Biological Invasions

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

--Manuscript Draft--

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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 had fewer arthropods overall and arthropods of lower protein quality 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.
Response to Reviewers:	Dear Associate Editor: Thank you for facilitating multiple reviews for our manuscript. We will start out by sharing that we understand concerns from reviewers that readers may draw

conclusions about invasive plant management which could be counterproductive. We have taken the suggestions seriously from the last two reviewers and believe the manuscript is improved. We have changed the title, introduction, and conclusions to better reflect the results and qualify the regional nature of the work. Importantly, we made efforts to highlight the rationale behind comparing the specific invasive and native plants in this experiment vs other potential species. We clarified issues on whether figures and results compare plant biomass or arthropod biomass as well.
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Please don’t hesitate to ask us for input or changes on any of these edits.
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Reviewer #2:
The authors have addressed my concerns in great detail and I appreciate that. They claim I misinterpreted the goal of their study and they are correct. But if I did, so will others, so I ask for a more explicit description of the goal. I concluded, based on phrases used throughout the paper, such as "Our finding that the predation effect of birds on arthropod biomass was similar between natives and non-natives shows that birds recognize the non-natives as a quality food source and exploit them just as often as the native plants." that the comparisons were based in large part on trophic contributions of the plants themselves. For example, the title "Are native plants always better for wildlife than invasives?" implies that it is the contributions of the plants themselves to local food webs, not of the surrounding habitat that is being examined. Birds do not eat plant architecture. I understand that the architecture may have attracted prey items from elsewhere and therefore made it available to the birds. But readers of the first version of this paper had to work hard to draw this conclusion. All I'm asking is that the authors recognize the potential for confusion here and work a little harder to make sure readers know what the paper is actually about.

The authors conclude their response to my review by saying: "Lastly, and most importantly, our objective was never to narrowly compare the insect productivity of native and non-native plants, despite the reviewer's interpretation as such. In fact, neither the word "produce" nor the word "productivity" appear once in the text of our manuscript. Instead, our stated goal on lines 89-92 of the introduction was to establish whether target invasive species offer lower quality food resources to insectivorous birds. The food resources on a plant available to birds potentially include all arthropods present, not just those "produced" by the plant and especially not just those "produced" in the very narrow sense of having direct trophic connections to the plant." The authors may think the difference between the word "produce" and "offer" is clear to all, but I still argue that the goal can be made more explicit. The explanation they provide above should be included in the introduction. They go on to say that "nontrophic contributions to food webs have been undervalued and understudied." and " The food resources on a plant available to birds potentially include all arthropods present, not just those "produced" by the plant and especially not just those "produced" in the very narrow sense of having direct trophic connections to the plant." This is the type of discussion I would like to see enhance throughout`. How about changing the title to something like "Do native plants always make more food available to local food webs?" I'm just

thinking out loud here.
We thank the reviewer for letting us know the goals of the study are not clear to them. We have restructured the last two paragraphs of the introduction (Lines 85-112) and changed the title to hopefully clarify our objectives better. We have also attempted to clarify that we considered the prey provided by plants to insectivorous birds to include all arthropods found on them because plants support arthropods both directly (e.g., host insects, herbivores) and indirectly (e.g., predators) (Introduction, lines 100-110).

Another point I wish the authors would address more thoroughly is the state of the habitats in which they did their study. The authors argue in their response to my review that it is appropriate to compare nonnatives to depauperate native plant communities because that is what is typically out there. I get that, but they should not use language that implies that nonnatives are equal in their trophic contributions to the natives like oaks etc. that actually drive productive food webs. I recommend that they discuss the point that their study did not include powerhouse natives. Their comparison is between invaded habitats and degraded native habitats. The authors suggest that because invaded habitats are just as productive as native habitats, we should be "more nuanced" in our treatment of invaded habitats. One could also interpret these results in the following way: the fact that degraded native habitats are no more productive than habitats invaded by Asian plants emphasizes how important it is to restore high producing natives to degraded sites.
To clarify, our study site is not considered to have depauperate plant communities and is only disturbed in the sense that nearly 100% of the forests of the northeastern U.S. are disturbed due to a long history of anthropogenic influences since European colonization. We would argue there is no such thing as a truly undisturbed forest in the Northeast. Our study site is an 825-acre nature preserve surrounded by thousands of acres of additional protected forest in CT and neighboring NY. As such, our study system is relatively undisturbed compared to the more densely developed and fragmented areas of western CT and southern NY. Our point was that across the entire region, oaks have been in steep decline for nearly a century and are being widely replaced by the native species we studied and others, even in large protected areas. In Connecticut specifically, red oak was formerly the most numerically dominant tree species but has been surpassed in recent decades by two of our study species (American beech, sweet birch), sugar maple, and red maple. Our study species are among the most realistic alternatives to non-native species when non-natives are removed by land managers without subsequent active planting and ongoing support of oak establishment. In other words, our study species, not oaks, are among the most likely natives to passively fill the void after invasive plants are removed. Our study therefore asked whether the replacement of invasives by such natives improves food abundance and quality for insectivorous birds and warrants the effort and cost to remove the invasives. Given the rapidly changing composition of northeastern forests, this has far greater application and relevance to invasive plant management than a comparison of invasive plants to disappearing oaks. We have revised the introduction (Lines 85-96), methods (Lines 129-136), and discussion (Lines 361-384) to better explain our rationale for using these native species and believe these changes have improved the manuscript.

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We did not calculate these mass percentages separately while doing lab work. Arthropod biomass even while pooling all arthropod taxa was at the lower threshold of sensitivity for our analytical balance.

I think your figure descriptions for Fig 1 and 2 are flipped.

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Reviewer #4: The authors perform an experiment comparing arthropod populations and songbird foraging on invasive and native plants. They found that some invasives, like honeysuckle, had a greater abundance of arthropods than native trees and shrubs, defying the notion that invasives are less beneficial foraging grounds for native birds. Conversely, species such as Japanese barberry hosted fewer, less nutritious arthropods. The study is thought-provoking and experimentally sound. However, to appeal to the broad readership of Biological Invasions I propose several recommendations that could make it both more useful for managers and engage with some big questions within the field of Invasion Ecology. Recognizing the authors' focus on bird foraging, I have attempted to balance their goals with my excitement for what this paper means for the bigger picture of the field. I have included several optional recommendations in addition to major and minor recommendations.

Major recommendations:
1. More details required about the experimental setup and to evaluate the appropriateness of the statistical methods. A map would be very helpful showing spacing and proximity to water, particularly in reference to aquatic insects. It could incorporate a birds-eye view of the study design. It can be put in the ESM but fills in a lot of the unknowns from the sample design.

Map of Experimental Setup is now included in Appendix S1.

2. At some point in the paper (in the Introduction or Discussion or both) it would be useful to discuss how plant invasions impact birds directly. This could include a mention in the introduction about birds feeding on fruit (e.g. Labbe and King 2020 and earlier papers by A. Rodewald), and something in the discussion about how plant invasions might select for birds that can eat arthropods and negatively impact those that predominantly feed on fruit.

Thank you for these suggestions. We now note in line 71 of the Introduction that invasive plants generally produce lower-quality fruits eaten by songbirds and in lines 78-81 some of the ways in which invasive plants have been found to impact birds. A longer discussion of this broad topic is beyond the scope of our paper, but we refer readers to a comprehensive review paper on the subject (Nelson et al. 2017).

3. There are a lot of moving pieces in this study. A conceptual figure specifying direct trophic and indirect explanations could be very useful. You could include a list or icons of the invertebrate group under each of those headings/pathways. It could potentially include multiple panels or arrows to demonstrate the 'limited food quality' and 'limited food quantity' hypotheses, as well as the hypothesis about bird foraging.
This is a good suggestion, but we are at the figure limit for a standard biological invasions article.

4. A previous reviewer (2) brought up interesting points about indirect and direct pathways arthropods may be impacted. A great strength of the experimental design is that you have this data collected and analysed in the ESM. Consider featuring it in the main text, providing a hypothesis, and including it in a conceptual figure. I strongly recommend including ESM figures 1-8 in the main body of the text. I think it is really interesting that you have so many plant species-specific differences, but when you pool them together they provide equivalent nutritional value to birds. This tension

between what scale (species, functional traits, stoichiometry) to think about invasive plant impacts is much more interesting and accurate than simply origin not mattering all that much. To me, this is one of the most interesting conclusions of the study. You could:
a. Analyze host plant species origin as a fixed effect and individual species as a random effect, or analyze individual species as fixed effects.
b. Add partially transparent points with different colors/patterns representing the different native species to existing figures or just use EMS figures 1-8 and add two additional points representing the mean invasive and mean native values.
5. There is a lot of value in running this study with existing invasive and native plant species, however there are some potential biases to contend with. Most of the native species selected are trees that aren't mature in the understory, and most of the invasive species will be fruiting. Another reason to present each plant species independently!
6. I would like to see the phenology, even if just in the supplementary materials. Invasive shrubs have very different phenology than native, and it would be interesting to know whether there is more variability in some shrubs than others. For example, in May I might expect the invasive plants that leaf out sooner to have more arthropods.
These are good suggestions, but ultimately the complexity of individual host-plant effects needed to be reduced in prior revisions. We have opted to include this information in the supplemental figures if readers want to dig deeper into individual host-plant effects. Since our original hypothesis focus on comparing invasive plants and native woody plants in the same habitat as groups, the primary figures highlight those pooled comparisons.

