous songbirds foraged as intensively on the invasive plants as they did on the native plants. We recommend a regionally tailored and species-specific approach to invasive plant management that targets species that provide low-quality foraging opportunities relative to the quality of the local native plant community.

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Introduction

Invasive species are widely considered to be a leading cause of global biodiversity decline (Bellard et al. 2016). Invasive species management totals \$120 billion spent annually (Pimentel et al. 2007). Invasive

plants are a particularly challenging category of invasives to manage in terrestrial ecosystems, with the cost of plant removal efforts still being difficult to estimate accurately for the U.S. or globally (Rai et al. 2022). Nevertheless, the costs of invasive plant management have not been trivial when quantified, reaching average annual totals of \$82 million in California (California Invasive Plant Council, 2022) and \$45 million in Florida (Hiatt et al. 2019). However, despite dramatic efforts to remove invasive plants, there are still doubts about how reliably these interventions benefit wildlife communities (Robichaud et al. 2022; Traylor et al. 2022). In some cases, invasive plant removal can even have unintended negative consequences (Zavaleta et al. 2001; Lehtinen et al. 2022). Consequently, invasive plant removal should consider whether these intensive activities are justified on a case-by-case basis (D'Antonio and Meyerson 2002). Because conservation resources are severely limited relative to the scale of non-native species invasions, prioritizing control on the most impactful invasives is necessary (Arponen 2012; Courtois et al. 2018; Eppinga et al. 2021).

Invasive plant management emphasizes physical or chemical removal to restore ecological dynamics prior to invasion. In principle, removing or otherwise killing invasive plants improves habitat quality for native plants (Hartman and McCarthy 2004) and native wildlife (Schneider and Miller 2014). One target for invasive plant removal is to allow native plants to reestablish, which is expected to provide more food resources to wildlife. Removal of invasive plant species can drive recovery of arthropod assemblages by allowing higher food-quality native plants to reestablish, facilitating an increase in insect prey abundance for songbirds and other insectivores (Gratton and Denno 2005). As such, native plants are recommended as replacements for exotic shrubs to provide more insect prey as well as higher quality fruits for birds (Smith et al. 2013; Narango et al. 2018; Kramer et al. 2019; Tallamy et al. 2021). Furthermore, invasive plants are assumed to be disruptive in ecological restoration efforts since invasive species are prevalent in already degraded habitats with a history of intensive land-use practices (Mosher et al. 2009; Wang et al. 2016; Seebens et al. 2017; Holmes et al. 2021).

Typically, invasive plants dominate or form monocultures and displace native plant species, sometimes negatively impacting native animals indirectly

(McCary et al. 2016; Fletcher et al. 2019). For example, some invasive plants have been linked to reduced nestling quality and reproductive success in insectivorous birds due to lower arthropod prey abundance (Narango et al. 2018; Tarr 2022), although evidence of negative impacts of invasive plants to birds remains largely mixed (reviewed by Nelson et al. 2017). Some studies have also shown lower quality arthropod prey is available to insectivorous birds and mammals in habitats dominated by invasive plants (Gerber et al. 2008; Riedl et al. 2018). The ecological mechanisms by which invasive plants impact arthropods range from chemical to behavioral. For example, compounds released from invasive plants through roots and decaying leaves can impact detritus-based food webs (Robison et al. 2021). Furthermore, the atypical architecture of invasive plants can modify the foraging behavior of arthropod communities, changing encounter rates between predatory arthropods and prey (Pearson 2009; Lind and Parker 2010; Landsman et al. 2021).

In managed forests, invasive plant removal is commonly conducted without active restoration of native plants and relies on local native plants to become established in recently cleared areas on their own (Flory and Clay 2009; Shields et al. 2015; Farmer et al. 2016; Cutway 2017). Presumably this approach is taken because active planting is costly and it is assumed that whatever native plants may naturally establish themselves in place of the removed invasives will improve food resources for birds and other wildlife. However, despite an abundance of literature showing negative effects of invasive plants on arthropods, it remains unknown for most invasive plant species how they compare to native plants of invaded areas in terms of the biomass and quality of arthropods they directly or indirectly support and the extent to which insectivores forage on them. We therefore drew these comparisons between four notorious invasive woody plants of northeastern U.S. secondary growth forests and six dominant native woody plants that are among those most likely to passively establish themselves in areas cleared of the invasives.

We tested three hypotheses: (1) the 'low food quantity hypothesis', (2) the 'low food quality hypothesis', and (3) the 'weaker predatory effects hypothesis'. In the low food quantity hypothesis, an invasive plant species is expected to have significantly less prey available for insectivores compared

to native plants coexisting in the same habitat patch. In the ‘low food quality’ hypothesis, prey items that are available on invasive plants are expected to have lower nutritional value (e.g., lower protein content) resulting from being low-quality food sources for herbivorous arthropods and the cascading effects of that on predatory arthropods (e.g., spiders) (Lieurance and Cipollini 2013; Haan et al. 2021; Lampert et al. 2022). In the weaker predatory effects hypothesis, insectivores are predicted to forage on invasive plants less than native plants because of lower prey abundance and quality (Riedl et al. 2018), which will be manifested as weaker top-down effects on insect prey. Because plants support arthropods directly (e.g., herbivores) as well as indirectly (e.g., predators), each hypothesis considers the food resources provided by plants to insectivores to include all arthropods. We tested these hypotheses through a predator exclusion experiment on four intensively managed invasive woody plant species of the northeastern U.S., using a set of six increasingly dominant, co-occurring native plants as a comparison point.

