Important notes from Rob:

*King and Tschinkel, 2008, our model PNAS paper is 3,500 words. Keep it short and to the point.*

Title(s):

Are invasive plants always poorer foraging opportunities for insectivorous songbirds?

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. Removal of invasive shrubs is a stated goal of habitat improvement, a practice that costs conservation organizations xxx million dollars a year. 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. In this project, we tested the hypothesis that food availability and food quality for insectivorous songbirds is lower on inside woody plants compared to native woody plants in the same habitat. However, relatively few studies compare communities of invasive shrubs to adjacent communities of native plants. We examined food webs among four species of invasive shrubs in contrast to six species of native woody plants 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. Notably, the predation effects of birds were not significantly different among plant species, suggesting insectivorous songbirds actively forage and prey on arthropods on invasive plants at the same rate as native plants. Our results suggest a more nuanced approach to invasive plant management that prioritizes species that are low-quality foraging opportunities in the context of the local plant community.

Keywords:

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

Introduction:

*P1 – The impacts of invasive plants and cost of removal*

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 benefit native plants or wildlife (citation from global plant invasions). One key gap in this understanding is under what contexts invasive species removal may not be necessary. This gap is crucial to fill since resources for habitat and species conservation are severely limited relative to the ecological challenge at hand (reference for general conservation biology needs).

*P2 – Negative impacts on wildlife as a case study in invasive plant biology*

Plant invasions have cascading impacts on all higher trophic levels by altering above-ground and below-ground food webs. Changes to food chains as a result of plant invasions has been documented in nearly every terrestrial ecosystem, and it is particularly prevalent in habitats experience frequent anthropogenic disturbance (meta-analysis citations). To ameliorate these negative impacts, invasive plant removal if a central feature of habitat improvement plans. In some systems, removal of invasive plants has promoted healthy wildlife populations and facilitate the recovery of declining species (find case studies). In many cases, invasive plant removal plans suggest removal of all non-native woody species. Frequently non-native co-occur and have overlapping impact areas (citation on co-occurring invasives). Understanding the impacts of non-natives on wildlife is an important goal as new invasive plant species are expected to accumulate (Seebens et al. 2017 citation from chapter 8 of GPI).

*P3 – Motivations for invasive plant management and the implicit assumptions about lower food quality in habitat restoration efforts*

The mechanisms by which invasive plants disrupt forest food webs has been well documented, but broad patterns still differ among host species. Typically, invasive plants are lower quality food sources for insect herbivores compared to native conspecifics (there are a million citations on this, a few from stuff like Norway maple would be ideal). As a result of lower nutritional quality, these invasive plants can host dramatically lower herbivore abundance and fewer species of herbivores. In cases where invasive plants have displaced natives, prey availability for insectivorous birds and mammals are significantly reduced. However, nutritional quality for herbivores is just one of multiple traits of invasive plants that impacts food webs. Allelopathic compounds released from invasive plants through roots and decaying leaves can impact soil food webs and insect prey. Furthermore, invasive plants have atypical architecture compared to native plants (spider paper citations), leading to different compositions of arthropods independent of the host plant quality (more of the spider paper citations).

*P3a – Setting up hypotheses and predictions*

It is expected that by removing invasive plants, native plants would grow in their place. But implicit in this assumption is that native plants typically found in disturbed forests (those prone to invasion) are higher quality. However, to our knowledge this is rarely tested. In landscaping scenarios native plants like cherry and white oak are suggested as replacements for exotic shrubs, but in managed forests just removal is suggested.

Really good quote from Wagner et al. PNAS paper:

*One way that researchers have dealt with the complexity of population-level stochasticity in insects is to aggregate data at higher taxonomic levels: For example, using total insect biomass as a proxy for biodiversity, or aggregating data across different sites. Studies that generalize across datasets, higher taxonomic categories, or ecological groups (e.g., refs. 17, 18, 51, and 52) provide much-needed perspectives relevant to ecological function as, for example, the amount of insect food available to nestlings (53) and other insectivores or the general health of a region’s pollinators.*

*P4 – Hypotheses and predictions (this paragraph is not in other PNAS papers, but its important to me to use it as a narrative tool)*

At the community level, non-native plants are expected to have significantly lower prey available for insectivores compared to native plants in the same environment. Furthermore, the insect prey found on non-native plants expected to have lower nutritional quality for these insectivores as well (citation on N content of bugs on invasives). Due to lower abundance and quality of prey, it is generally anticipated that vertebrate insectivores will make optimal foraging decisions and invest less effort into finding food on invasives. As a consequence, the predatory effects of these insectivores should be weaker overall on non-natives vs. native plants. In our system, we tested these three paired hypotheses & predictions. First, that in a shared habitat a group of native woody plant species should have more insect prey than non-native woody species. Second, predation effects will be weaker on native vs non-natives plants overall in the same habitat where insectivore habitats overlap. Third, the nutritional quality of herbivores and other arthropods should be lower on natives vs. natives within these same managed habitats as well.