Optional recommendations:
1. Framing this paper within the discussion about whether invasive plants are drivers or passengers of environmental change would be really useful to couch this in a bigger discussion within Invasion Biology (e.g. MacDougall and Turkington 2005).
2. One thing that jumps out at me from the ESM figures is how traits, rather than origin of introduced species might be a way to prioritize invasive species management (e.g. Cohen et al. 2012).
3. I think the connection to management is really important and could have a big impact. Consider build out manager recommendations further. Invasive plants are visible and management success is measured with weight of plants removed. But the focus should be on getting back that ecosystem function rather than celebrating a pile of garlic mustard you pulled.
4. As deer browsing intensifies and limits the regeneration of canopy trees, coupled with the proliferation of tree diseases and insect/disease outbreaks (e.g. beech trees), native canopy trees might be replaced by shrubby woody species, both invasive and native. This shift in forest composition suggests that forest managers might need to prioritize managing these changes in forest structure and species composition, rather than focusing solely on the origin (native vs. invasive) of these species.
5. A given invasive plant may have neutral, negative, or positive, impacts depending on what you are looking at (different species or even ecosystem function). So if you want to make management decision based on impacts rather than origin (e.g. the Davis vs Simberloff debate), you need to look at a broad suite of things.
6. I don't think that it is at all expected that invasive plants will be lower in food quality for herbivores. Many of them are fast-growing species with high nitrogen litter. I would expect honeysuckle, in particular to have the highest SLA. I know plant traits aren't the focus of the paper, but encouraging a trait-based approach to prioritizing invasive species management could tie in nicely to the applied arguments in this paper.
7. As deer browsing intensifies and limits the regeneration of canopy trees, coupled with the proliferation of tree diseases and insect/disease outbreaks (e.g. beech trees), native canopy trees might be replaced by shrubby woody species, both invasive and native. This shift in forest composition suggests that forest managers might need to prioritize managing these changes in forest structure and species composition, rather than focusing solely on the origin (native vs. invasive) of these species.

Each of these topics is the subject of long debate and many review papers, and well outside the scope of revisions at this phase of the manuscript. Our manuscript is meant to address one ecological restoration scenario that we, as scientists active in conservation work in the state of Connective, have observed repeatedly with respect to these four target invasive plants in secondary forests. We believe the applications of our results to invasive plant management are adequately discussed in the Discussion and will be of use to a wide audience of land managers in the northeastern U.S, and an insightful case study outside the region.

Minor recommendations:
1. Line 40 - traits not just region and species?

The sentence in line 40 has been modified to say:

“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.”

2. Line 58 - not just which species but what are drivers.
Apologies we don’t understand the suggestion.

3. Line 63 - be more specific and cite - who is proposing this? This paper (rephrase) or external (cite)
Citations are included in the following lines.

4. Line 71 - (disturbed habitats) this is a key, not an afterthought
Correct, that’s why its in the introduction and later comes up in the discussion.

5. Line 78 - specify which compounds. This could be a good place for talking about fruit consumption on native/introduced plants.
We had discussion of chemical compounds in prior revisions but they were removed because the hypotheses and data collection do not contain any information on the role of specific compounds like secondary metabolites.

6. Line 83 - no restoration after removal seems a tangent to the argument about prioritizing some invasive plants.
Disagree. Lack of native plant restoration supports our comparison of co-occurring native plants with invasive plants. If removals of invasive plants occur, these will typically be the species left to provide food resources to migratory songbirds.

7. Line 92 - in Connecticut
Sentence just shortened to say ‘secondary forest’ because location information is provided lateri n the methods.
“Our study involved a comparison of invasive and native members of a plant community within a secondary forest.”

8. Hypotheses are confusing. I would recommend only naming the food quality and food quantity hypotheses. Then having a hypothesis about bird effect. If you use one of my optional comments above you can also include a hypothesis about direct trophic vs indirect (e.g. structural) impacts.
We would like to stick with the use of hypotheses as currently described. We had included indirect vs direct impacts in prior revisions. In earlier versions of this manuscript, we had comments that readers found it confusing that all three hypotheses were not explicitly named, making tracking the complicated statistical results difficult.

9. Line 127 - convert to metric
Half-inch is how the product is sold and labeled, we would like to keep this reference so other scientists using this method will be able to source the same product.

10. Lines 188-190 sentence doesn't make sense, revise
Changed. Line 188 now reads:
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.

11. Figure 2 - y axis would be more descriptive as 'bird exclusion'

	Disagree. This is the Log-Response Ratio, not simply bird exclusion effect. 12. (Throughout the manuscript)- Edit the statement "target invasive species offer lower quality food resources to insectivorous birds," to be more general (e.g. support a larger and/or more nutritious community of food resources) Prior revisions suggested being more specific rather than more general. 13. Specify how you categorized arthropods as aquatic insects (e.g. which classes, orders) Aquatic arthropods are stoneflies. 14. In ESM figures specify mean rather than average. Average changed to mean. 15. Where possible, stay consistent in text and figures - stick to a consistent taxonomic, trophic, or common group name. 16. The van Hengstum et al. 2014 paper talks about food quality in terms of herbaceous vs woody as an explanation for differences between native and invasive, but your species are all woody. The meta-analysis cited looks at both woody and herbaceous invasive plants. We qualified this and edited the sentence to read: First, leaf tissue is expected to be of lower quality or more highly defended on invasive woody plants than on native plants woody plants, reducing biomass of arthropods on invasive plants (van Hengstum et al. 2014). 17. 'higher quality native plants' is vague and value laden. Choose something like nitrogen rich or specify you are talking about food quality. We added the clause “(e.g. those that contain nitrogen-rich leaf tissue)” to the discussion section on high-quality food plants.

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b. Add partially transparent points with different colors/patterns representing the different native species to existing figures or just use EMS figures 1-8 and add two additional points representing the mean invasive and mean native values.
5. There is a lot of value in running this study with existing invasive and native plant species, however there are some potential biases to contend with. Most of the native species selected are trees that aren't mature in the understory, and most of the invasive species will be fruiting. Another reason to present each plant species independently!
6. I would like to see the phenology, even if just in the supplementary materials. Invasive shrubs have very different phenology than native, and it would be interesting to know whether there is more variability in some shrubs than others. For example, in May I might expect the invasive plants that leaf out sooner to have more arthropods.

These are good suggestions, but ultimately the complexity of individual host-plant effects needed to be reduced in prior revisions. We have opted to include this information in the supplemental figures if readers want to dig deeper into individual host-plant effects. Since

our original hypothesis focus on comparing invasive plants and native woody plants in the same habitat as groups, the primary figures highlight those pooled comparisons.

Optional recommendations:
1. Framing this paper within the discussion about whether invasive plants are drivers or passengers of environmental change would be really useful to couch this in a bigger discussion within Invasion Biology (e.g. MacDougall and Turkington 2005).
2. One thing that jumps out at me from the ESM figures is how traits, rather than origin of introduced species might be a way to prioritize invasive species management (e.g. Cohen et al. 2012).
3. I think the connection to management is really important and could have a big impact. Consider build out manager recommendations further. Invasive plants are visible and management success is measured with weight of plants removed. But the focus should be on getting back that ecosystem function rather than celebrating a pile of garlic mustard you pulled.
4. As deer browsing intensifies and limits the regeneration of canopy trees, coupled with the proliferation of tree diseases and insect/disease outbreaks (e.g. beech trees), native canopy trees might be replaced by shrubby woody species, both invasive and native. This shift in forest composition suggests that forest managers might need to prioritize managing these changes in forest structure and species composition, rather than focusing solely on the origin (native vs. invasive) of these species.
5. A given invasive plant may have neutral, negative, or positive, impacts depending on what you are looking at (different species or even ecosystem function). So if you want to make management decision based on impacts rather than origin (e.g. the Davis vs Simberloff debate), you need to look at a broad suite of things.
6. I don't think that it is at all expected that invasive plants will be lower in food quality for herbivores. Many of them are fast-growing species with high nitrogen litter. I would expect honeysuckle, in particular to have the highest SLA. I know plant traits aren't the focus of the paper, but encouraging a trait-based approach to prioritizing invasive species management could tie in nicely to the applied arguments in this paper.
7. As deer browsing intensifies and limits the regeneration of canopy trees, coupled with the proliferation of tree diseases and insect/disease outbreaks (e.g. beech trees), native canopy trees might be replaced by shrubby woody species, both invasive and native. This shift in forest composition suggests that forest managers might need to prioritize managing these changes in forest structure and species composition, rather than focusing solely on the origin (native vs. invasive) of these species.