Methods

Study System. We performed a selective predator exclusion experiment on ten woody host plant species at Great Hollow Nature Preserve in New Fairfield, Connecticut, USA (41.507998 N, -73.530032 W). The preserve is 334 ha and comprised predominantly of mature, closed-canopy, second-growth deciduous and mixed forest. Historic disturbance of the land, mostly from past agricultural uses, has favored the establishment of many of the invasive plants that are now ubiquitous to the northeastern U.S. and often aggressively targeted for removal by land managers and conservation practitioners. We focused our experiment on a subset of these invasive plants: Japanese barberry (*Berberis thunbergii*), Morrow’s honeysuckle (*Lonicera morrowii*), burning bush (*Eunonymus alatus*), and autumn olive (*Eleagnus umbellata*). These four species are designated as invasive by the Connecticut Invasive Plants Council, formed via Connecticut General Statutes §22a-381a through §22a-381d (<https://cipwg.uconn.edu/ipc/>). For comparison, we chose six native woody plants that often co-occur with these invasive shrubs in the region’s second-growth forests and are the

most dominant native trees in the understory of our study system: striped maple (*Acer pennsylvanicum*), shadbush (*Amelanchier canadensis*), musclewood (*Carpinus caroliniana*), witch-hazel (*Hamamelis virginiana*), sweet birch (*Betula lenta*), and American beech (*Fagus grandifolia*). In the common stewardship practice of removing invasives without actively planting natives afterwards (Flory and Clay 2009; Shields et al. 2015), these six native species are among those most likely to fill the void left by invasive plant removal in secondary growth forests in our region. They are therefore among the most realistic alternatives to invasive plants facing managers of such forests, as opposed to native species like oaks (*Quercus* spp.) that are generally considered high quality sources of insect prey for wildlife, but have been in steep decline in the eastern U.S. for nearly a century due to a combination of anthropogenic factors (Dey 2014; Peracchio 2020). In Connecticut, for example, red oak (*Quercus rubra*) has been surpassed by two of our study species (American beech, sweet birch) and maples (*A. rubrum*, *A. saccharum*) as the most numerically dominant trees (Peracchio 2020). Performing our experiment across our 10 coexisting non-native and native species thus provided a community-wide perspective on the impacts of invasive plants on food webs, in the context in which invasive plant management decisions should be made (Westman 1990).

Bird exclusion experiment. From 4–27 May, 2021, we set up a predator exclusion experiment in a paired design following Singer et al. (2012). Briefly, insectivorous birds were prevented from foraging on branches of our 10 study species via mesh netting (1/2-inch Bird-X Protective Netting, Elmhurst, IL, USA) that was folded and sown into a bag that was slid over a single branch of a target plant, and affixed using plastic zip-ties (“exclusion treatment”). This is an effective method of excluding birds while allowing arthropods access to branches in Connecticut forests (Singer et al. 2012; Clark et al. 2016). Although the mesh size could have prevented some large adult lepidoptera from accessing branches for oviposition, our study began after the primary oviposition period of forest lepidoptera in our area (Wagner 2005). We paired each exclusion branch with a nearby (2–10 m away) unmanipulated control branch of the same species and similar apparent leaf area. When trees with larger understory canopies were variable, control and

removal pairs were erected on the same tree (Clark et al. 2016). We set up 12 treatment pairs for each of the 10 focal plant species (240 total individual host plants), which were located at least 10 m from actively used trails and 50 m from any conspecific pair. At the end of the set-up period on 27 May, all 240 branches were struck with a 0.3 m wooden dowel to dislodge arthropods and reset colonization to avoid bias caused by the disturbance of setting up the exclusion netting. After a 2-wk waiting period, we then sampled foliage-foraging arthropods with a branch-beating technique (Wagner 2005) every other week from 24 May until 2 July, to coincide with the peak breeding period of most forest birds in our region. We struck each branch with a 0.3 m dowel while held over a 1m² ripstop fabric beat sheet and collected all invertebrates from the beat sheet into plastic vials or plastic zip-top bags using aspirators or soft-touch aluminum forceps. Each branch was sampled this way three times with 14 d between samples. We kept the collected arthropods cool in the field in coolers with ice packs and then transferred them to a -80° C freezer at the end of each day.

Taxonomic identification of arthropods. We combined the three repeated samples from a given branch to provide a tally of total arthropod abundance (Clark et al. 2016) and then weighed (wet mass) the arthropods together on a 10⁻⁴ g microbalance. After identifying all invertebrates from a given branch to class, we sorted all insects in the orders Lepidoptera, Hemiptera, Hymenoptera to family. We identified true spiders (Araneae) and Opiliones to family as well. Following identification, we transferred each taxonomic group from a given branch to separate 0.6–2 mL Eppendorf tubes and stored them at -80° C. In all, the four numerically dominant taxonomic groupings of arthropods included (1) Lepidoptera (caterpillars), (2) true spiders (Araneae), (3) herbivorous Hemiptera families (Aphidae, Cicadellidae, Membracidae, Miridae, and Pentatomidae), and (4) Orthoptera (families Gryllidae and Tettigoniidae).

