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Are native plants always better for wildlife than invasives? Insights from a community-level bird-exclusion experiment

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	species, such as honeysuckle (Lonicera morrowii), supported higher arthropod biomass and protein content than the native plants. Conversely, one NNI, Japanese barberry, had fewer arthropods overall and spiders from it had significantly lower protein content. Contrary to predictions from other food web experiments, the predation effects of birds were of similar magnitude on native and NNI plants, demonstrating that insectivorous songbirds foraged as intensively on the NNI plants as they did on the native plants. We recommend a more nuanced, regionally tailored and evidence-based approach to NNI plant management that targets species that provide low-quality foraging opportunities relative to the quality of the local native plant community.

Ecological Applications Article

Title:

Are native plants always better for wildlife than invasives? Insights from a community-level bird-exclusion experiment

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Keywords:

Invasive species, invasive plants, non-native plants, insectivores, songbirds, forests, food webs, habitat restoration

Abstract:

Biological invasions can threaten biodiversity by outcompeting native species and disrupting food webs. Non-native invasive (NNI) species are now ranked as a leading driver of biodiversity and protected species declines around the world. In temperate forests of eastern North America understory plant communities are frequently dominated by NNI woody shrubs and trees. For many species of insectivorous birds and mammals, there is concern that these NNI plants can threaten populations by providing fewer food resources and/or foods of lower quality. Conservation practitioners expend significant resources to remove NNI plants, but evidence that this removal improves food abundance or quality to wildlife is scant. Using a bird exclusion experiment, we compared arthropod abundance, biomass, and quality (protein content of herbivores and spiders), and bird foraging intensity among four NNI and six native woody plant species in a Connecticut, USA forest to examine how NNI plants affect the tri-trophic relationship among forest understory plants, branch-dwelling arthropods, and insectivorous songbirds. All four lines of evidence suggested the NNI plants were not poorer foraging opportunities for songbirds. Some NNI species, such as honeysuckle (*Lonicera morrowii*), supported higher arthropod biomass and protein content than the native plants. Conversely, one NNI, Japanese barberry, had fewer arthropods overall and spiders from it had significantly lower protein content. Contrary to predictions from other food web experiments, the predation effects of birds were of similar magnitude on native and NNI plants, demonstrating that insectivorous songbirds foraged as intensively on the NNI plants as they did on the native plants. We recommend a more nuanced, regionally tailored and evidence-based approach to NNI plant management that targets species that provide low-quality foraging opportunities relative to the quality of the local native plant community.

Introduction:

Non-native invasive (NNI) species are widely considered to be a leading cause of global biodiversity decline (Bellard et al. 2016). In the United States alone, NNI species are estimated to also cause a yearly average of $19.9 billion in economic losses (Fantle-Lepczyk et al. 2021) and $120 billion is annually spent on their management (Pimentel et al. 2007). NNI plants are particularly challenging to manage in terrestrial ecosystems, with the cost of removal efforts still being difficult to estimate accurately for the U.S. or globally (Rai et al. 2022). Nevertheless, the costs of NNI 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). Despite the high cost, NNI plant removal is often thought to be a necessity for restoring ecosystem services and biotic integrity. However, despite dramatic efforts to remove NNI plants, there is still not a consensus on whether such practices actually benefit wildlife communities (Robichaud et al. 2021, Traylor et al. 2022), and in some cases, NNI plant removal can even have unintended negative consequences (Zavaleta et al. 2001, Lehtinen et al. 2022) . Effective management requires knowledge of when removal of a given NNI species may not be justified based on restoration goals (D'Antonio and Meyerson 2002). Decisions about prioritizing some NNI species removal over others is critical since conservation resources are severely limited relative to the ecological challenge at hand (Arponen 2012, Courtois et al. 2018, Eppinga et al. 2021).

In principle, removing NNI plants improves habitat quality for native plants (Hartman and McCarthy, 2004) and native wildlife (Schneider and Miller, 2014). Notably, removal of particularly aggressive NNI plant species that form monocultures can drive recovery of arthropod assemblages, which are an important food source for other wildlife (Gratton and

Denno, 2005). Plant invasions often have cascading impacts on ecological communities because they can directly modify both above-ground and soil food webs (McCary et al. 2016). NNI plants are prevalent in degraded habitats with a history of intensive land-use practices (Mosher et al. 2009, Wang et al. 2016. Furthermore, new non-native plant species are expected to become established in anthropogenically modified habitats over time (Seebens et al. 2017, Holmes et al. 2021). Consequently, understanding the mechanisms by which non-native plants disrupt food webs and identifying effective solutions have become priorities for ecologists and land managers.

Typically, NNI plants dominate or form monocultures and displace native plant species, negatively impacting native animals indirectly (Fletcher et al. 2019). Some studies have shown lower quality arthropod prey is available to insectivorous birds and mammals in habitats dominated by non-native plants. (Gerber et al. 2008, Riedl et al. 2018). However, nutritional quality for herbivores is just one of multiple traits of non-native plants that impact food webs. For example, compounds released from NNI plants through roots and decaying leaves can impact detritus-based food webs (Robison et al. 2021). Additionally, non-native plants have atypical architecture compared to native plants, leading to different compositions of arthropods independent of the host plant quality (Pearson 2009, Landsman et al. 2021). Each of these trait-based mechanisms provides some insight into the consequences of plant invasion, but interspecific comparisons are needed to help elucidate these pathways. For example, Lind and Parker (2010) compared a range of plant species testing the hypothesis that non-native plants have significantly different defensive chemistry than natives, but this hypothesis was only supported for a small proportion of the NNI plants examined.