Each of these topics is the subject of long debate and many review papers, and well outside the scope of revisions at this phase of the manuscript. Our manuscript is meant to address one ecological restoration scenario that we, as scientists active in conservation work in the state of Connective, have observed repeatedly with respect to these four target invasive

plants in secondary forests. We believe the applications of our results to invasive plant management are adequately discussed in the Discussion and will be of use to a wide audience of land managers in the northeastern U.S, and an insightful case study outside the region.

Minor recommendations:
1. Line 40 - traits not just region and species?

The sentence in line 40 has been modified to say:

"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."

2. Line 58 - not just which species but what are drivers.

Apologies we don't understand the suggestion.

3. Line 63 - be more specific and cite - who is proposing this? This paper (rephrase) or external (cite)

Citations are included in the following lines.

4. Line 71 - (disturbed habitats) this is a key, not an afterthought

Correct, that's why its in the introduction and later comes up in the discussion.

5. Line 78 - specify which compounds. This could be a good place for talking about fruit consumption on native/introduced plants.

We had discussion of chemical compounds in prior revisions but they were removed because the hypotheses and data collection do not contain any information on the role of specific compounds like secondary metabolites.

6. Line 83 - no restoration after removal seems a tangent to the argument about prioritizing some invasive plants.

Disagree. Lack of native plant restoration supports our comparison of co-occurring native plants with invasive plants. If removals of invasive plants occur, these will typically be the species left to provide food resources to migratory songbirds.

7. Line 92 - in Connecticut

Sentence just shortened to say ‘secondary forest’ because location information is provided lateri n the methods.

“Our study involved a comparison of invasive and native members of a plant community within a secondary forest.”

8. Hypotheses are confusing. I would recommend only naming the food quality and food quantity hypotheses. Then having a hypothesis about bird effect. If you use one of my optional comments above you can also include a hypothesis about direct trophic vs indirect (e.g. structural) impacts.

We would like to stick with the use of hypotheses as currently described. We had included indirect vs direct impacts in prior revisions. In earlier versions of this manuscript, we had comments that readers found it confusing that all three hypotheses were not explicitly named, making tracking the complicated statistical results difficult.

9. Line 127 - convert to metric

Half-inch is how the product is sold and labeled, we would like to keep this reference so other scientists using this method will be able to source the same product.

10. Lines 188-190 sentence doesn't make sense, revise

Changed. Line 188 now reads:

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.

11. Figure 2 - y axis would be more descriptive as 'bird exclusion'

Disagree. This is the Log-Response Ratio, not simply bird exclusion effect.

12. (Throughout the manuscript)- Edit the statement "target invasive species offer lower quality food resources to insectivorous birds," to be more general (e.g. support a larger and/or more nutritious community of food resources)

Prior revisions suggested being more specific rather than more general.

13. Specify how you categorized arthropods as aquatic insects (e.g. which classes, orders)

Aquatic arthropods are stoneflies.

14. In ESM figures specify mean rather than average.

Average changed to mean.

15. Where possible, stay consistent in text and figures - stick to a consistent taxonomic, trophic, or common group name.

16. The van Hengstum et al. 2014 paper talks about food quality in terms of herbaceous vs woody as an explanation for differences between native and invasive, but your species are all woody.

The meta-analysis cited looks at both woody and herbaceous invasive plants. We qualified this and edited the sentence to read:

First, leaf tissue is expected to be of lower quality or more highly defended on invasive woody plants than on native plants woody plants, reducing biomass of arthropods on invasive plants (van Hengstum et al. 2014).

17. 'higher quality native plants' is vague and value laden. Choose something like nitrogen rich or specify you are talking about food quality.

We added the clause "(e.g. those that contain nitrogen-rich leaf tissue)" to the discussion section on high-quality food plants.

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.

Map of Experimental Setup. Blue crosses indicate bird exclusion branches/trees while red lines indicate controls (no bird exclusion applied). Trail systems are shown with hashed lines and waterways are shown in light blue. Forested areas shown in green.

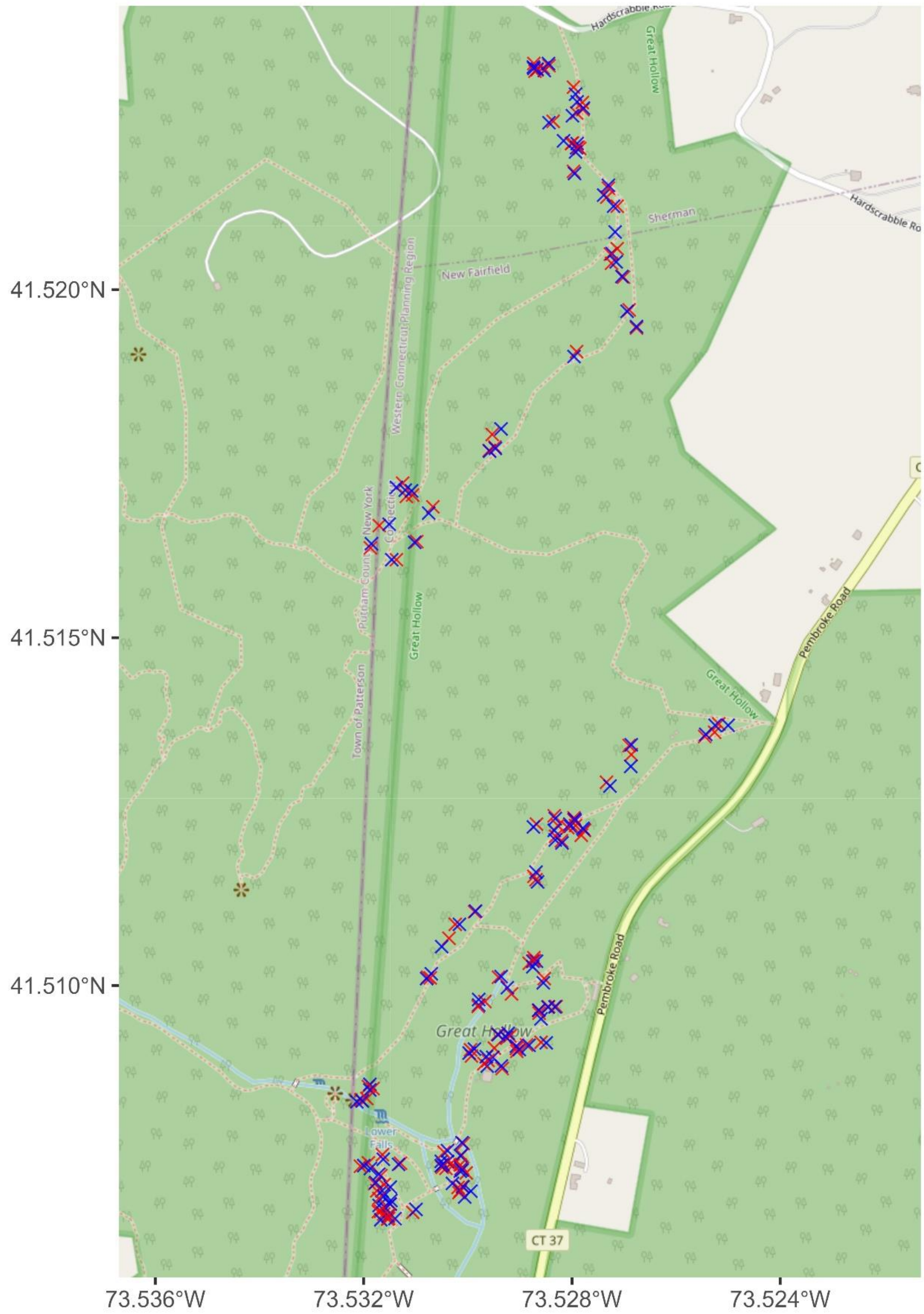


Fig. S1. Mean abundance of aquatic insects (# per bagged branches) among ten sampled host-plant species. Bar height indicates estimated mean from GLMM, and error bars indicate 95% confidence intervals. Bars with non-overlapping confidence intervals are significantly different. Bars ranked by estimated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