Elemental analysis of arthropods. As an indicator of arthropod quality as prey for songbirds, we used elemental analysis to compare the protein content (percent elemental Nitrogen) of arthropods collected from native plants and invasive plants (Smets et al. 2021). Protein is a macronutrient that strongly mediates food selection by breeding birds and is critical to offspring development (Klasing 1998; Birkhead et al.

1999; Robbins et al. 2005; Razeng and Watson 2015). Our preliminary analyses suggested that two broad functional groups responded strongly to bird predation effects and varied significantly among native and invasive host plants, each representing a different trophic level above host plants: foliage-feeding herbivores (see Online Resource 1, Fig S1–S3) and predatory true spiders (Araneae). These two groupings of arthropods are prey for foliage-gleaning, insectivorous birds, should differ in protein content because of their different trophic levels (Reeves et al. 2021), and are impacted by experimental manipulation of bird predation (Gunnarsson et al. 1996). Generally, insects feeding on plants have a similar C:N ratio as their host (Abbas et al. 2014). To assay elemental composition, we first pooled foliage-feeding herbivore taxa and true spiders across sampling periods for each branch in the bird exclusion treatment group. We limited our analyses to branches with birds excluded to quantify the nutritional quality of the arthropod community as it would be for the first bird foraging on a given branch. We then oven-dried arthropod samples at 60 °C to a constant mass and homogenized any samples that weighed > 3 mg. Samples (1.5–3.5 mg) were measured for carbon and nitrogen concentrations on a Flash 1112 CHNSO elemental analyzer (CE Elantech inc. Lakewood, NJ, USA) by comparing results with aspartic acid and L-cystine standards. We analyzed replicates for a subset of branches, producing mean within-sample coefficients of variation of 4.2% for nitrogen and 2.9% for carbon.

Statistical analyses. We employed a series of Generalized Linear Mixed Models (GLMMs) using the *lme4* package (Bates et al. 2015) in R version 4.1.2 (R Development Core Team 2022). We included the following as response variables for successive models: (1) total arthropod biomass sampled per plant, (2) spider abundance (Araneae), (3) caterpillar abundance (Lepidoptera), (4) herbivorous true bug abundance (Hemiptera) (5) tree cricket and katydid abundance (Orthoptera) (6) N content of herbivorous insects and (7) N content of spiders. Arthropod biomass log-transformed and included both host plant species and bird exclusion treatment as fixed effects, and branch as a random effect in a GLMM. All abundance models were fitted with a negative binomial GLMM. In abundance models, host-plant species with bird-exclusion treatment were fitted as fixed effects, and branch was included as a random effect.

Nitrogen content models were fit with a normal distribution and all arthropod samples were pooled across sampling periods. In these analyses, host-plant species was used as a main effect (GLM). Post-hoc tests comparing changes in biomass, abundance, and nitrogen content were run using the *emmeans* package in R (Lenth 2016). Differences were investigated between pooled native plants and each individual invasive plant using Dunnett's method for P-value adjustment in unplanned contrasts. P-values and critical values were determined using the *car* package with analysis of deviance tests and χ^2 test statistics (Fox et al 2015).

Log-response ratios. A follow-up GLM was employed using LRRs (log-response ratios) of exclusion treatments to investigate the interspecific variation in bird predation effects across all host plant species (Singer et al. 2012). LLRs, when used to evaluate the effects of natural enemy exclusion, provide insight into whether the interaction strength of top-down effects vary according to different environmental variables (Chaguaceda et al. 2021, Wootton 1997). In this case, we used a LRR modified from Hedges et al. (1999) as the natural log of the combined arthropod biomass on exclusion branches divided by the arthropod biomass on control branches. LLR calculated in this way tests the prediction that bird predation is weaker on invasive plants, testing the predictions of the 'weaker predatory effects hypothesis'.

Results

We observed significant variation in total arthropod biomass among our ten focal host-plant species (Fig. S4, GLMM, $P=0.001$, $\chi^2=26.62$, d.f.=9). Collectively, invasive plants did not have significantly lower arthropod biomass than surrounding native plants in Dunnett's tests (vs autumn olive: $P=0.27$, vs barberry: $P=0.21$, vs burning bush: $P=0.28$, vs honeysuckle: $P=0.56$, Fig. 1, Table S1). Honeysuckle had higher arthropod biomass than the three other invasive plant species (Fig. 1D). Native plants varied in arthropod biomass, with musclewood, sweet birch and witch-hazel exhibiting higher arthropod biomass than the other plants (Fig S4). We did not observe statistically significant variation among plant species in the effect size of bird predation as measured by LRR (Fig. S5, GLM, $P=0.294$, $\chi^2=10.73$,

d.f.=9). Furthermore, bird predation LLR was not significantly lower on any invasive species compared to the native species group in Dunnett's tests (vs autumn olive: $P=0.99$, vs barberry: $P=0.38$, vs burning bush: $P=0.94$, vs honeysuckle: $P=0.99$, Fig. 2, Table S2). Bird predation reduced biomass of arthropods on all plant species except musclewood (Fig. S6). Musclewood branches were associated with relatively high occupancy of aquatic insect orders (Fig S1).