It is expected that by removing NNI plants, native plants have an opportunity to recover, thus restoring ecosystem services (Hopfensperger et al. 2017). In residential landscaping scenarios, native plants are recommended as replacements for exotic shrubs to provide more insect prey for birds (Narango et al. 2018, Kramer et al. 2019). By contrast, in managed forests, NNI plant removal is typically conducted without active restoration of native plants and relies on local native plants to move into recently cleared areas on their own (Flory and Clay 2009, Shields et al. 2015, Farmer et al. 2016, Cutway 2017). Removal is suggested since habitats dominated by NNI plants often have lower abundances of plant-feeding arthropods which could be prey for birds, particularly caterpillars or spiders (Richard et al. 2019, Clark and Seewagen 2019). For wildlife at higher trophic levels, the success of this management strategy depends on the presumed superiority of arthropod quantity or quality on native compared to non-native plants. However, this assumption has not been rigorously tested, both in general and particularly in the temperate forests of eastern North America.

Our study involved a comparison of NNI and native members of a plant community within a Connecticut, USA mature forest. We tested two hypotheses: (1) a 'low food quantity hypothesis', and (2) a 'low food quality hypothesis'. In the low food quantity hypothesis, NNI plants are expected to have significantly lower prey available for insectivores compared to native plants coexisting in the same environment. In other forest regions in eastern North America, some non-native plants have relatively lower insect abundance and diversity (Tallamy et al. 2020). For example, caterpillar prey taken by birds were found to be less abundant on NNI than native plants in the suburbs around Washington, D.C. (Narango et al. 2018). Conversely, in the 'low food quality' hypothesis, prey items that are available on non-native plants are expected to have lower nutritional value (e.g., lower protein content) because non-natives are often low-quality food sources for herbivorous arthropods (Lieurance and Cipollini 2013, Haan et al. 2021, Lampert et al. 2022). We predicted lower arthropod quality on non-native plants than natives. Finally, in both hypotheses, insectivores are predicted to forage on non-native plants less than native plants because of lower prey abundance and quality (Riedl et al. 2018). We tested both hypotheses through a predator exclusion experiment on multiple widely distributed NNI woody plant species of the northeastern, U.S., using forest songbirds as model insectivores. We expected NNI woody plants to support lower arthropod biomass and lower quality arthropods than native woody plants coexisting in the same system.

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 NNI 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 NNI plants, including Japanese barberry (*Berberis thunbergii)*, Morrow's honeysuckle (*Lonicera morrowii*), burning bush (*Eunonymous alatus*), and autumn olive (*Eleagnus umbellata*). For comparison, we chose six native shrubs and trees that commonly occur with these NNI woody plants in the understory of closed-canopy northeastern U.S. forests: striped maple (*Acer pennsylvanicum*), shadbush (*Amelanchier canadensis*), musclewood (*Carpinus caroliniana*), witch-hazel (*Hamamelis virginiana*), sweet birch (*Betula lenta*), and American beech (*Fagus grandifolia*). These ten NNI and native species collectively represented the dominant woody plants in the understory of our study area. Performing our experiment across these 10 species thus provided a community-wide perspective on the impacts of non-native plants on food webs, in the context in which NNI plant management decisions should be made (Westman 1990).

Bird exclusion experiment. From 4-27 May, 2021, we employed 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* a mesh netting that was draped over a single branch of a target plant and affixed using plastic zip-ties ("exclusion treatment"). Each of these branches were paired with a nearby (< 10 m away) unmanipulated control branch of the same species. We set up 12 treatment pairs for each of the 10 focal plant species, resulting in a total of 240 individual host plants in the study. At the end of the set-up period on 27 May, all 240 branches were gently tapped to dislodge arthropods 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, for a total of three repeated samples per branch. We struck each branch with a 0.3 m dowel while held over a $1 m^2$ 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. We kept the collected arthropods cool in the field in coolers with ice packs and then transferred them to a -80^{o} 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 0.6-2mL Eppendorf tubes and stored them at -80º 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 NNI plants. These C:N ratios were used to assess the protein content of invertebrates as an indicator of their quality as food for birds (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 non-native host plants, each representing a different trophic level above host plants: foliage-feeding herbivores (see Appendix S1: Selection of herbivores for C:N analysis) and predatory true spiders (Araneae). These two groupings of arthropods are prey for foliage-gleaning, insectivorous birds, and should differ in protein content because of their different trophic levels (Reeves et al. 2021), and their abundances are impacted by experimental manipulation of bird predation (Gunnarsson et al. 1996). Generally, insects feeing 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 in order 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 each model: (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 was fitted as a normally distributed GLMM after log-transformation and included both host plant species and bird exclusion treatment as fixed effects, and branch as a random effect. All abundance models were fitted with a negative binomial GLMM. In abundance models, non-native status (yes or no) was a fixed effect along with bird-exclusion treatment, and branch and host-plant species were included as random effects. Samples taken across the two sampling periods were pooled together in arthropod models to avoid pseudoreplication (Clark et al. 2016). Nitrogen content models were fit with a normal distribution, but since all arthropod samples were pooled across sampling periods and only taken from exclusion branches, only 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 across all groupings using Scheffe's method (following Midway et al. 2020) for P-value adjustment in unplanned contrasts. P-values and critical values were determined using the *car* package with analysis of deviance tests and $\chi 2$ test statistics (Fox et al 2015).

