Title:

Context matters when comparing the impacts of native and non-native plants on food webs: insights from a bird-exclusion experiment in a managed forest

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Abstract:

Biological invasions threaten biodiversity by outcompeting native species and disrupting food webs. Invasive species are now ranked as a leading cause for decline of biodiversity and protected species. Non-native woody plants are one group of invasive species that now occupy the majority of terrestrial ecosystems as a result of human activity. In eastern North American temperate forests, understory plant communities are frequently dominated by non-native shrubs. For many species of insectivorous birds and mammals, invasive plants threaten populations by provided less food resources and/or food resources of lower quality. Conservation organizations expend significant effort to remove invasive plants, but evidence that this removal improves food availability to wildlife is lacking. In this project, we examined food webs among four species of invasive shrubs in contrast to six species of native woody plants found in the same habitats. Using a predator-exclusion experiment bird predation effect size, arthropod biomass available to insectivorous birds, abundance of major arthropod taxonomic groups, and the nitrogen content of herbivores and spiders as a proxy for protein availability. All four lines of evidence suggest that invasive plants do not always provide poorer foraging to songbirds. Compared to nearby native plants, some invasive plant species like Honeysuckles provided higher arthropod biomass with a higher nitrogen content. Conversely, Japanese barberry had fewer arthropods and spider prey had significantly lower nitrogen content. Contrary to predictions, the predation effects of birds were of similar magnitude on both native and non-natives, suggesting insectivorous songbirds actively forage non-native plants for prey. A more nuanced approach to invasive plant management should be considered that prioritizes species that are low-quality foraging opportunities relative to the local plant community.

Keywords:

Invasive species, invasive plants, insectivores, songbirds, forests, food webs, habitat improvement

Introduction:

*P1 – The impacts of invasive species and why prioritizing removal is important*

Invasive species are a leading cause of biodiversity decline globally (Bellard et al. 2016), with an estimate impact and cost of management totaling $120 billion dollars in the United States alone (Pimental et al. 2007). Removal of invasive species is costly, but it can potentially be an effective way to improve habitat for wildlife. Invasive 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). For example, however, the cost of management in just one U.S. state, California, totals $82 million dollars annually for invasive plant removal efforts (California Invasive Plant Council, 2022). In principle, removing invasive species improves the quality of habitat for native plants (Hartman and McCarthy, 2004) and native wildlife (Schneider and Miller, 2014). Notably, removal of particularly aggressive invasive plant species that form monocultures can drive recovery of arthropod assemblages, which are an important indicator of food availability for wildlife (Gratton and Denno, 2005). However, despite the dramatic efforts to remove established invasive plant populations from managed habitats, there is still not a consensus on whether such practices actually impact the arthropod communities that are prey for wildlife (Robichaud et al. 2021, Traylor et al. 2022). One key gap in effective management decision making is establishing under what contexts invasive species removal may not be necessary. Decisions about prioritizing some invasive species removal over others is critical since the financial resources for habitat and species conservation are severely limited relative to the ecological challenge at hand (Arponen 2012).

*P2– Broad mechanisms by which invasive plants disrupt food webs*

Plant invasions have cascading impacts on ecological communities because they directly modify both above-ground and soil food webs (McCary et al. 2016). Invasive plants are particularly prevalent in habitats that have experienced frequent anthropogenic disturbance (Mosher et al. 2009, Wang et al. 2016), meaning their impacts are most pronounced in areas where wildlife may already be distressed. Furthermore, new invasive plant species are expected to continue to accumulate in anthropogenically modified habitats (Seebens et al. 2017). Consequently, a significant amount of ecological research has focused on understand them mechanism by which invasive plants disrupt food webs and wildlife. Typically, invasive plants dominate or form monocultures and displace native plant species, negatively impacting native animals indirectly (Fletcher et al. 2019). In habitats dominated by invasive plants, less or lower quality arthropod prey is available to insectivorous birds and mammals (Gerber et al. 2008, Riedl et al. 2018). However, nutritional quality for herbivores is just one of multiple traits of invasive plants that impacts food webs. Compounds released from invasive plants through roots and decaying leaves can impact detritus-based food webs (Robison et al. 2021). Additionally, invasive 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. 2020). Each of these trait-based mechanisms provides some insight into the consequences of plant invasion, but cross-species comparisons are needed to help elucidate these pathways. For example, Lind and Parker, 2010 compared a range of plant species testing the hypothesis that invasive plants have significantly different defensive chemistry than natives, but this hypothesis was only supported for a small proportion of the invasive plants examined. For this reason, our study includes a comparison of a community of non-native plants to a community of native plants in a shared environment.