Bird predation effects on abundance of arthropods among native and invasive plants differed for each taxonomic group. Araneae abundance was higher on invasive plants overall (Fig. S6A, GLMM, $P<0.001$, $\chi^2=19.19$, d.f.=1), while bird effects on Araneae abundance were significant on both native and invasive plants (Fig. S6A, GLMM, $P<0.001$, $\chi^2=57.18$, d.f.=1). Hemiptera abundance was not significantly different between native and invasive plants (Fig S6B, GLMM, $P=0.488$, $\chi^2=0.479$, d.f.=1), and bird predation did not significantly reduce Hemipteran abundance (Fig. S6B, GLMM, $P=0.141$, $\chi^2=2.15$, d.f.=1). Bird predation effects were significant for Lepidoptera (Fig. S6C, GLMM, $P<0.001$, $\chi^2=25.7$, d.f.=1) and although there were fewer Lepidoptera on invasive plants (Fig. S6C, GLMM, $P=0.022$, $\chi^2=5.19$, d.f.=1), bird predation effects on Lepidoptera did not significantly differ between natives and invasives (GLMM interaction term for native vs. invasive plants and bird predation effect, $P=0.614$, $\chi^2=0.25$, d.f.=1). Finally, we observed similar abundances of Orthoptera on both native and invasive plants (Fig. S6D, GLMM, $P=0.941$, $\chi^2=0.005$, d.f.=1). Birds significantly reduced the abundance of orthoptera on both plant groups (Fig. S6D, GLMM, $P<0.001$, $\chi^2=15.6$, d.f.=1).

We observed significant variation in the %N by mass for herbivores among host plants (Fig. S7, GLM, $P<0.001$, $\chi^2=38.4$, d.f.=9). A Dunnett's test showed significantly higher %N by mass on honeysuckle compared to native plants (Fig. 3A, $P<0.001$, Table S3), and %N was higher on honeysuckle than any other plant (Fig. S7). Other invasive plants were not significantly different to the native group (vs autumn olive: $P=0.19$, vs barberry: $P=0.99$, vs burning bush: $P=0.88$, Fig. 3, Table S3). Spider %N varied significantly among plants overall (Fig. S8, GLM, $P<0.001$, $\chi^2=59.61$,