Log-response ratios. A follow-up GLM was employed using the LRR of exclusion treatments to investigate the interspecific variation in bird predation effects across all host plant species (Singer et al. 2012). Log-response ratios, 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, Wooton 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 NNI plants, an implicit assumption of both the ‘low food quantity hypothesis’ and the ‘low food quality hypothesis’. LRR values above zero indicate that predator effects are biologically and statistically significant, while those that intersect with zero are not.

Results:

We observed significant variation in total arthropod biomass among our ten focal host-plant species (Fig. 1, GLMM, $P = 0.001$, $\chi 2 = 26.62$, d.f. = 9). Collectively, native plants did not have significantly higher biomass than non-native plants in a grouped planned contrast ($P = 0.133$, t ratio = 1.5, d.f. = 223). Honeysuckle had higher biomass than the three other non-native plant species (Fig 1). Native plants varied in biomass, with musclewood, sweet birch and witch-hazel exhibiting relatively higher biomass than the other plants (Fig 1). We did not observe statistically significant variation among plant species in the effect size of bird predation as measured by LRR (Fig. 2, GLM, $P = 0.294$, $\chi2 = 10.73$, d.f. = 9). Furthermore, bird predation LLR was not significantly lower on NNI species than native species in a grouped planned contrast ($P = 0.364$, *t* ratio = 0.954, d.f. = 106). Bird predation reduced biomass of arthropods on all plant species except musclewood. Musclewood branches were associated with relatively high occupancy of aquatic insect orders (Fig S1).

Bird predation effects on abundance of arthropods among native-and non-native plants differed for each taxonomic group. Araneae abundance was higher on non-native plants overall (Fig. 3A, GLMM, $P < 0.001$, $\chi2 = 19.19$, d.f. = 1), while bird effects on Araneae abundance were significant on both native and non-native plants (Fig. 3A, GLMM, $P < 0.001$, $\chi2 = 57.18$, d.f. = 1). Hemiptera abundance was not significantly different between native and NNI plants (Fig 3B, GLMM, $P = 0.488$, $\chi2 = 0.479$, d.f. = 1), and bird predation did not significantly reduce Hemipteran abundance (Fig. 3B, GLMM, $P = 0.141$, $\chi2 = 2.15$, d.f. = 1). Bird predation effects were significant for lepidoptera (Fig. 3C, GLMM, $P < 0.001$, $\chi2 = 25.7$, d.f. = 1) and although there were fewer Lepidoptera on non-native plants (Fig. 3C, GLMM, $P = 0.022$, $\chi2 = 5.19$, d.f. = 1), bird predation effects on Lepidoptera did not significantly differ between natives and non-natives (GLMM interaction term for native vs. non-native plants and bird predation effect, $P = 0.614$, $\chi2 = 0.25$, d.f. = 1). Finally, we observed similar abundances of Orthoptera on both native and non-native plants (Fig. 3D, GLMM, $P = 0.941$, $\chi2 = 0.005$, d.f. = 1). Birds significantly reduced the abundance of orthoptera on both plant groups (Fig. 3D, GLMM, $P < 0.001$, $\chi2 = 15.6$, d.f. = 1).

We observed significant variation in the %N content by mass for herbivores among host plants (Fig. 4A, GLM, $P < 0.001$, $\chi2 = 38.4$, d.f. = 9). A grouped planned contrast showed significantly higher %N content by mass on the NNI than native plants (Fig 4A, planned contrast, $P = 0.001$, t ratio = -3.33, d.f. = 341). %N content was higher on honeysuckle than any other plant (Fig 4A). Spider %N content varied significantly among plants overall (Fig. 4B, GLM, $P < 0.001$, $\chi 2 = 59.61$, d.f. = 9), with lower values on non-native than native plants (Fig 4B, planned contrast, $P = 0.002$, t ratio = 3.19, d.f. = 341). Spider %N content was dramatically lower on Japanese barberry than any other plant species (Fig 4B).

Discussion:

The prevailing paradigm in habitat management and restoration assumes that all NNI plants are of little value or harmful to native wildlife. However, this broad-brush approach is based on region-specific case studies in which a single NNI plant is compared to a high-quality native plant, underemphasizing any contributions a NNI 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 (Shakleton et al. 2020). Our study found that NNI plants were not universally poorer hosts for insectivorous wildlife. These mixed results show that negative impacts of NNI should be demonstrated, not assumed, before extensive removal efforts are made— an approach proposed as early as Westman (1990). Furthermore, we provide a direct comparison between four incredibly widespread NNI plants and their co-occurring native plants. Given the tremendous drive for NNI plant removal in our region, we were surprised to see NNI plants supporting comparable abundances and protein-rich arthropod prey for songbirds. Moreover, songbirds appear to be foraging on these NNI plants with similar intensity, with strong bird predation effects found on all NNI and native plants. While our study does not suggest NNI plants have no negative ecological consequences, it does call into question whether the fervor with which NNI plants are removed, and the amount of conservation resources allocated towards their removal is sensible without more species-specific evidence that the NNI species being targeted are detrimental to wildlife.

