*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

Author(s):

Robert E. Clark\*1,2, Wales A. Carter1, Timothy C.W. Ku3, and Chad L. Seewagen1

Affiliations:

1 Great Hollow Nature Preserve & Ecological Research Center, 225 State Route 37

New Fairfield, CT USA

2 EcoData Technology LLC, 59 Lagana Ave, Plantsville CT USA

3 Wesleyan University, Department of Earth & Environmental Sciences, 45 Wyllys Ave, Middletown, CT USA

\* Corresponding author: robclark@ecodata.tech

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 1m2 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 χ2 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, χ2 = 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, χ2 = 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).

**A group of graphs with black dots

Description automatically generated with medium confidenceFig. 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.

A graph of bird effect on bombs

Description automatically generated**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, χ2 = 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, χ2 = 57.18, d.f. = 1). Hemiptera abundance was not significantly different between native and invasive plants (Fig S6B, GLMM, *P* = 0.488, χ2 = 0.479, d.f. = 1), and bird predation did not significantly reduce Hemipteran abundance (Fig. S6B, GLMM, *P* = 0.141, χ2 = 2.15, d.f. = 1). Bird predation effects were significant for Lepidoptera (Fig. S6C, GLMM, *P* < 0.001, χ2 = 25.7, d.f. = 1) and although there were fewer Lepidoptera on invasive plants (Fig. S6C, GLMM, *P* = 0.022, χ2 = 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, χ2 = 0.25, d.f. = 1). Finally, we observed similar abundances of Orthoptera on both native and invasive plants (Fig. S6D, GLMM, *P* = 0.941, χ2 = 0.005, d.f. = 1). Birds significantly reduced the abundance of orthoptera on both plant groups (Fig. S6D, GLMM, *P* < 0.001, χ2 = 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, χ2 = 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, χ2 = 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).

A group of black and white graphs

Description automatically generated

**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.

A graph of different sizes of spiders

Description automatically generated

**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.

References:

Abbas M, Klein A-M, Ebeling A, Oelmann Y, Ptacnik R, Weisser WW, Hillebrand H (2014) Plant Diversity Effects on Pollinating and Herbivorous Insects can be Linked to Plant Stoichiometry. Basic Appl Ecol 15:169–178.

Arponen A (2012) Prioritizing Species for Conservation Planning. Biodivers Conserv 21:875–893.

Bairlein F (1998) The Effect of Diet Composition on Migratory Fuelling in Garden Warblers *Sylvia borin*. J Avian Biol 29:546–551.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48.

Bellard C, Cassey P, Blackburn TM (2016) Alien Species as A Driver of Recent Extinctions. Biol Lett 12:20150623.

Birkhead TR, Fletcher F, Pellatt EF (1999) Nestling Diet, Secondary Sexual Traits, and Fitness in the Zebra Finch. Proc R Soc B: Biol Sci 266:385 – 390.

Bultman TL, DeWitt DJ (2007) Effect of An Invasive Ground Cover Plant on The Abundance And Diversity Of A Forest Floor Spider Assemblage. Biol Invasions 10:749.

Chaguaceda F, Scharnweber K, Dalman E, Tranvik LJ, Eklöv P (2021) Short-Term Apparent Mutualism Drives Responses of Aquatic Prey to Increasing Productivity. J Anim Ecol 90:834–845.

Clark RE, Farkas TE, Lichter-Marck I, Johnson ER, Singer MS (2016) Multiple Interaction Types Determine the Impact of Ant Predation Of Caterpillars In A Forest Community. Ecology 97:3379–3388.

Clark RE, Seewagen CL (2019) Invasive Japanese Barberry, Berberis thunbergii (Ranunculales: Berberidaceae) Is Associated with Simplified Branch-Dwelling and Leaf-Litter Arthropod Communities in a New York Forest. Environ Entomol 48:1071–1078.

Courtois P, Figuieres C, Mulier C, Weill J (2018) A Cost–Benefit Approach for Prioritizing Invasive Species. Ecol Econ 146:607–620.

Crystal-Ornelas R, Hudgins EJ, Cuthbert RN, Haubrock PJ, Fantle-Lepczyk J, Angulo E, Kramer AM, Ballesteros-Mejia L, Leroy B, Leung B, López-López E, Diagne C, Courchamp F (2021) Economic Costs of Biol Invasions Within North America. NeoBiota 67:485–510.

Cutway HB (2017) Effects of Long-Term Manual Invasive Plant Removal on Forest Understory Composition. Nat Areas J 37:530–539.

D’Antonio C, Meyerson LA (2002) Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis. Restor Ecol 10:703–713.

Dey, D.C., 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. Forest Science, 60(5), pp.926-942.

Eppinga MB, Baudena M, Haber EA, Rietkerk M, Wassen MJ, Santos MJ (2021) Spatially Explicit Removal Strategies Increase the Efficiency Of Invasive Plant Species Control. Ecol Appl 31:1–13.