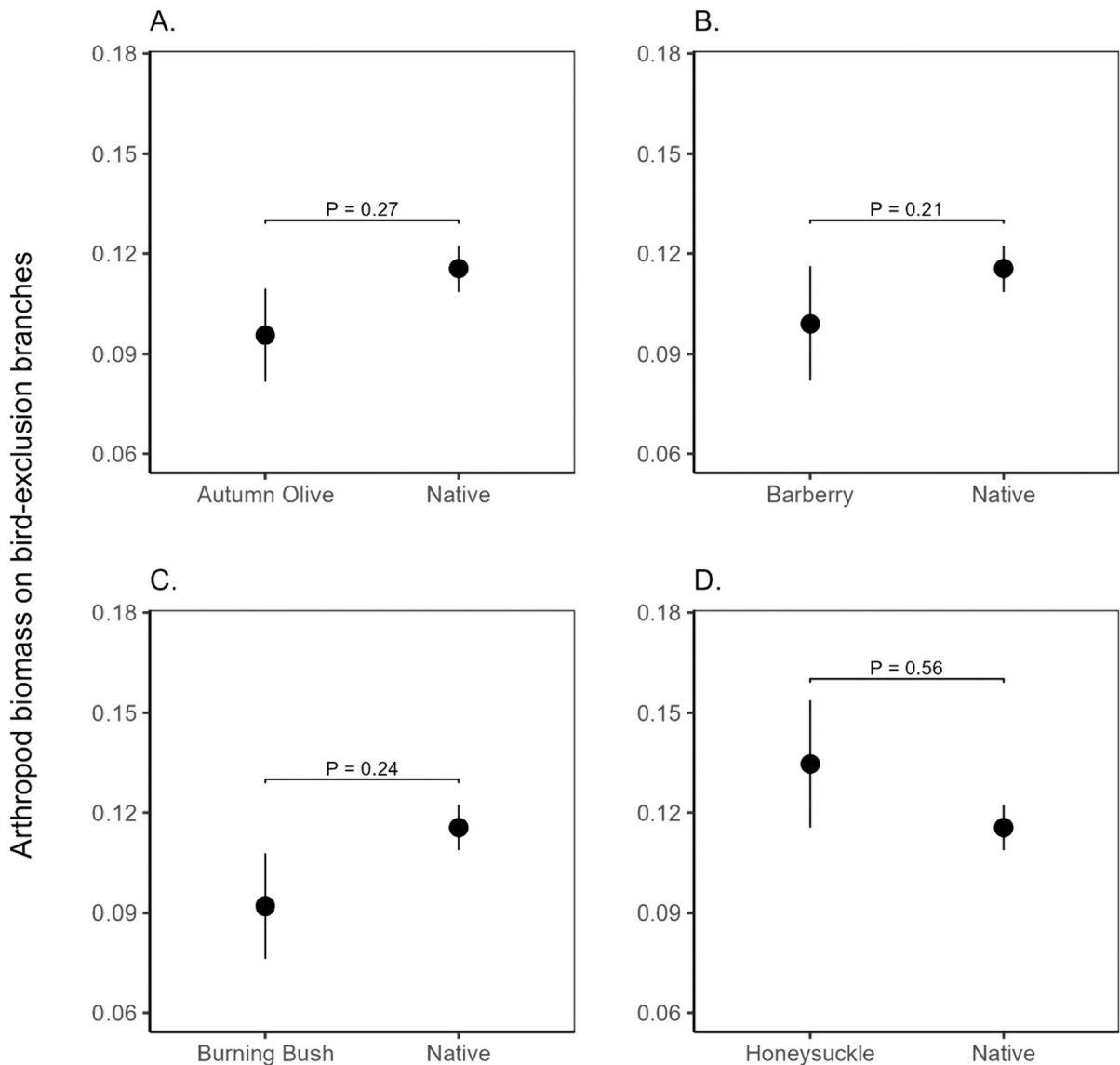


Fig. 1 Arthropod biomass (total grams per branch) with pooled comparisons between native plants and each invasive plant species for bird-exclusion branches. Biomass is reported

as total wet mass collected from branches. Mean \pm SEM is plotted, with levels of significance illustrated for native versus each invasive plant species using grouped, planned contrasts

d.f.=9), with lower values on Japanese barberry than native plants (Fig. 4B, $P < 0.001$, Table S4). Spider %N was dramatically lower on Japanese barberry than any other plant species (Fig. S8), while other invasive plants were not significantly different to the native group (vs autumn olive: $P = 0.08$, vs burning bush: $P = 0.96$, vs honeysuckle: $P = 0.98$, Fig. 4, Table S4).

Discussion

In the United States alone, invasive species are estimated to cause a yearly average of \$19.9 billion in economic losses (Fantle-Lepczyk et al. 2022). Consequently, the prevailing paradigm is that all invasive species are of little value or harmful. However, this broad-brush approach prevents prioritization of management efforts on the most ecologically impactful