Few studies have evaluated the simultaneous value of arthropod prey in terms of both quantity and quality at a plant community level. The results of our holistic approach revealed not all NNI 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'. Furthermore, support for the 'low food quality hypothesis' was mixed, with extremely variable arthropod protein content across NNI and native plants. We anticipated that herbivorous insects would be significantly lower in protein content on NNI plants but found no evidence for this assertion. However, on NNI plants like Japanese barberry, the protein content of spiders was significantly lower. Investigation of host plant-specific patterns suggest that the variance in food quality on non-native plants encompasses the range of quality of food found on native plants in the same habitat.

Our results suggest that common NNI plants in our study system are used as a foraging substrate by a major group of forest insectivores, birds, just as intensively as natives. Similar predation effect sizes are surprising given two established mechanisms that cause non-native plants to have different arthropod communities. First, leaf tissue is of lower quality or more highly defended than on native plants, reducing biomass of arthropods on NNI plants (van Hengstum et al. 2014). Second, the branch architecture or leaf shape of NNI 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). Spider abundance was higher on lowlying Japanese barberry, similar to other observations with NNI 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). Nevertheless, despite these differences we were surprised to see comparably strong predation effects on native and non-native plants. Thus, it appears that the introduction of non-native plants has not greatly impacted the interactions among higher trophic levels at our study site. 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 non-native 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 survey did not include *Prunus* (cherries) and *Quercus* (oaks), which are conventionally-known high-quality food plants for forest insects like caterpillars (Wagner 2005). One of the key priorities for NNI species research includes understanding the context of the invaded habitat (Ricciardi et al. 2021), and at our site, our study suggests that removal of NNI plants would not improve habitat quality without the subsequent establishment of higher-quality native plants. In other systems, it should be established in a given region whether native woody plants are superior foraging resources for songbirds, especially since the disturbances created by NNI plant removal can have unintended, negative impacts (Kettenring and Adams 2001). One particularly surprising observation in this study was the range in arthropod prey availability on our focal native plants. Witch hazel supported a greater total biomass than all species surveys, but native shadbush was substantially lower and statistically indistinguishable from non-natives. Consequently, the relative value of removing a non-native shrub will depend on the particular pairwise comparisons being made at a given site, as well as the density of NNI shrubs (Tarr 2022). Overall, our results suggest that a more nuanced management strategy for habitat improvement goals in eastern North American forests in which the native plant community is considered as the reference point in invaded habitats rather than assume that all non-natives are poorer food resources for wildlife.

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Figure captions

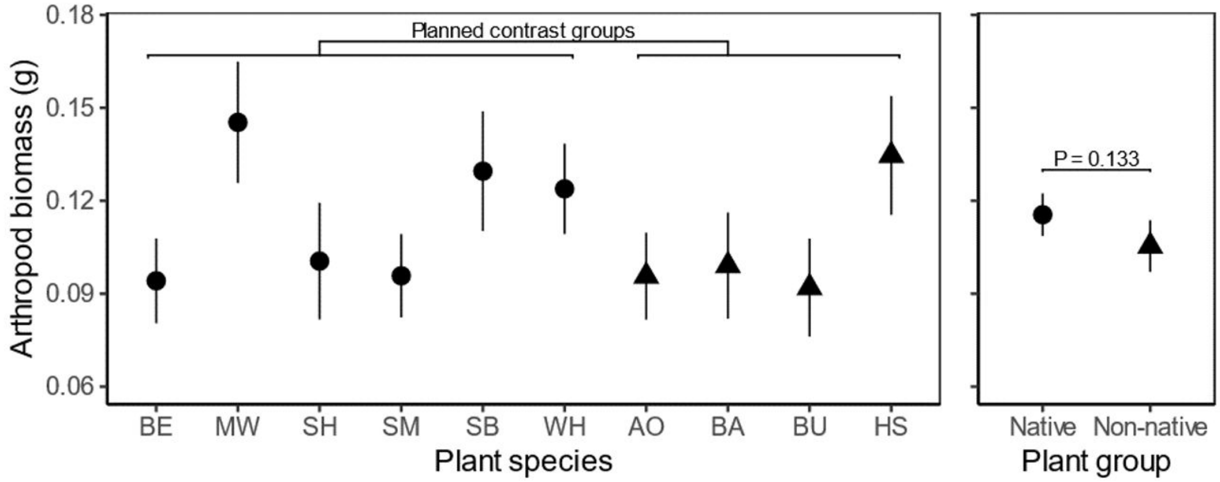
Fig. 1. Arthropod biomass (total grams per branch) among the ten sampled host-plant species. Pooled comparisons are between native and non-native plant groups. Biomass is reported as total wet mass collected from branches. Mean ± SEM is plotted, with levels of significance illustrated for native versus non-native plant groups using grouped, planned contrasts. BE is American beech (Fagus grandifolia), MW is musclewood (*Carpinus caroliniana)*, SH is shadbush (*Amelanchier canadensis*), SM is striped maple (*Acer pennsylvanicum*), SB is sweet birch (*Betula lenta*), WH is witch-hazel (*Hamamelis virginiana*), AO is autumn olive (*Eleagnus umbellata*), BA is Japanese barberry (*Berberis thunbergii*), BU is burning bush (*Eunonymous alatus*) and HS is Morrow's honeysuckle (*Lonicera morowii*).