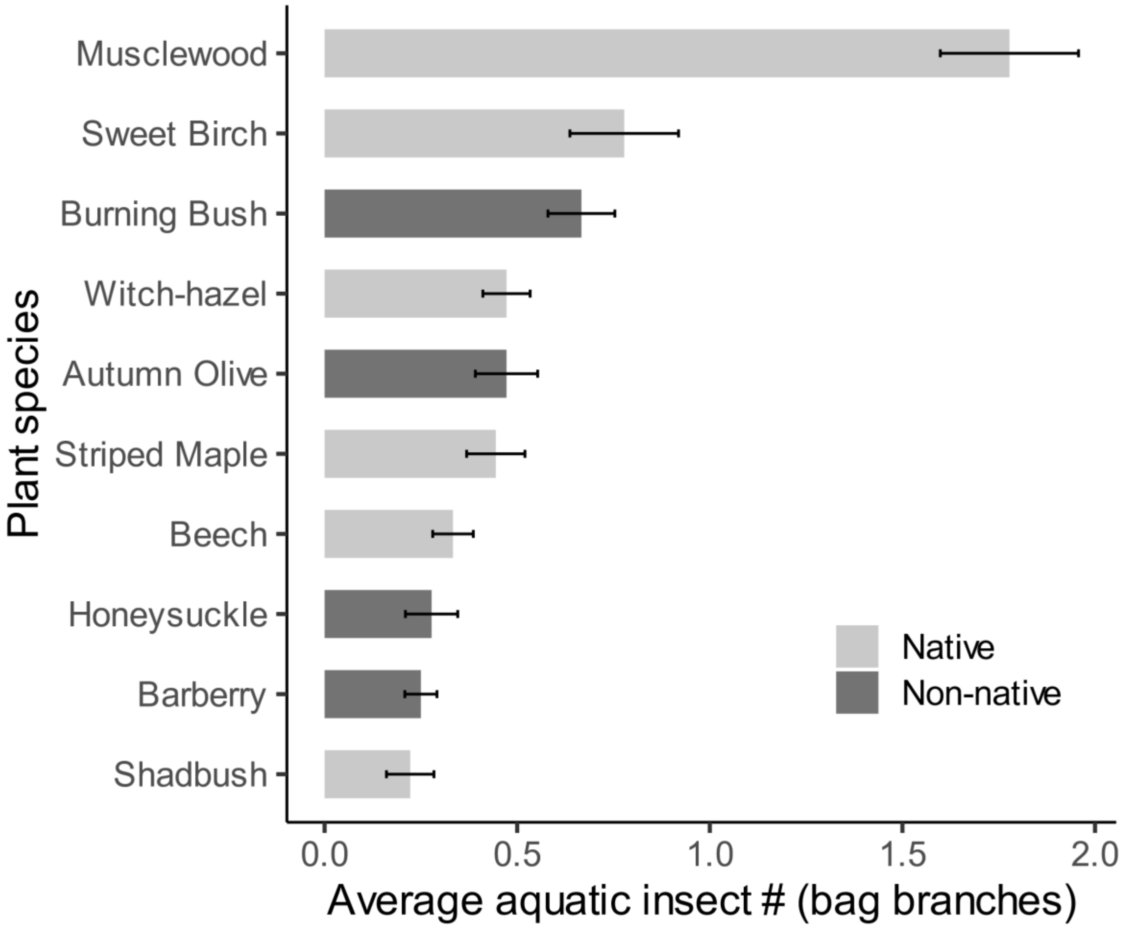


Fig. S2. Mean abundance of lepidoptera (# of caterpillars per bagged branches) among ten sampled host-plant species. Bar height indicates estimated mean from GLMM, and error bars indicate 95% confidence intervals. Bars with non-overlapping confidence intervals are significantly different. Bars ranked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

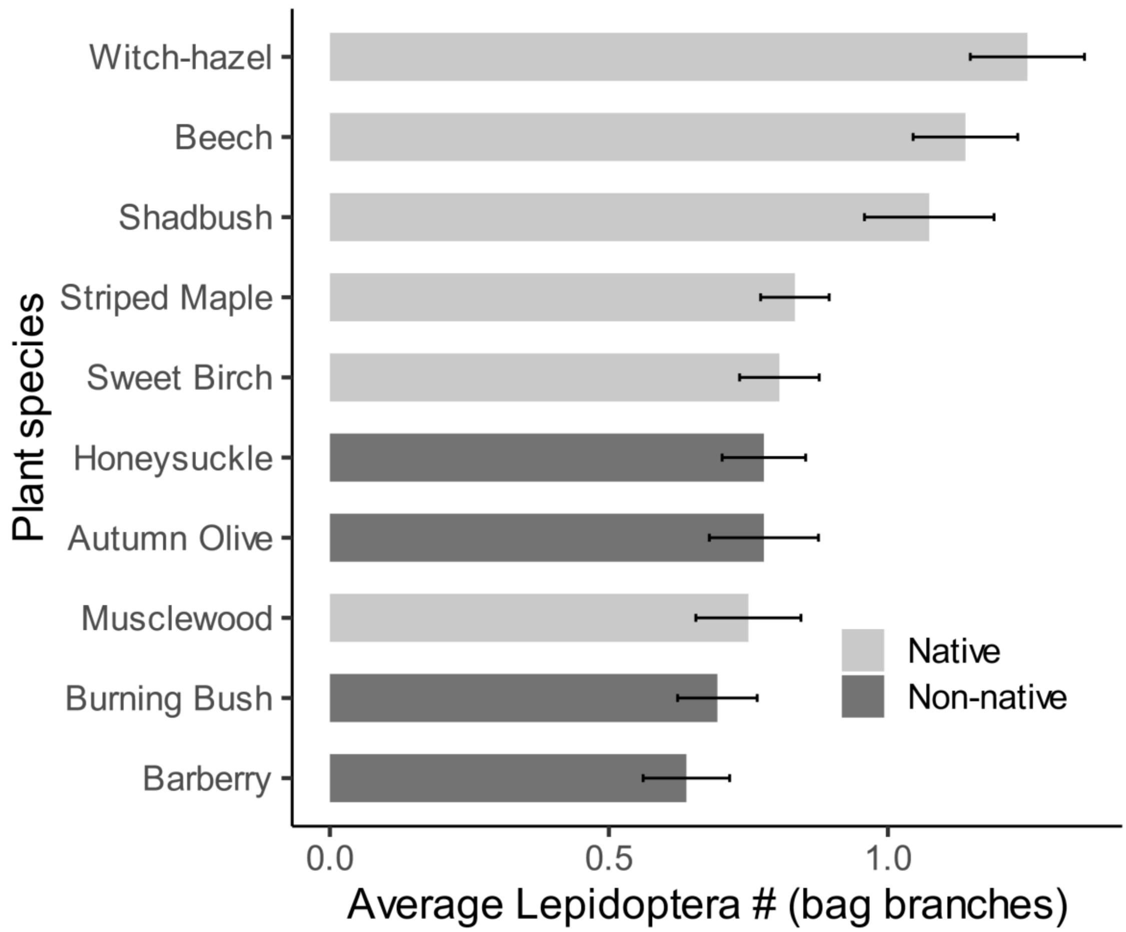
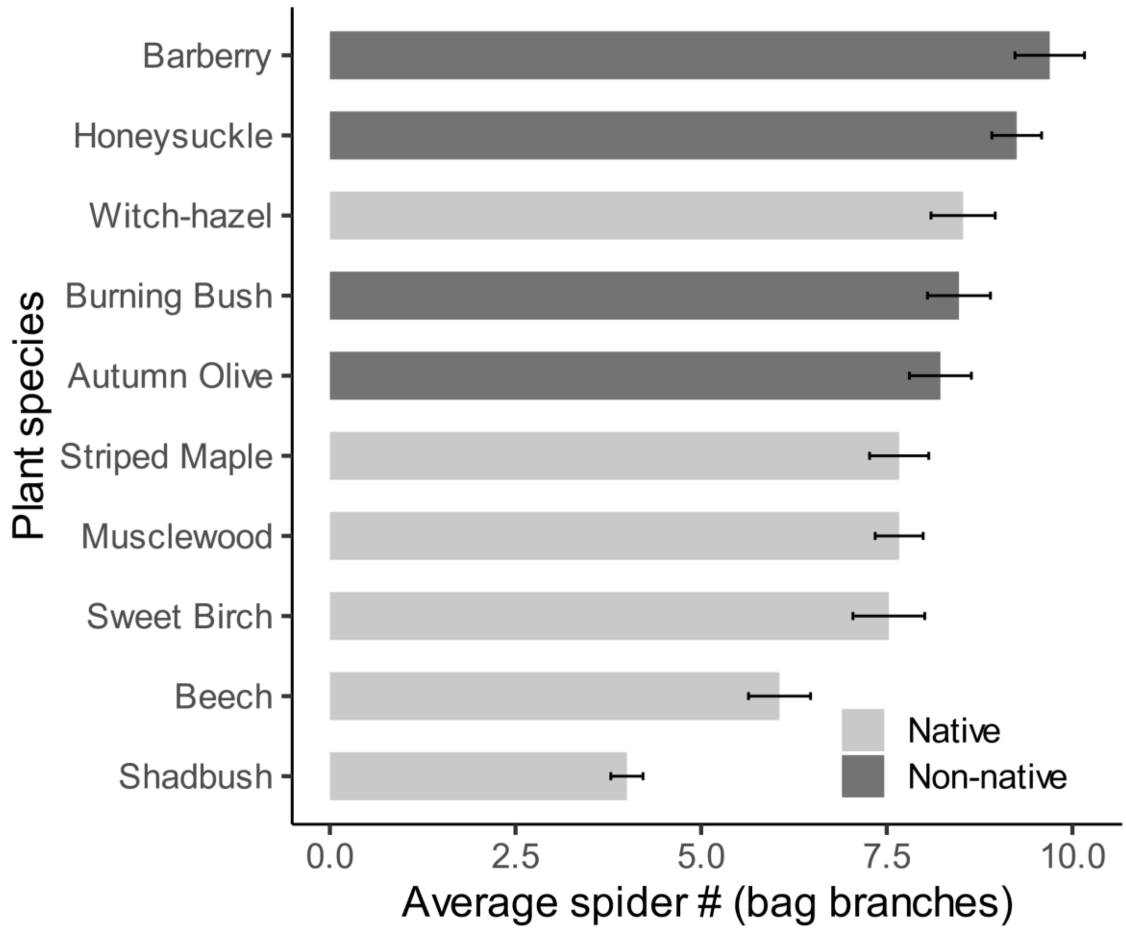