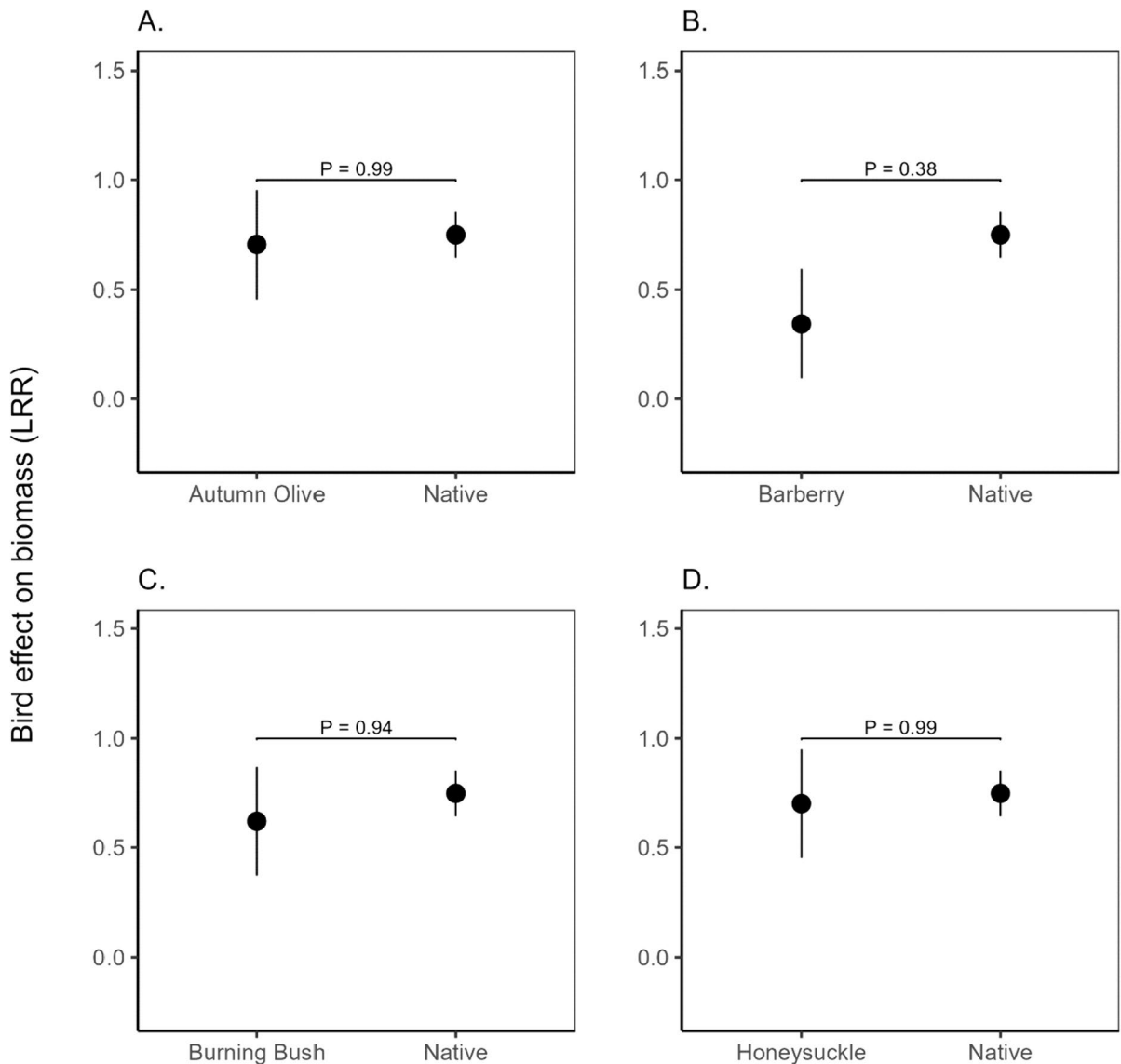


Fig. 2 Effect size of bird exclusion treatment showing pooled comparisons between native plants and each invasive plant species. Bird exclusion effect size reported as Log-Response Ratios (LRR), in which positive values >0 indicate a sig-

nificant reduction in arthropod abundance in response to bird predation. Mean \pm SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts

species. For invasive plants, most research is based on region-specific case studies in which a single invasive plant is compared to a high-quality native plant, underemphasizing any contributions an invasive plant may make to biodiversity (Schlaepfer 2018). Recent perspective surveys of conservation biologists and practitioners reveal conflicting opinions about impacts as being the criteria for ‘invasiveness’ rather than spread alone (Shackleton et al. 2020). Here, we

found multiple lines of evidence to suggest common invasive plants in our study system are comparable to the dominant native plants in their value as foraging resources for insectivorous birds. Arthropod biomass and protein content, and bird foraging intensity were broadly similar between native and non-native plant species that are major components of second-growth, hardwood and mixed forests of the northeastern U.S. Our results suggest that it should first be

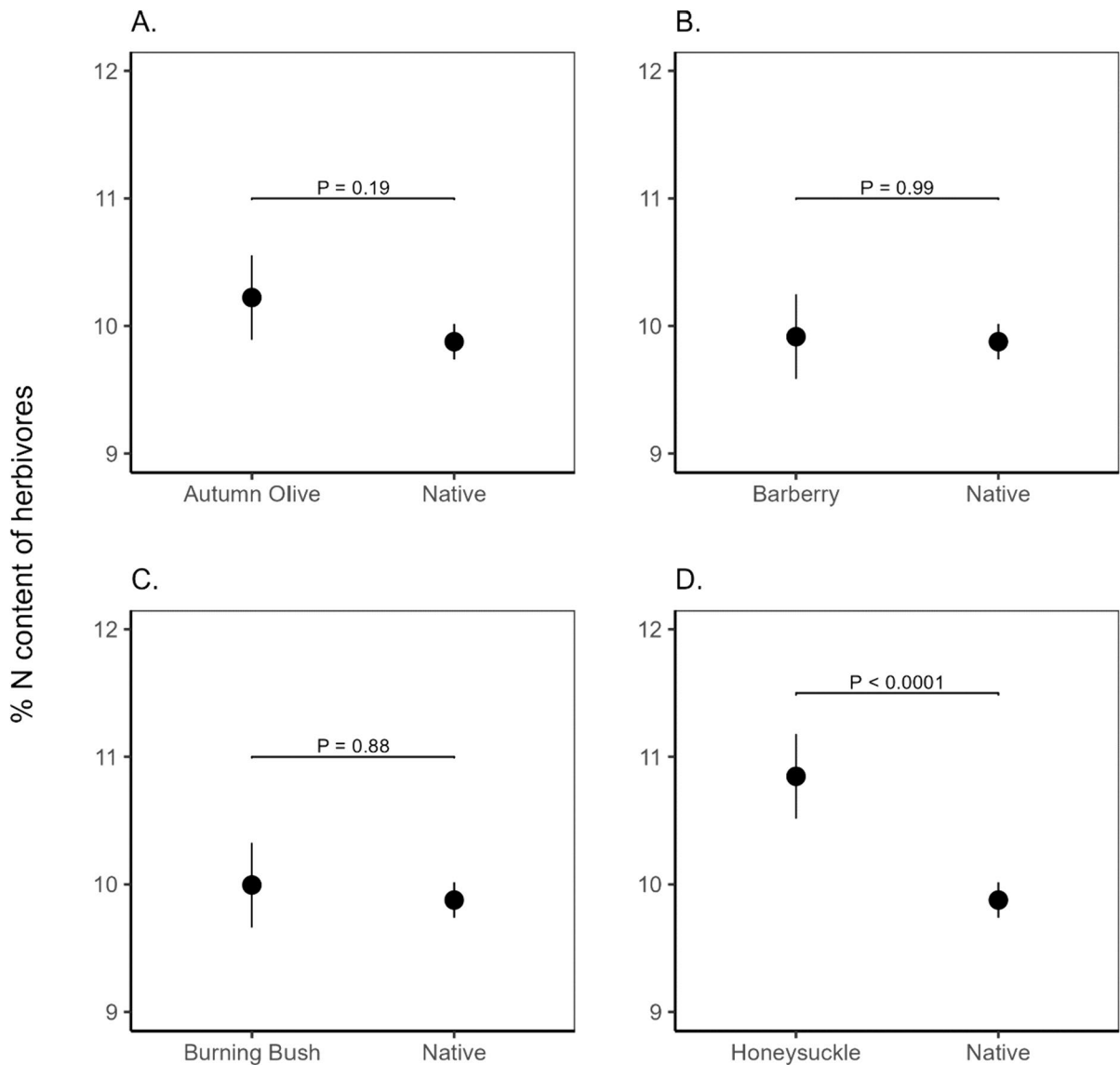


Fig. 3 Total % nitrogen for insect herbivores on bird-exclusion branches. Nitrogen content is measured as the total molecular mass of elemental nitrogen relative to total mass of a single