Fig. 2. Effect size of bird exclusion treatment among ten sampled host-plant species and pooled comparison between native and non-native plant groups. Bird exclusion effect size reported as Log-Response Ratios (LRR), in which positive values > 0 indicate a significant reduction in arthropod abundance in response to bird predation. Mean ± SEM is plotted, with levels of significance illustrated for native versus non-native plant groups using grouped, planned contrasts. BE is American beech (Fagus grandifolia), MW is musclewood (*Carpinus caroliniana)*, SH is shadbush (*Amelanchier canadensis*), SM is striped maple (*Acer pennsylvanicum*), SB is sweet birch (*Betula lenta*), WH is witch-hazel (*Hamamelis virginiana*), AO is autumn olive (*Eleagnus umbellata*), BA is Japanese barberry (*Berberis thunbergii*), BU is burning bush (*Eunonymous alatus*) and HS is Morrow's honeysuckle (*Lonicera morowii*).

Fig. 3. Effects of bird-bag exclusion treatment under the context of native versus non-native host-plant groups. Points with lines connecting them are significantly different from each other if they have different letters (Scheffe's test for pairwise comparisons were completed for each of the eight sub-panels). Each panel indicates the response of a single taxonomic group and changes in Mean ± SEM abundance: 3a. Araneae (true spiders), 3b. Hemiptera (herbivorous true bug families), 3c. Lepidoptera (caterpillars), and 3d. Orthoptera (tree crickets and katydids).

Fig. 4. Total % nitrogen for insect herbivores (4a) and true spiders (4b) among ten host-plant species and pooled comparisons between native and non-native plant groups. 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. Only bagged branches were included in analysis (see Fig 1). Mean ± SEM is plotted with levels of significance illustrated for native versus non-native plant groups using grouped, planned contrasts. BE is American beech (Fagus grandifolia), MW is musclewood (*Carpinus caroliniana)*, SH is shadbush (*Amelanchier canadensis*), SM is striped maple (*Acer pennsylvanicum*), SB is sweet birch (*Betula lenta*), WH is witch-hazel (*Hamamelis virginiana*), AO is autumn olive (*Eleagnus umbellata*), BA is Japanese barberry (*Berberis thunbergii*), BU is burning bush (*Eunonymous alatus*) and HS is Morrow's honeysuckle (*Lonicera morowii*).

39 Fig. 1.



Planned contrast groups
Arthropod biomass (g)
0.18
0.15
0.12
0.09
0.06
BE
MW
SH
SM
SB
WH
AO
BA
BU
HS
Plant species
P = 0.133
Native
Non-native
Plant group

40

41

Fig 2.