Methods:

*In PNAS Methods are presented at the end. To save space some methods are put into the supporting information documents*

Results:

P6 – 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).

P7 – 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).

P8 – 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:

P9 – *Recapping results in a big picture way*

Our results validate the overwhelming evidence that invasive plants disrupt food webs in managed ecosystems (key trophic invasive plant papers). We observed major ecological differences in the composition of arthropod communities among native and non-native plants. The structure of arthropod food webs was distinctly different than those seen on native plants. However, our results also contradict work arguing that non-native plants provide little or no food resources to migratory songbirds. This is troubling since invasive plant removal is the leading focus of habitat improvement, costing government and non-profit organizations millions of dollars a year. With respect for nutritional quality of arthropod prey on invasive plants, our results suggest that a more nuanced management strategy be in place that prioritizes removal of invasive plants that are exceptionally poor foraging opportunities for songbirds. In some cases, there are clearly invasive plants that are not significantly worse in terms of abundance or nitrogen availability, and it would be up to the stakeholders to decide if it is still worth investing significant resources to remove such species.

P10 – 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.

P11 – *Linking it to bird nutritional ecology done by other people in the region*

Despite the differences in arthropod community composition 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 take less biomass from invasive species.

P12 – *Take it home: broader implications and future work needed*

Methods:

P13 – 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 834-hectare forest preserve follows a USDA forestry conservation plan aimed at managing for outdoor recreation and wildlife habitat. We intentionally chose locations that would typically be targeted for invasive shrub removal, with a dense understory including Japanese barberry (*Berberis thunbergii)*, invasive bush honeysuckles, *Lonicera* spp. (primarily *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 native woody plants.

P14 – Predation manipulation

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”). Each of these branches were paired with a nearby (< 10m) unmanipulated control branch (“+ birds”). We set up treatments on 12 pairs for each of ten focal woody plant species, consequently a total of 240 plants were sampled this way. At the end of the set-up period after May 27th branches were gently tapped to dislodge arthropods so the sampling occurring exactly 2 weeks later was measured from the same exact starting point. Afterwards, each of these 240 plants were sampled three times in the same order and with the same time duration (in days) between set up and sampling. These three repeated sampled brought the number of arthropod community samples up to 720 (sampling methods following Clark et al 2016). Arthropod abundance was quantified by collecting all foliage-foraging invertebrates using branch-beating (branch beating citation). Each branch was struck with a 0.3m 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.

P14 – 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. All invertebrate sorting and taxonomic identifications were completed from June 2021 to August 2021. Once identifications were complete, all taxonomic groups from each individual branch sample and placed into 0.6mL and 2mL Eppendorf tubes kept in the lab freezer for later processing.

P15 – nutritional quality 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. Foliage-feeding herbivores included the three most common insect orders collected in our experiment: Hemiptera (True bugs not including predatory true bugs), Orthoptera, and Lepidoptera. Several families of known insect herbivores were included in this method (see Appendix 1) in order to assure a complete picture of the nutritional quality of insect herbivore likely to be eaten by insectivores. Spiders (Araneae) were among the most abundant arthropod orders and are known to be important prey for insectivorous, migratory songbirds (birds eating spidahs citation). These two groupings of arthropod samples were assayed for percent nitrogen content as a proxy for nutritional quality for insectivores (i.e. relative protein content). [Can you guys write up the technical details of the C:N methods?]

P16 – stats methods 1

We employed a series of Generalized Linear Mixed Models (GLMMs) using the lme4 package (citation) in R version 4.1.2 (citation). These univariate analyses use the following as response variables: (1) total arthropod biomass sampled per plant in grams, (2) spider abundance (Araneae), (3) caterpillar abundance (Lepidoptera), (4) Hemiptera abundance, and (5) aquatic insect abundance (Stoneflies and Mayflies), (6) C:N Content of spiders, and (7) C:N content of putative herbivores. Arthropod biomass (1) was fitted as normally distributed variable after a log-transformation. All abundance models were fitted using the negative binomial distribution (citations). C:N ratio models were fit using the xxx distribution (or this fitted as % mass that is N). Related to these GLMM’s, we performed a set of diagnostic tests to determine the impact of leaf counts on arthropod biomass among host-plant species (Appendix 1). Posthoc tests comparing changes in biomass, spider abundance, true bug abundance, caterpillar abundance, and tree cricket & katydid abundance were run using the emmeans package in R (Lenth 2009). Differences were investigated across all groupings using Scheffe’s method (following Midway et al. 2020) for P-value adjustment in unplanned contrasts.

P16 – stats methods 2 **[overflow for field methods information or C:N ratio analyses. We probably want more about the experimental design and location, maybe each in their own paragraph]**

P18 – **(K&T had 6 short methods paragraphs, but I don’t think we need that much, save the space for the intro or results)**