Fig. S3. Mean abundance of spiders (# of spiders per bagged branch) among ten sampled-host plant species. Bar height indicates estimated mean from GLMM, and error bars indicate 95% confidence intervals. Bars with non-overlapping confidence intervals are significantly different. Bars ranked by estimated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



Appendix S2: Supporting analyses

In support of our results, we also tested for differences among all plant species (Fig. S4, S5, S7, S8), and for the effects of bird-bag exclusion on arthropod abundance (Fig. S6). Abbreviations are as follows: 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. S4. Arthropod biomass (total grams per branch) among the ten sampled host-plant species. Biomass is reported as total wet mass collected from branches. Mean ± SEM is plotted. Circles are native species, triangles are invasive species, see Appendix S2 overview for description of abbreviations.

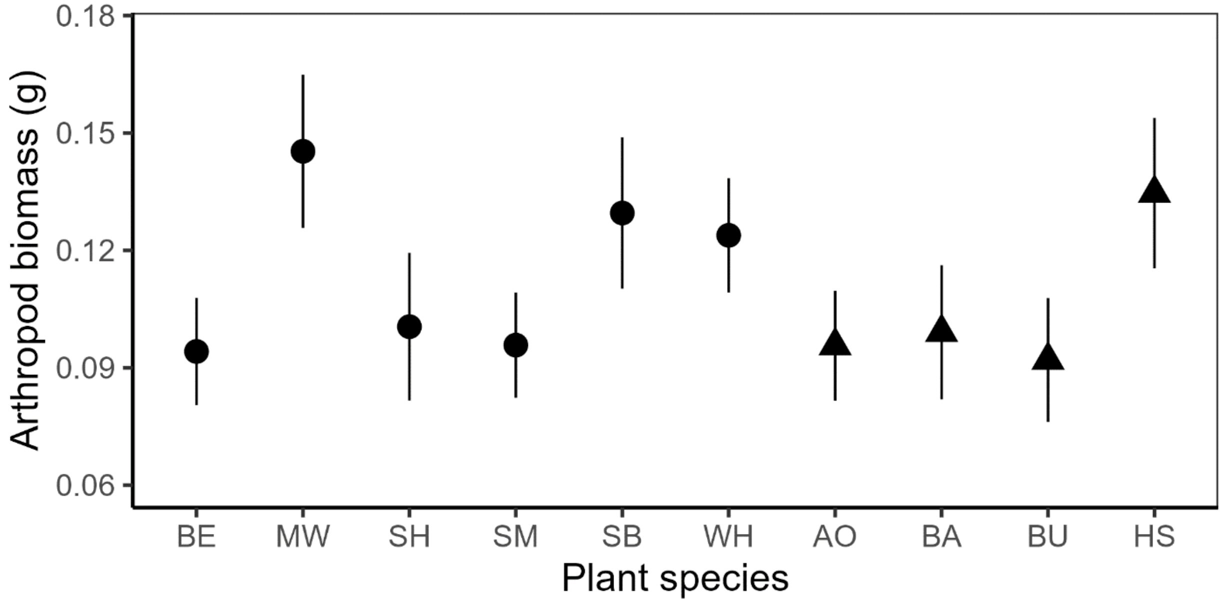


Fig. S5. Effect size of bird exclusion treatment among ten sampled host-plant species. Bird exclusion effect size reported as Log-Response Ratios (LRR), in which positive values > 0 indicate a significant reduction in arthropod abundance in response to bird predation. Mean ± SEM is plotted. Circles are native species, triangles are invasive species, see Appendix S2 overview for description of abbreviations.

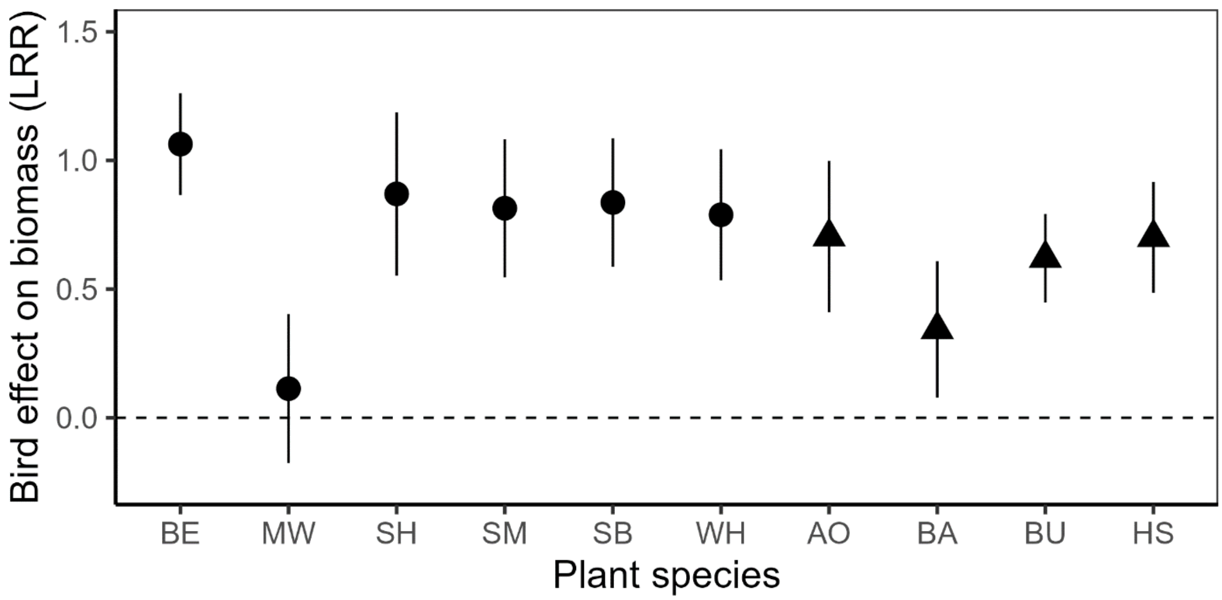


Fig S6. Effects of bird-bag exclusion treatment under the context of native versus non-native host-plant groups. Points with lines connecting them are significantly different from each other if they have different letters (Scheffe's test for pairwise comparisons were completed for each of the eight sub-panels). Each panel indicates the response of a single taxonomic group and changes in Mean ± SEM abundance: S6a. Araneae (true spiders), S6b. Hemiptera (herbivorous true bug families), S6c. Lepidoptera (caterpillars), and S6d. Orthoptera (tree crickets and katydids).