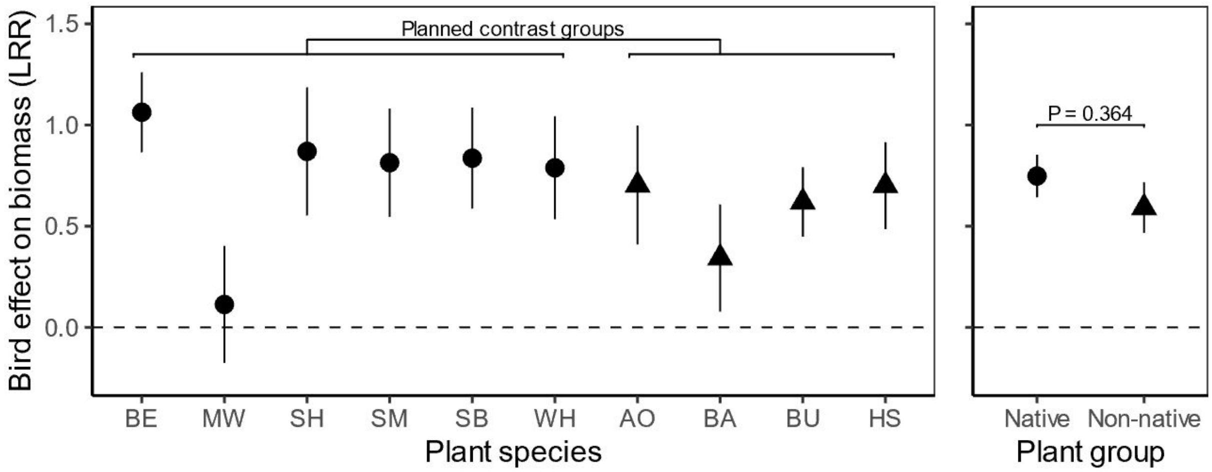
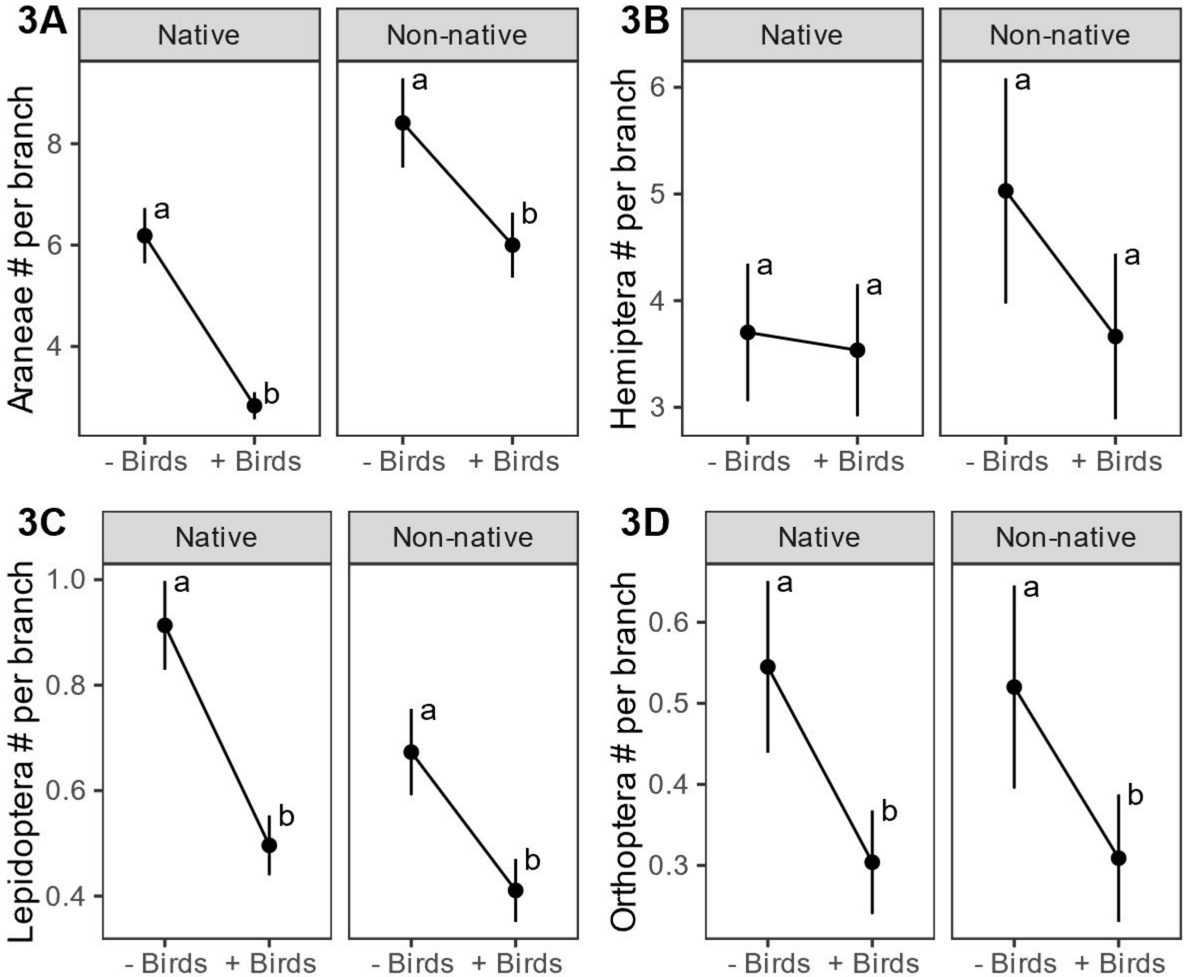
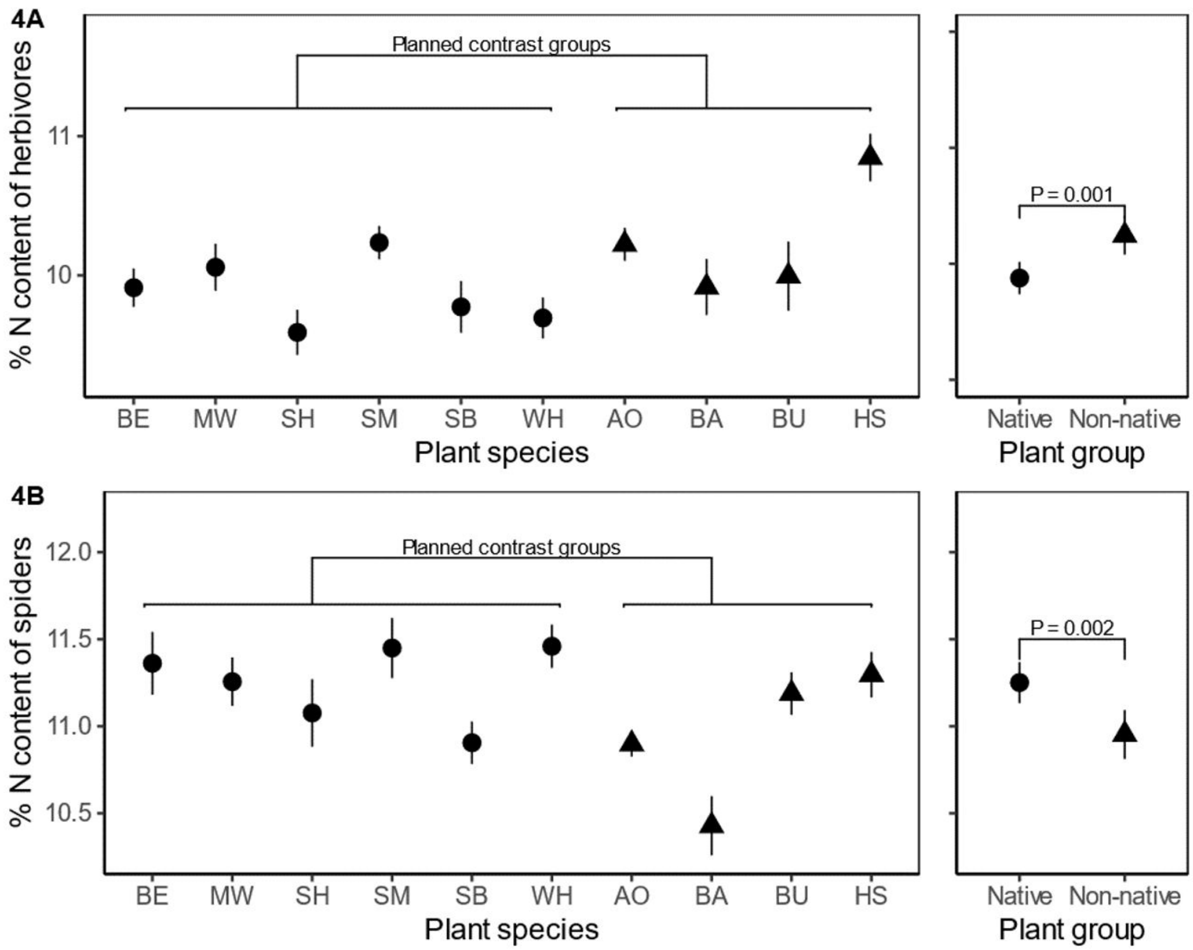