sample from an experimental host-plant branch. Mean \pm SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts

demonstrated, not assumed, that a given non-native, invasive plant is of inferior quality to dominant surrounding native plants before extensive removal efforts are made—an approach proposed as early as Westman (1990). Given the tremendous drive for invasive plant removal in our region, we were surprised to see some invasive plants supporting comparable abundances and protein-rich arthropod prey for songbirds. Moreover, songbirds appear to be foraging

on these invasive plants with similar intensity, with significant bird predation effects found on both invasive and native plants. While our study does not suggest invasive plants have no negative ecological consequences, it highlights that nearby native plants do not always yield significant differences in arthropod prey abundance and quality for songbirds.

Few studies have evaluated the simultaneous value of arthropod prey in terms of both quantity

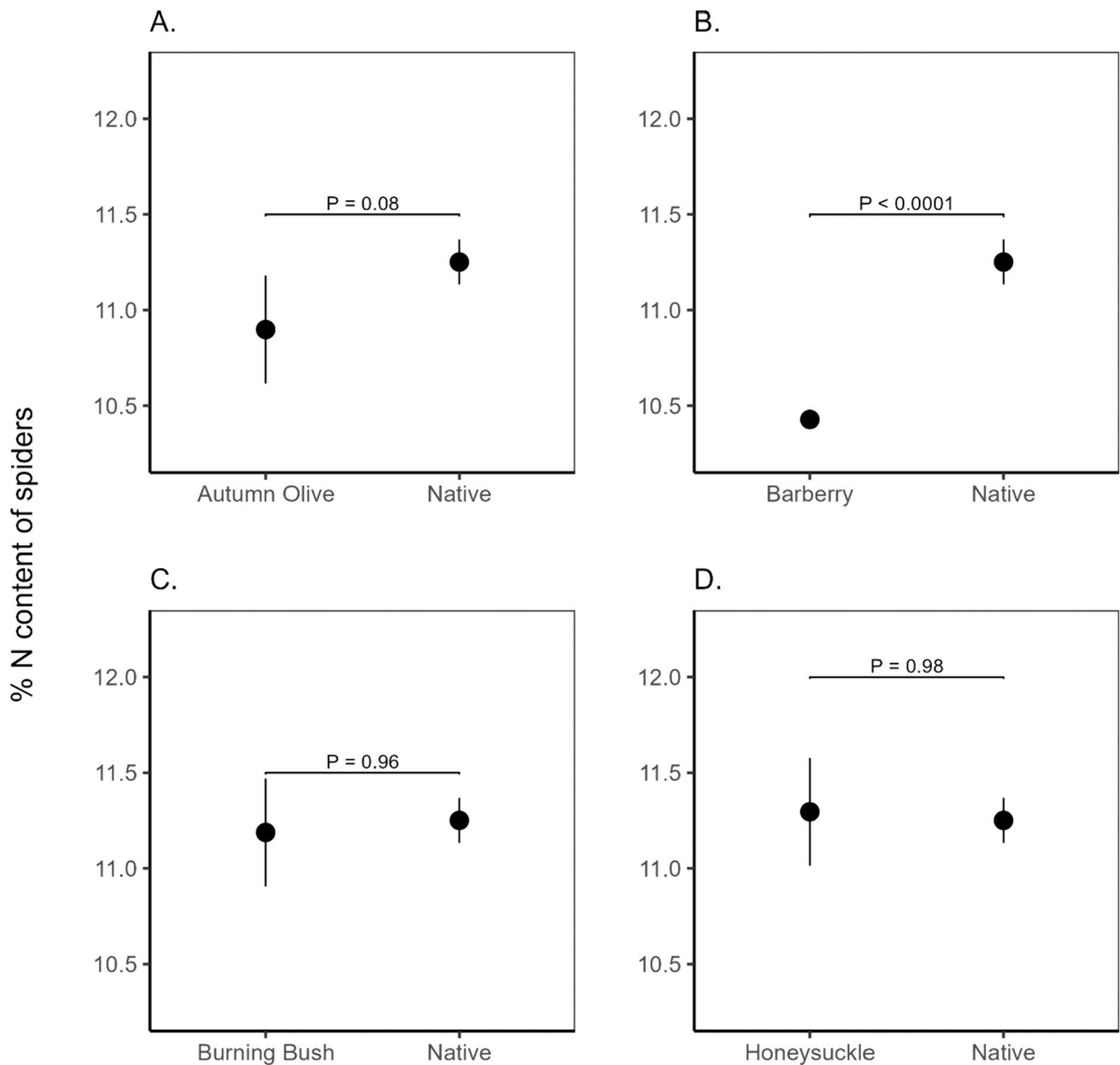


Fig. 4 Total % nitrogen for true spiders on bird-exclusion branches. Nitrogen content is measured as the total molecular mass of elemental nitrogen relative to total mass of a single