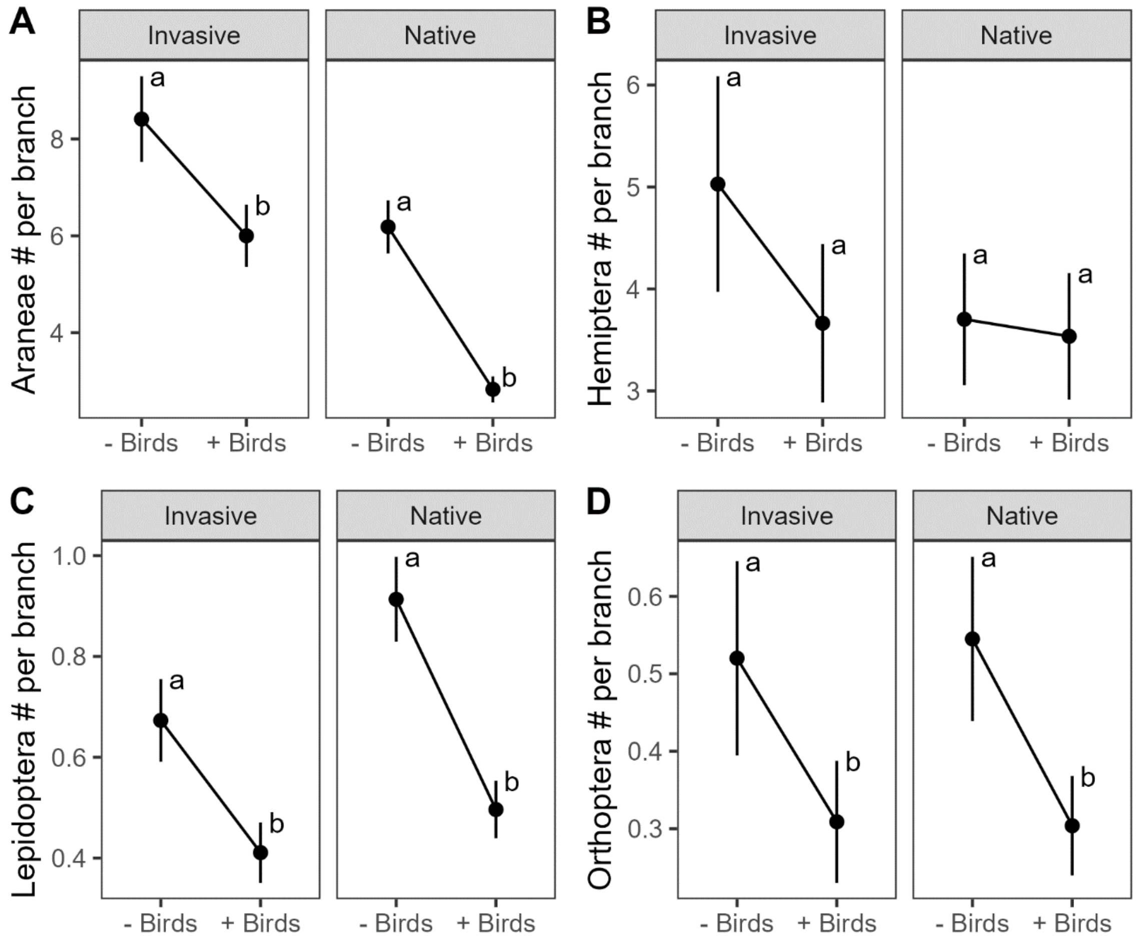


Fig S7. Total % nitrogen for insect herbivores among ten host-plant species. Nitrogen content is measured as the total molecular mass of elemental nitrogen relative to total mass of a single sample from an experimental host-plant branch. Only bagged branches were included in analysis, mean ± SEM is plotted. Circles are native species, triangles are invasive species, see Appendix S2 overview for description of abbreviations.

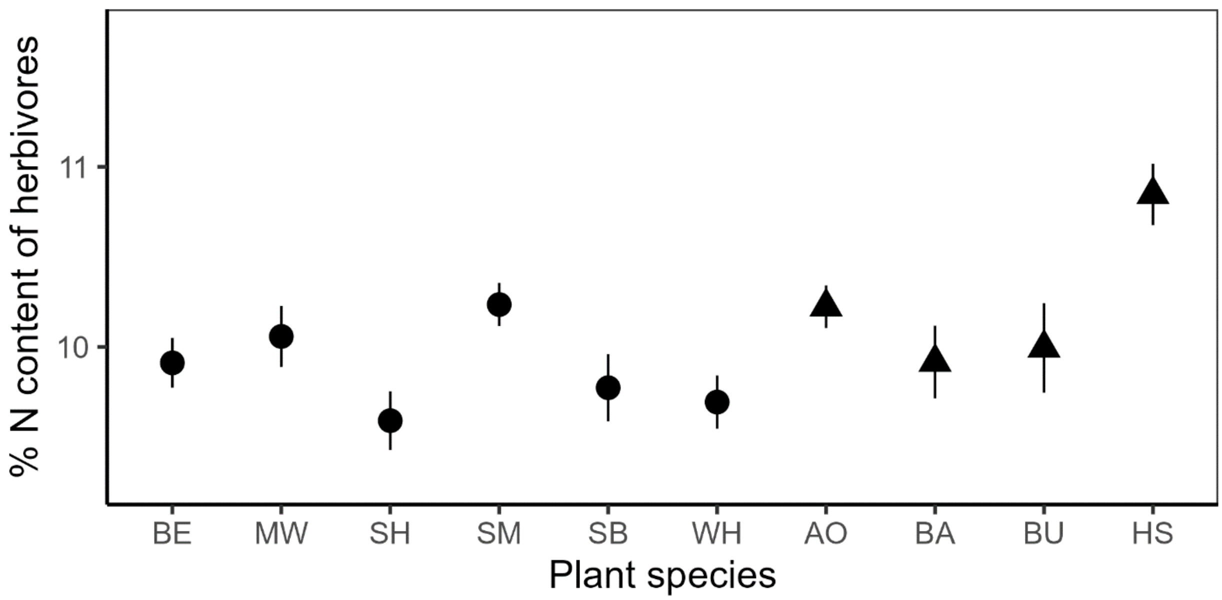
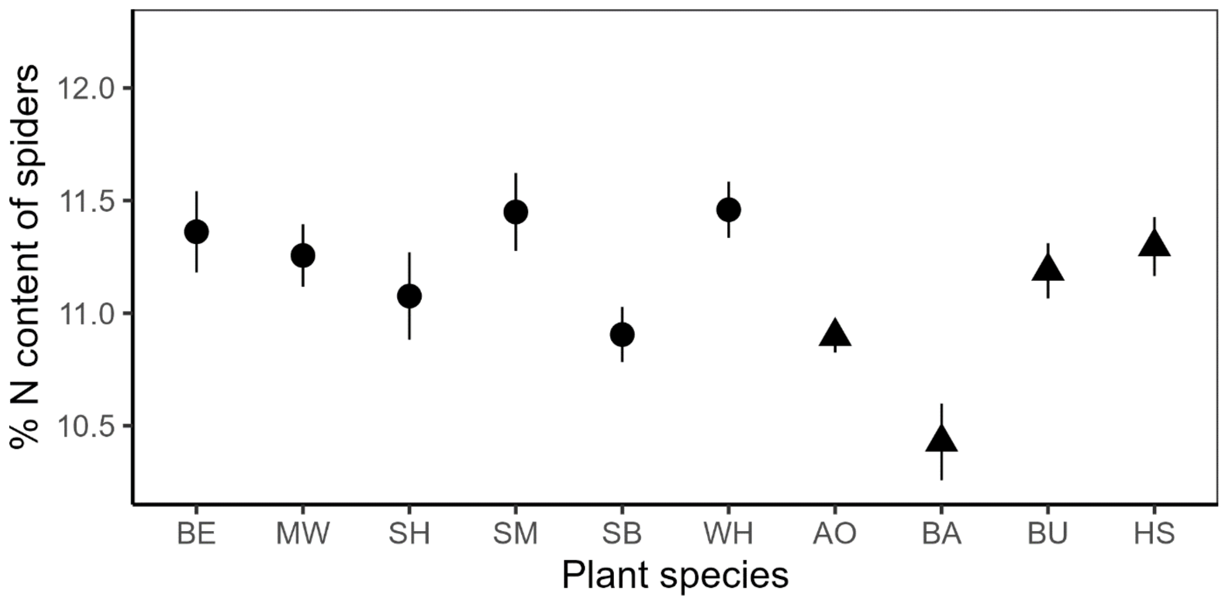


Fig. S8. Total % nitrogen for true spiders among ten host-plant species. Nitrogen content is measured as the total molecular mass of elemental nitrogen relative to total mass of a single sample from an experimental host-plant branch. Only bagged branches were included in analysis, mean ± SEM is plotted. Circles are native species, triangles are invasive species, see Appendix S2 overview for description of abbreviations.



Biological Invasions Research Paper

Title:

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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Keywords:

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

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 had fewer arthropods overall and arthropods of lower protein quality 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.