Planned contrast groups
P = 0.364
Bird effect on biomass (LRR)
1.5
1.0
0.5
0.0
BE
MW
SH
SM
SB
WH
AO
BA
BU
HS
Plant species
Native
Non-native
Plant group

Fig 3a, 3b, 3c, 3d.



52 Fig 4a, 4b.



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Supporting information (SI)

Appendix S1: Selection of arthropods for C:N analysis

We selected two broad functional groups to evaluate the differences in % nitrogen among native and non-native plants. Spiders (Araneae) were selected as indicators of the %N content of the third trophic level as arthropod predators. Our other function group were insect herbivores. We selected insect herbivores from families that were most likely to feed on plant foliage, particularly the foliate of woody plants included in our experiment. These represent the nutritional content of insect prey primarily available to bird and the numerical majority of arthropods collected. Insect herbivore families selected included: All families of Lepidoptera collected (primarily Geometridae and the superfamily Noctuoidea), Hemipteran families including Tingidae, Miridae, Coreidae, Pentatomidae, Acanthosomatidae, and Thyreocoridae. We included sawfly families Cimbicidae and Tenthrediniadae. The only beetle families selected were those likely to feed on foliage as adults or larvae, including Brentidae, Chrysomelidae, Cleridae, Curculinidae (only the subfamily Entiminae) and Melolonthinae.

Figure. S1. Average abundance of aquatic insects (# per bagged branches) among ten sampled host-plant species. Bar height indicates estimated mean from GLMM, and error bars indicate 95% confidence intervals. Bars with non-overlapping confidence intervals are significantly different. Bars ranked by estimated means.

