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.

We are somewhat concerned that the manuscript is starting to become a “moving target” where new suggestions made by reviewers are calling for content removed or modified based on earlier reviewer suggestions. We’re confident the current changes will help with the high-level concerns of the reviewers. However, some suggestions from both reviewers would require an almost total rewrite of the hypotheses & results sections. We are very open to working with you, as the editor, to make changes that address concerns without, for example, require creating completely new figures for the entire manuscript this late in the revisions.

Please don’t hesitate to ask us for input or changes on any of these edits.

Rob Clark and Chad Seewagen

COMMENTS TO THE AUTHOR:

Associate Editor: The authors have significantly improved this manuscript, but additional revision is needed before further consideration. The reviewers have made important suggestions that should be considered in the next revision. Additionally, I agree with Reviewer two that the authors did not completely resolve comments made on the original submission. In addition to the reviewers' comments, I would like to add that the authors need to make it clear when they are talking about plants or arthropods. For example, in lines 208-220 the authors repeatedly refer to plant biomass but I believe it is arthropod biomass on the plants that is being referenced.  
  
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.**

Methods. I disagree that a mesh size of ½" allows access to plants by all but the largest invertebrates. It excludes all Saturniids, and most Noctuids, Arctiids and Geometrids, i.e. most macromoth adults that lay the eggs that make the caterpillars that are the bread and butter of terrestrial food webs, particularly for breeding birds.

**We added text acknowledging the possibility that some adult lepidoptera could be excluded by the mesh size of the netting. However, we also note that this is a published method that has been used successfully in other experiments in Connecticut forests, and because oviposition happens before the mesh is put onto the branches, it does not prevent caterpillars from moving onto branches once they hatch from eggs in spring (Lines 148-150).**

Results:  
I would have liked to see actual abundances (or biomass) of the taxa you collected. What % were the valuable arthropods used by breeding birds (Lepidoptera, Orthoptera, Spiders) and what percentage were taxa unimportant in breeding bird nutrition (Hemiptera, Homoptera)?

**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.  
  
**Thanks for catching that, we have moved figures around many times in revisions and flipped the figures. Fig 1 is now arthropod biomass and figure 2 is bird effect on branch biomass.**   
  
  
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.**