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. 2021, 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, Hopfensperger et al. 2017). 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. 2020). 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’, and (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 (*Eunonymous 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 1m^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. 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 -80º 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 -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 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, but since all arthropod samples were pooled across sampling periods to gain enough biomass for the assay. 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 $\chi 2$ 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, 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 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 relatively 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).

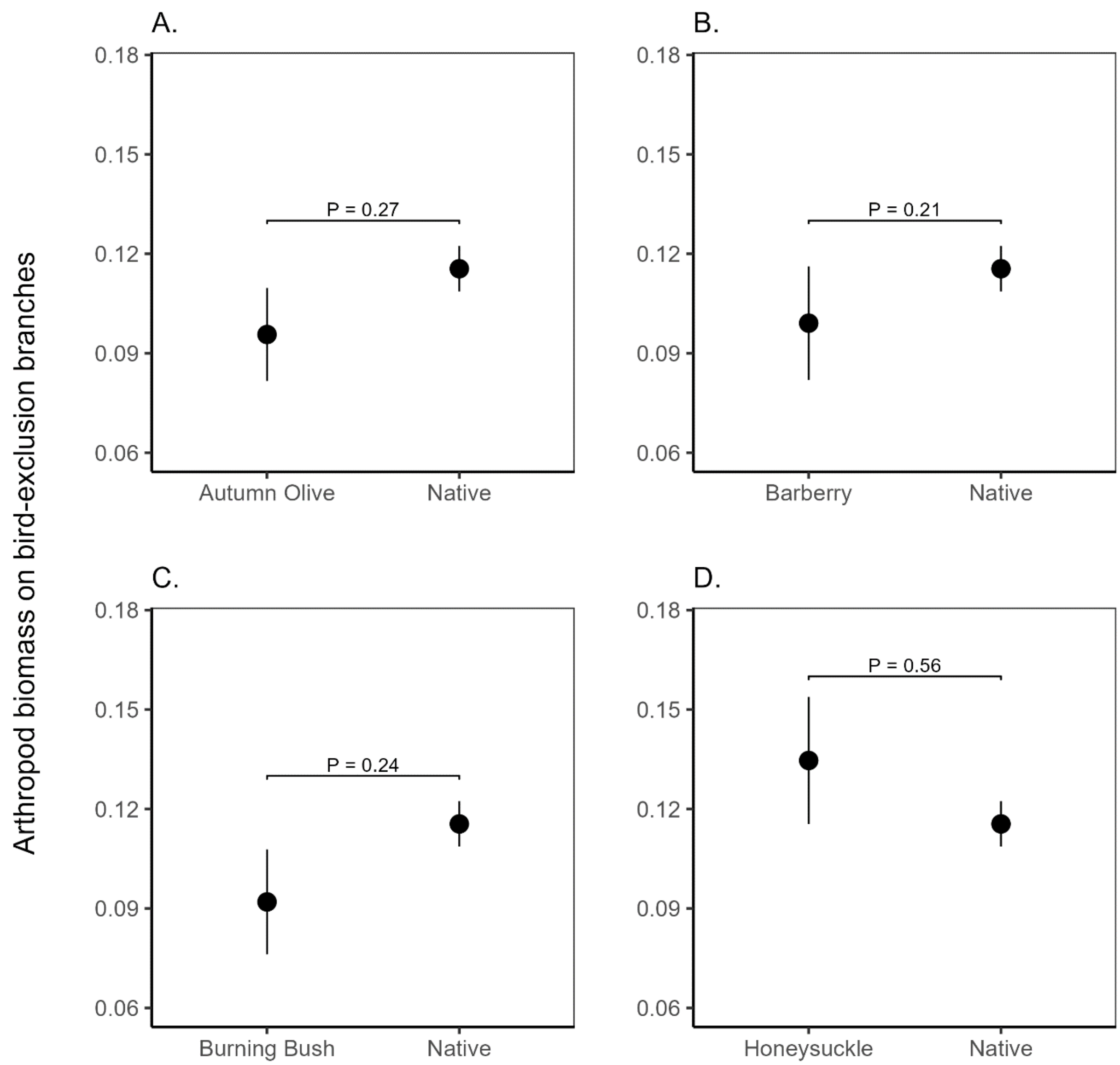

Fig. 1 Arthropod biomass (total grams per branch) with pooled comparisons between native plants and each invasive plant species for bird-exclusion branches. Biomass is reported as total wet mass collected from branches. Mean ± SEM is plotted, with levels of significance illustrated for native versus each invasive plant species using grouped, planned contrasts.

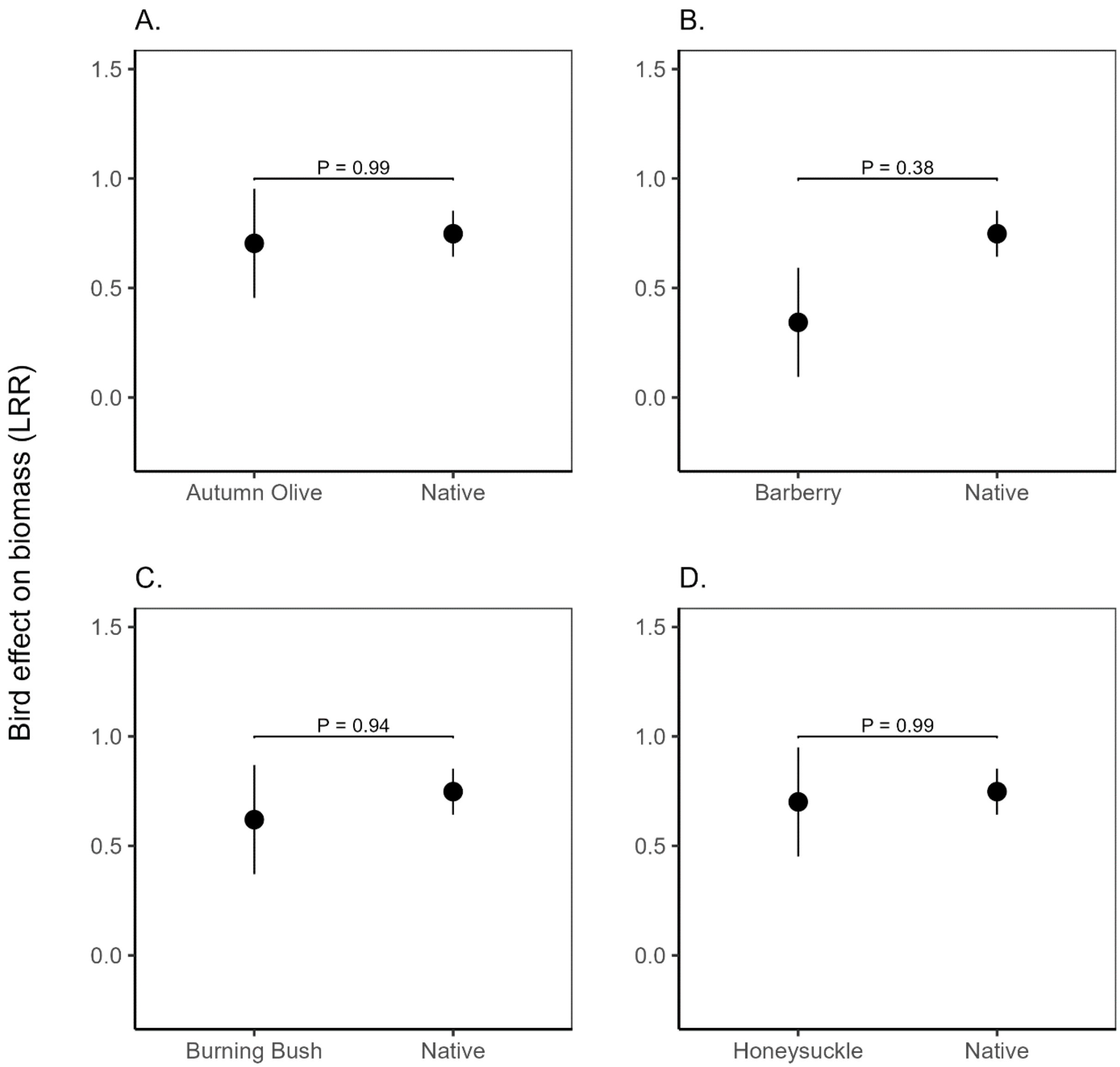

Fig. 2 Effect size of bird exclusion treatment showing pooled comparisons between native plants and each invasive plant species. Bird exclusion effect size reported as Log-Response Ratios (LRR), in which positive values > 0 indicate a significant reduction in arthropod abundance in response to bird predation. Mean ± SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts.