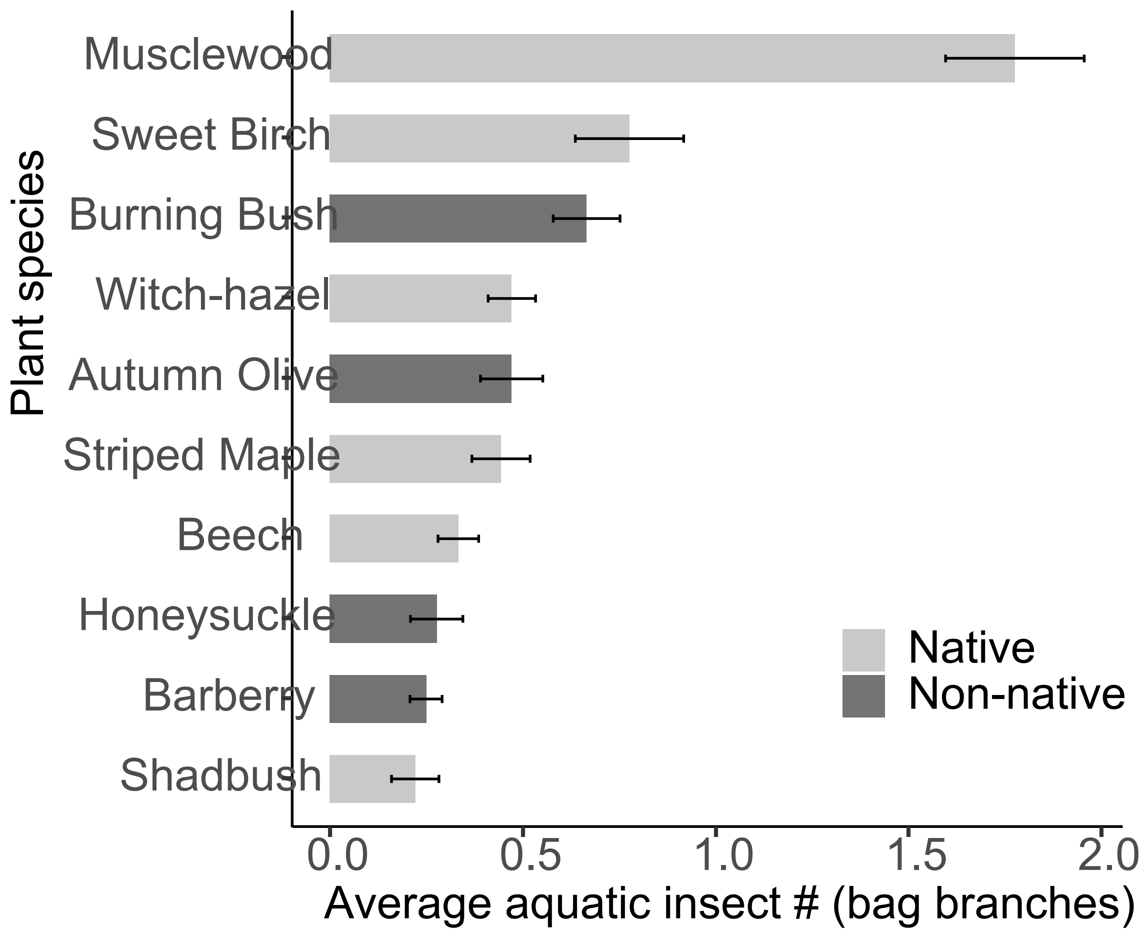

Fig. S2. Average abundance of lepidoptera (# of caterpillars per bagged branches) among ten sampled host-plant species. Bar height indicates estimated mean from GLMM, and error bars indicate 95% confidence intervals. Bars with non-overlapping confidence intervals are significantly different. Bars ranked by estimated means.

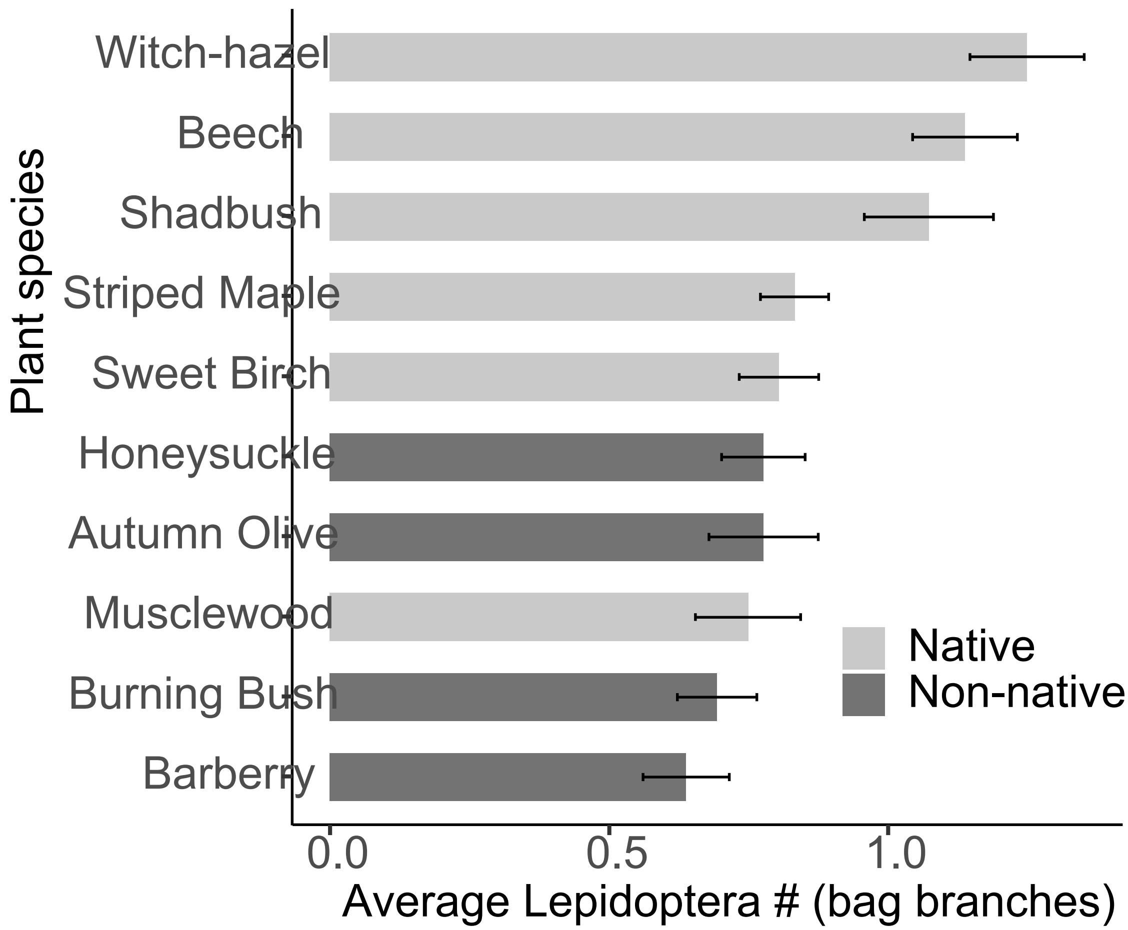

Fig. S3. Average abundance of spiders (# of spiders per bagged branch) among ten sampled-host plant species. Bar height indicates estimated mean from GLMM, and error bars indicate 95% confidence intervals. Bars with non-overlapping confidence intervals are significantly different. Bars ranked by estimated means.