*P3 – Setting up the background for hypotheses and predictions*

Often for studies on arthropod food webs, comparisons are made between native and non-native species that are in the same genera and are expected to have similar phytochemistry and thus shared defensive traits (Lampert et al. 2022, many other studies). Similarly, in comparable habitats, locations dominated by invasive plants often have lower abundances of plant-feeding arthropods, particularly caterpillars (Richard et al. 2019). As a result of lower nutritional quality, invasive plants may have fewer herbivores, shrinking the biomass in the second trophic level (Clark and Seewagen 2019). It is expected that by removing invasive plants, native plants would have an opportunity to recover, thus restoring ecosystem services (Hopfensperger et al. 2017). In landscaping scenarios native plants which provide more insect prey are suggested as replacements for exotic shrubs to help bird populations (Narango et al. 2018, Kramer et al. 2019). However, in managed forests just removal is typically employed without replacement and local native plants recover that were already within that habitat fragment (Flory and Clay 2009, Shields et al. 2015, Farmer et al. 2016, Cutway 2017). However, for wildlife, implicit in this assumption is that native plants typically found in the same disturbed forests provide more arthropod prey or higher quality arthropod prey. To our knowledge this has not been tested in northeastern US forests or any other system for that matter.

*P4 – Hypotheses and predictions*

We tested two hypotheses (1) a ‘low food availability’ hypothesis (2) ‘low food quality hypothesis’. In the low food availability hypothesis, non-native plants are expected to have significantly lower prey available for insectivores compared to native plants in the same environment. Indeed, there is broad, community-level evidence that non-native plants have lower insect abundance and diversity (Tallamy et al. 2020). In the ‘low foraging oppurtunity’ hypothesis, taxonomic groups of high value (e.g., caterpillars) are expected to be less available (Narango et al. 2018). Conversely, in the ‘low food quality’ hypothesis, those prey items that are available on non-native plants are lower in protein content compared to native plants (citation?). In this study we used percent nitrogen content of arthropods as an indicator to protein availability and quality (Reeves et al. 2021). Thus, we predicted lower arthropod nitrogen content in non-native plants compared to natives. Finally, in both hypothesis, predators forage on invasive plants less, leading to weaker predator effects on arthropods. Due to lower abundance and quality of prey, insectivorous songbirds will make optimal foraging decisions and invest less effort into finding food on invasives (Riedl et al. 2018).

Methods:

*P5– Site information*

We performed a selective predator exclusion treatment on ten woody host plant species at Great Hollow Nature Preserve & Ecological Research center (Fairfield Co., Connecticut, USA). This 334-hectare forest preserve follows a forest conservation plan managing for wildlife habitat and outdoor education. We intentionally chose closed-canopy plots within this site that would be candidates for invasive shrub removal targeting Japanese barberry (*Berberis thunbergii)*, invasive bush honeysuckles, *Lonicera* spp. (our experiments only sampled *Lonicera mackii*), burning bush (*Eunonymous alatus*), and autumn olive (*Eleagnus umbellata*). Native understory shrubs and understory trees included striped maple *Acer pennsylvanicum*, shadbush (*Amelanchier canadensis*), musclewood (*Carpinus caroliniana*), and witch-hazel (*Hamamelis virginiana*). Our experiment occurred in areas where the overstory tree composition is dominated by sweet birch (*Betula lenta*) and American beech (*Fagus grandifolia*). As these ten species were the dominant woody plants in the selected habitat, we performed experiments on all to provide a community-wide perspective on the impacts of invasive plants on food webs compared to adjacent native woody plants.

*P6 – Predator exclusion methods*

From May 4th to May 27th, 2021, we employed a predator exclusion experiment in a paired design (following Singer et al. 2012). Insectivorous birds were prevented from foraging on branches *via* a mesh netting that was draped over branches and affixed to the base of the branch using Velcro (“- birds” treatment). Each of these branches were paired with a nearby (< 10m) unmanipulated control branch (“+ birds” treatment). We set up treatments on 12 pairs for each of ten focal woody plant species for a total of 240 individual host plants. At the end of the set-up period after May 27th branches were gently tapped to dislodge arthropods from all branches to avoid bias caused by the disturbance of setting up bag treatments. For sampling, arthropod abundance was quantified by collecting all foliage-foraging invertebrates using a branch-beating technique employed for sampling forest caterpillars (e.g. Wagner 2005). Each branch was struck with a 0.3m long dowel while hanging over a 1m2 ripstop fabric beat sheet. All invertebrates that landed on the sheet were collected via aspirators or soft-touch aluminum forceps. Each of these 240 plants were sampled in this same manner, every other week for a total of three repeated samples. We combined these repeated samples in all analyses to produce a broader-scale estimate of total arthropod prey availability per plant (following Clark et al. 2016).