sample from an experimental host-plant branch. Mean \pm SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts

and quality at a plant community level. The results of our holistic approach revealed not all invasive plants are equally disruptive to trophic interactions between forest plants, arthropods, and insectivorous birds. To this point, our study showed surprisingly more arthropod prey on honeysuckle (*Lonicera*) compared to natives, failing to support the 'low food quantity hypothesis'. Similarly, Seraniak et al. (2023) found an invasive honeysuckle (*L.*

maackii) to be associated with a higher abundance and diversity of arthropods and birds than native shrubs in Ohio, U.S.A. forests. Support for our 'low food quality hypothesis' was mixed, with extremely variable arthropod protein content across invasive and native plants. We anticipated that herbivorous insects would be significantly lower in protein content on invasive plants, but found no evidence for this assertion. Investigation of host plant-specific

patterns suggest that the variance in food quality on invasive plants encompasses the range of quality of food found on native plants in the same habitat.

We found that common invasive plants in our study system are used as a foraging substrate by insectivorous songbirds just as intensively as natives. The similar predation effect sizes we observed between invasive and native plants were unexpected given two established mechanisms that cause invasive plants to have different arthropod communities. First, leaf tissue is expected to be of lower quality or more highly defended on invasive woody plants than on native woody plants, reducing biomass of arthropods on invasive plants (van Hengstum et al. 2014). Our finding of comparable numbers of herbivorous hemipterans and orthopterans on invasive and native plants (Figure S6) suggests that this is not universally true. Second, the branch architecture or leaf shape of invasive plants provide novel microhabitat for arthropods and thus create a distinct community from those found on native plants (Bultman and DeWitt 2007; Landsman et al. 2021). These differences in architecture may explain why spider abundance was higher on low-lying Japanese barberry, matching other observations with invasive plants like Japanese stiltgrass (Landsman et al. 2020).

One of the gaps in past research on non-native plant invasions is the limited ability of previous studies to assess how much invader-driven changes in arthropod communities translate into altered interactions between arthropods and their predators. Our study allowed us to investigate this question by combining quantification of the arthropod community on a range of host plants with a predator exclusion experiment to quantify top-down effects. Moreover, we considered trends in broad taxonomic groups, which can be informative for aggregating effects over complex systems (sensu Wagner et al. 2021). Accordingly, differences in nitrogen content of caterpillars and spiders ranged from around 0.5% in aggregate to 1% in specific contrasts. These differences in nitrogen content translate to differences in protein content of approximately 3–6% (McDonald et al. 2011; Smets et al. 2021), which, while not extreme, are detectable by songbirds and can affect their body condition (Bairlein 1998; Klasing 1998; Razeng and Watson 2015). However, it is unknown whether there are any notable downstream nutritional consequences of shifts in arthropod abundance and nitrogen content

for songbirds, even in the absence of changes in predatory behavior.

Current management practices attempt to ameliorate the impacts of invasive plants on wildlife through physical or chemical removal (Weidlich et al. 2020). However, our results suggest that the native plant community is a critical comparison point. Our study did not include oaks, which are known to be high-quality (e.g. those that contain nitrogen-rich leaf tissue) food plants for forest insects like caterpillars (Wagner 2005), because they are regenerating poorly and have been in steep decline in eastern U.S. forests (including our study site) for nearly a century due to a variety of anthropogenic factors (reviewed by Dey 2014). We expect that oaks support higher prey abundance and quality for insectivorous birds than the invasive plants we studied, but such comparison is not reflective of forest composition trends in the eastern U.S. and the realistic alternatives to invasive plants in the absence of active planting and maintenance – a practice few land managers have the resources to implement on meaningful scales. One of the key priorities for invasive species research includes understanding the context of the invaded habitat (Ricciardi et al. 2021), and thus we chose for comparison the native trees and shrubs that are increasingly dominant in our region's forests and would therefore replace invasives in the absence of efforts to actively restore *Quercus*, *Prunus*, or similarly high-quality native plants. The lack of distinction between invasives and the present native-plant community in our study suggests that in many northeastern forests the removal of invasive plants must be paired with restoration of these higher-quality native plants, especially since the process of physical or chemical removal of invasive plants can have unintended, negative impacts (Kettenring and Adams 2011). For management, the relative value of removing an invasive shrub should depend on the particular pairwise comparisons being made at a given site, as well as the density of invasive shrubs (Tarr 2022). Overall, we suggest a more nuanced management strategy for habitat improvement goals in eastern North American forests where the species identity is considered against the backdrop of surrounding native plants.

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Author contributions RC, WC, CS completed fieldwork. TK completed elemental analysis. RC completed data analysis. All authors wrote and revised the manuscript.

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Data availability All data and R Code for this manuscript are available through Open Science Framework (osf.io) at DOI 10.17605/OSF.IO/BVFNA

Declarations

Competing interests The authors have no conflicts of interest to declare.

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