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 content 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 content by mass on honeysuckle compared to native plants (Fig 3A, $P < 0.001$, Table S3), and %N content 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: $P = 0.88$, Figure 3, Table S3). Spider %N content varied significantly among plants overall (Fig. S8, GLM, $P < 0.001$, $\chi 2 = 59.61$, d.f. = 9), with lower values on Japanese barberry than native plants (Fig 4B, $P < 0.001$, Table S4). Spider %N content 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: $P = 0.98$, Figure 4, Table S4).

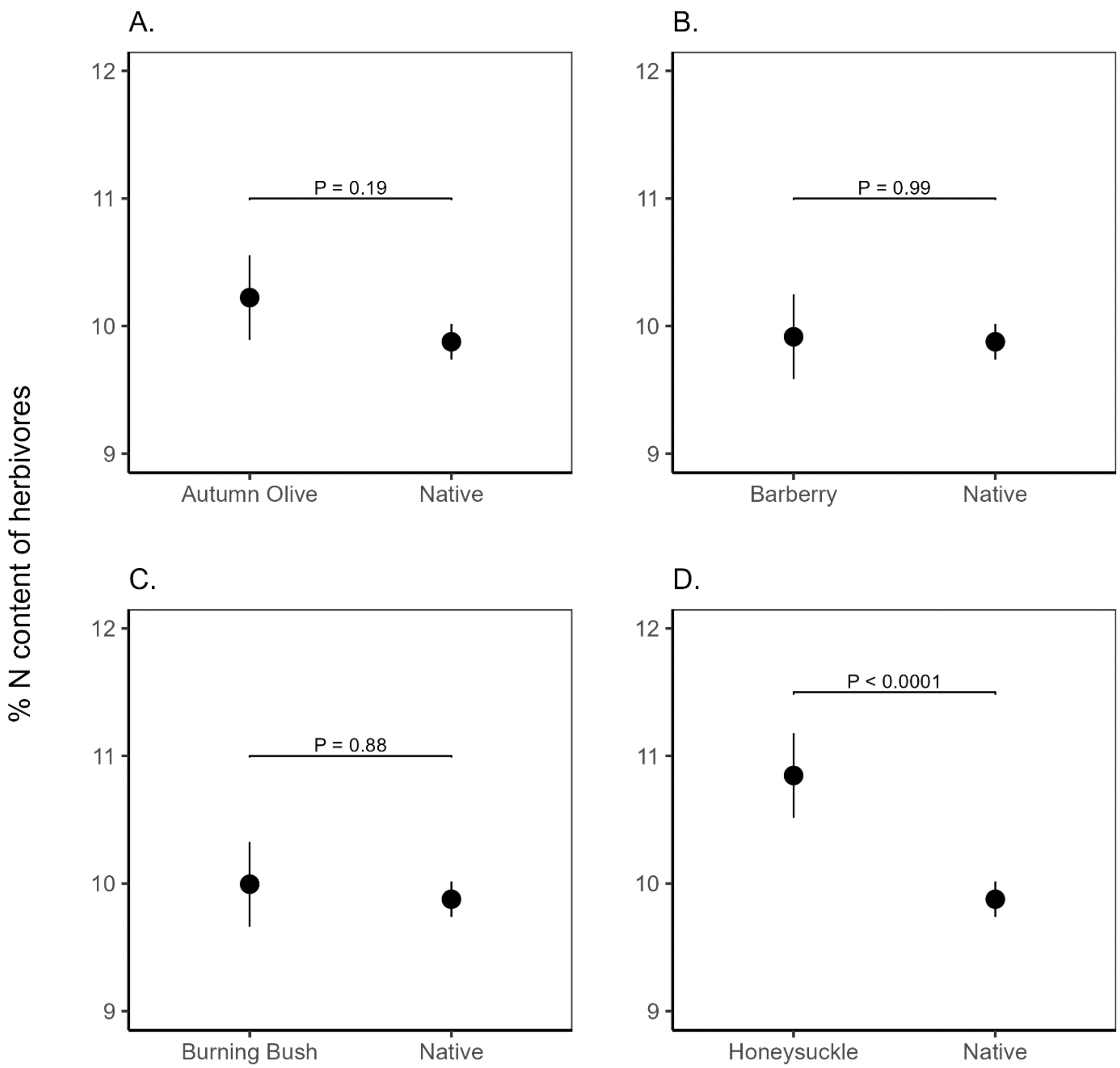

Fig. 3 Total % nitrogen for insect herbivores on bird-exclusion branches. Nitrogen content is measured as the total molecular mass of elemental nitrogen relative to total mass of a single sample from an experimental host-plant branch. Mean ± SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts.

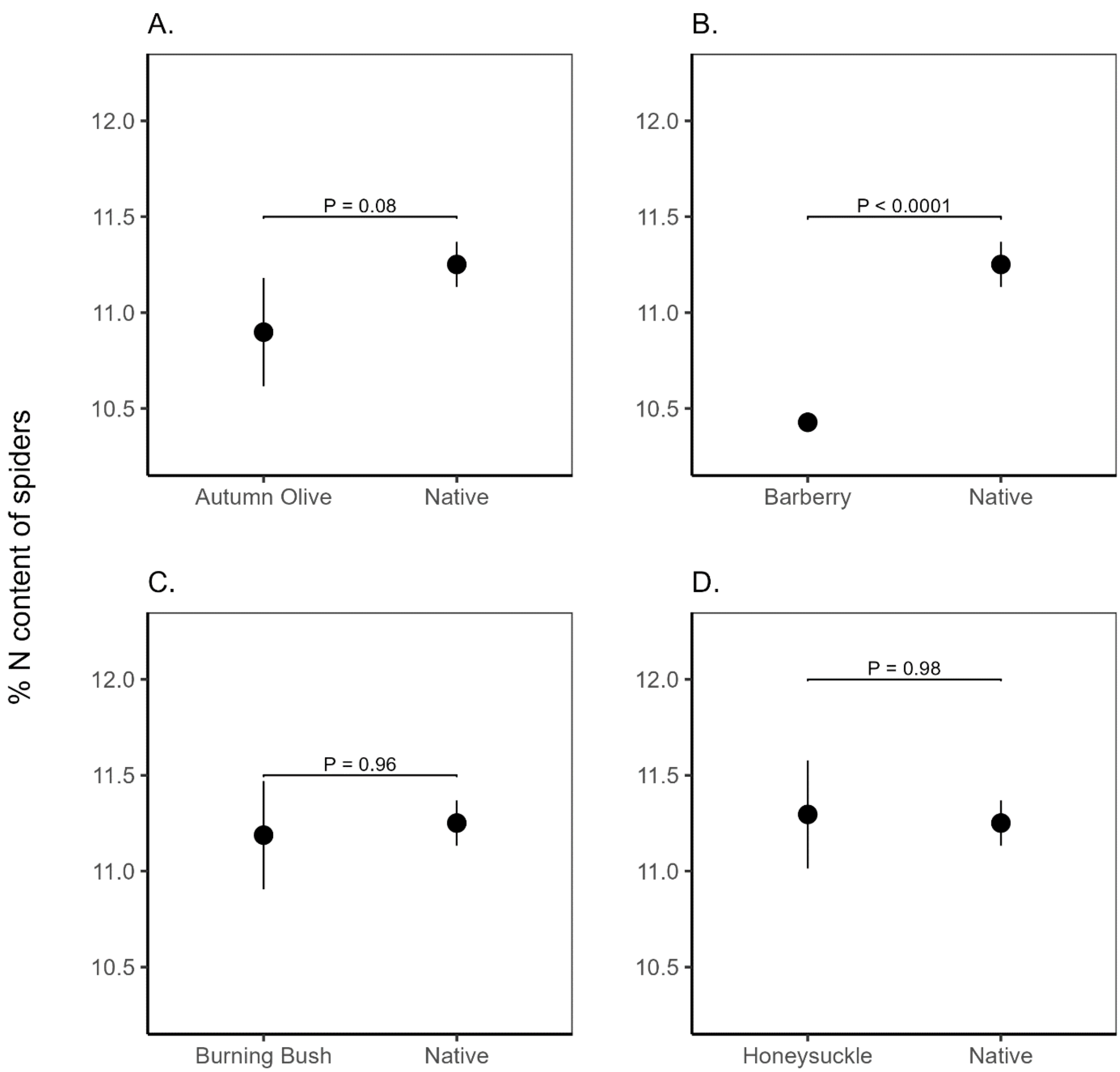

Fig. 4 Total % nitrogen for true spiders on bird-exclusion branches. Nitrogen content is measured as the total molecular mass of elemental nitrogen relative to total mass of a single sample from an experimental host-plant branch. Mean ± SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts.

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. 2021). 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 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 (Shakleton 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 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 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, Serniak 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 plants 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 invasive 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 2001). 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, our results suggest that 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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