*P7 – arthropod id and processing*

All invertebrates collected in the field were transferred immediately to 7 × 3cm plastic vials or 16 × 8cm plastic zip-top bags and preserved in a –18° C lab freezer. Afterwards, specimens collected on entire experimental branches were weighed (wet mass) on a 10^-4 g microbalance. All invertebrates were identified to class. Common arthropod species (those observed > 25 times) were then identified to order, and all insects in the orders Lepidoptera, Hemiptera, Hymenoptera were identified to family. True spiders (Araneae) and Opiliones were identified to family as well. Once identifications were complete in August 2021, all taxonomic groups from each individual branch sample and placed into 0.6mL and 2mL Eppendorf tubes kept in a -80C lab freezer. 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.

*P8 – Nitrogen content methods*

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 1a: Selection of herbivores for C:N analysis) and predatory true spiders (Araneae). These two groupings of arthropods are prey for insectivorous birds on trees and their abundances are impacted by experimental manipulation of bird predation (e.g. Gunnarsson et al. 1996). Samples were assayed for C:N ratios as an indirect measure of protein availability, a nutritional factor which strongly mediates food selection behavior (Robbins et al. 2005). To do so we did the following…

*P9 – Stats methods*

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). These univariate analyses use the following as response variables for each model: (1) total arthropod biomass sampled per plant in grams, (2) spider abundance (Araneae), (3) caterpillar abundance (Lepidoptera), (4) Hemiptera abundance (5) Orthoptera abundance, (6) N Content of herbivorous insects and (7) N content of spiders. Arthropod biomass (1) was fitted as normally distributed variable after a log-transformation. All abundance models were fitted using the negative binomial distribution. Finally, nitrogen content models were fit as a normal distribution using % mass out of the total mass of a sample. Posthoc 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 (Fox et al 2015).

*P10 –Leaf count diagnostics*

In addition to our primary seven models outlined above, we performed a set of diagnostic tests to determine the impact of leaf counts on arthropod biomass among host-plant species. Leaf density or leaf area are traits relevant to herbivore community composition (Barbour et al. 2015), and leaf traits may be different in invasive plants compared to co-occurring native plants (Leishman et al. 2007). At the conclusion of the primary experiment in summer 2022, we counted all leaves for all 240 trees and shrubs sampled in the project. In this diagnostic step, we found no evidence that leaf counts significantly impacted arthropod abundance, biomass, or bird treatment effects in this experiment (Appendix 1b: Leaf counting methods and data analysis).

Results:

*P11 – Arthropod biomass across the ten species (Fig 1) and bird treatments (Fig 2)*

We observed significant variation in the available, total biomass of arthropods among our ten focal host-plant species (Tree effect on biomass on bagged branches). Native plants exhibited higher biomass compared to invasive plants in a grouped planned contrast (P = 0.089), however this difference was only significant at α = 0.1. Investigation of biomass means suggests that honeysuckle may have higher biomass than other invasive plant species, autumn olive, Japanese barberry, and burning bush. Native plants varied in biomass, with witch-hazel appearing relatively higher than other native plants. Following these results, we observed significant variation in the effect size of bird predation as measured by LRR. Bird predation effects were higher than zero for all host-plant species except for musclewood (Fig. 2). We observed no evidence that bird predation was weaker on non-native species in a grouped plant contrast (P = 0.364).

*P12 – community composition reporting what taxonomic groups birds are removing from native and non-native plants*

Our analysis of bird predation among native-and non-native plants for each of four separate taxonomic groups suggested bird effects are relatively similar on both groups of plants. Araneae (true spiders) were more common on non-native plants overall (cite table rather than figure here), while bird effects were significant on both native and non-native plants (Fig. 3A, Table x). Hemiptera were more common on non-native plants as well (cite table rather than figure here too), but bird predation effects were not significant for this group (Fig. 3B, Table x). Fitting with predictions from other studies on caterpillar abundance, we observed fewer Lepidoptera on non-native plants. Despite the lower abundance, bird predation effects were significant on both natives and non-natives (Fig. 3C, Table x). Finally, we observed similar abundances of Orthoptera (tree crickets and katydids) on both native and non-native plants. Bird significantly reduced the abundance of orthoptera on both plant groups as well (Fig. 3D, Table x).

*P13 – Nutritional quality data*

We observed significant variation in the %N content by mass for herbivores among the ten sampled host-plant species (Fig. 4A, Table x). For non-native plants, our grouped planned contrast suggested significantly higher %N content by mass compared to natives (Fig 4A, P = 0.001). Mirroring our observed higher arthropod biomass result, we saw the highest N content on honeysuckle. For spider %N content by mass, we also saw significant variation among the ten sampled host-plant species (Fig 4B, Table x). Conversely, spider %N content was significantly lower on non-native plants compared to native plants. Japanese barberry had the lowest %N content.

Discussion:

*P14 –* *Recapping results in a big picture way*

Invasive species is an environmental problem on a massive scale. Introduced organisms have had a dramatic impact on ecosystems and economies, with some conservative estimates for monetary impacts of $1.26 trillion US dollars in North America since 1960 (Crystal-Ornelas et al. 2021). A problem of this scope requires careful strategic planning in which the most damaging invasive species are prioritized. Our results address a long-standing question on whether some invasive species in the same habitat are more damaging than others. While we have evidence that invasive plants certainly disrupt food webs and have altered trophic interactions, most were not strictly poorer foraging opportunities than native woody plants in the same habitat. More specifically, we observed major ecological differences in the composition of arthropod communities among native and non-native plants, with lower biomass and fewer caterpillars on most invasive plant species. However, our results also contradict work arguing that non-native plants provide little or no food resources to migratory songbirds since songbirds removed prey at equal rates and there was no consistent drop in nutritional quality.

*P15 –* *Linking it to past work on arthropod food webs and invasive plants*

Two primary mechanistic hypotheses have been tested with respect to invasive plants and their impacts on above-ground food webs. First, the nutritional quality of these plants is considered lower due to reduced nitrogen content (nutritional quality citations) and contextually higher defenses (non-co-evolved defenses citations) compared to native plants. Consequently, herbivores are less abundant, making the base of arthropod food webs less robust (rephrase later). Second, the architecture is often unique, providing a different microhabitat for arthropods and thus creating a distinct community compared to native plants (citations from spider work). While our study does not distinguish between either of these mechanisms nor tests these hypotheses directly, their predictions help explain several of the patterns we observed. Fitting with observations on other woody invasive plants, we observed higher spider abundance on our invasive plants. Likely differences in twig and leaf architecture provide superior scaffolding and hunting territory (citations from spider behavior). Interestingly, bird predation effects were still of a similar magnitude compared to natives, suggesting that spiders do not achieve enemy free space from insectivorous songbirds (e.g. enemy free space papers). Conversely, herbivores like caterpillars (Lepidoptera) were less abundant on invasive plants, likely owing to their inferior nutritional quality, but other mechanisms, such as increased threat from spider predation may also be important. Equivalent abundances of another major herbivore functional group, the Orthoptera, suggest that mobile grazing generalists may not be as constrained by the lower nutritional quality of invasive plants as they can forage on both types of hosts.

*P16 –* *Linking it to bird nutritional ecology done by other people in the region*

One of the key gaps in past research is demonstrating not only that differences in arthropod communities are different among native and non-native plants, but also that predators have altered top-down effects. We chose to use broad taxonomic groups of arthropods as that approach can be informative for aggregating effects over complex systems (*sensu* Wagner et al. 2021). Despite the differences in the abundance of caterpillars and spiders among native and non-natives hosts, we were surprised to see similar rates of bird predation effects on arthropod biomass. It stands to reason that insectivorous songbirds actively forage on and take prey from invasive plants, and there was no evidence that these predators have weaker effects on invasives either. It is important to note that in our specific case study, some high-quality plants are rare or absent from the understory in which invasive plants were dominant (how to cite this).

*P17 –* *Take it home: broader implications and future work needed*

Overall, our results suggest that a more nuanced management strategy for habitat improvement goals in northeastern US forests. First, the comparison to native plants that have been displaced by invasives are a critical comparison point. It should be stablished in a given region whether native woody plants are superior foraging opportunities for songbirds. In other words, management should prioritize removal of some invasive plants. Conversely, habitat improvement should facilitate the recovery of higher-quality host plants for caterpillars like Oak and Cherry if possible since these provide more prey for migratory songbirds (Tallamy citation). Insectivorous songbirds may compensate by shifting diet to other insect prey other than caterpillars (Tarr 2022).