Fantle-Lepczyk JE, Haubrock PJ, Kramer AM, Cuthbert RN, Turbelin AJ, Crystal-Ornelas R, Diagne C, Courchamp F (2022) Economic Costs of Biol Invasions in The United States. Sci Total Environ 806:151318.

Farmer S, Ward J, Horton J, Clarke D (2016) Southern Appalachian Urban Forest Response To Three Invasive Plant Removal Treatments. Manag Biol Invasions 7:329–342.

Fletcher RA, Brooks RK, Lakoba VT, Sharma G, Heminger AR, Dickinson CC, Barney JN (2019) Invasive Plants Negatively Impact Native, But Not Exotic, Animals. Glob Chang Biol 25:3694–3705.

Flory SL, Clay K (2009) Invasive Plant Removal Method Determines Native Plant Community Responses. J Appl Ecol 46:434–442.

Fox J, Weisberg S, Adler D, Bates D, Baud-Bovy G, Ellison S, Firth D, Friendly M, Gorjanc G, Graves S, Heiberger R, Laboissiere R, Monette G, Murdoch D, Nilsson H, Ogle D, Ripley B, Venables W, Winsemius D, Zeileis A, R-Core (2015) car: Companion to Applied Regression.

Gerber E, Krebs C, Murrell C, Moretti M, Rocklin R, Schaffner U. (2008) Exotic Invasive Knotweeds (Fallopia spp.) Negatively Affect Native Plant and Invertebrate Assemblages In European Riparian Habitats. Biol Conserv 141:646–654.

Gratton C, Denno RF (2005) Restoration of Arthropod Assemblages in a Spartina Salt Marsh following Removal of the Invasive Plant Phragmites australis. Restor Ecol 13:358–372.

Haan NL, Bowers MD, Bakker JD (2021) Preference, Performance, And Chemical Defense in An Endangered Butterfly Using Novel And Ancestral Host Plants. Sci Rep 11:992.

Hartman KM, McCarthy BC (2004) Restoration of a Forest Understory After the Removal of an Invasive Shrub, Amur Honeysuckle (Lonicera maackii). Restor Ecol 12:154–165.

van Hengstum, T, Hooftman DAP, Oostermeijer JGB, van Tienderen PH (2014) Impact of Plant Invasions on Local Arthropod Communities: A Meta-Analysis. J Ecol 102:4–11.

Hedges LV, Gurevitch J, Curtis PS (1999) The Meta-Analysis of Response Ratios in Experimental Ecology. Ecology 80:1150–1156.

Hiatt D, Serbesoff‐King K, Lieurance D, Gordon DR, Flory SL (2019) Allocation of Invasive Plant Management Expenditures For Conservation: Lessons from Florida, USA. Conserv Sci Pract 1:1–10.

Holmes MA, Whitacre JV, Bennion LD, Poteet J, Kuebbing SE (2021) Land-Use History and Abiotic Gradients Drive Abundance of Non-Native Shrubs In Appalachian Second-Growth Forests With Histories Of Mining, Agriculture, And Logging. For Ecol Manag 494:119296.

Kettenring KM, Adams CR (2011) Lessons Learned from Invasive Plant Control Experiments: A Systematic Review And Meta-Analysis. J Appl Ecol 48:970–979.

Klasing KC (1998) Comparative Avian Nutrition. CAB International, Wallingford, UK.

Kramer AT, Crane C, Downing J, Hamrick JL, Havens K, Highland A, Jacobi SK, Kaye TN, Lonsdorf EV, Ramp Neale J, Novy A, Smouse PE, Tallamy DW, White A, Zeldin J (2019) Sourcing Native Plants to Support Ecosystem Function In Different Planting Contexts. Restor Ecol 27:470–476.

Lampert EC, Cylkowski ZR, McDonough KA, Young CR (2022) Arthropod Associations Show Naturalization with Non-Native Quercus Species in the Georgia Piedmont. J Entomol Sci 57:323–332.

Landsman AP, Schmit JP, Matthews ER (2021) Invasive Plants Differentially Impact Forest Invertebrates, Providing Taxon-Specific Benefits by Enhancing Structural Complexity. Front Ecol Evol 9.

Landsman AP, Burghardt KT, Bowman JL (2020) Invasive Grass (Microstegium Vimineum) Indirectly Benefits Spider Community by Subsidizing Available Prey. Ecol Evol 10:11133–11143.

Lehtinen RM, Hartman H, Marlowe B, Rojas A (2022) Evidence for Negative Impacts on Terrestrial Salamanders following Invasive Plant Removal. J Herpetol 56:92–98.

Lenth RV (2016) Least-squares means: The R Package lsmeans. J Stat Softw 69:1–33.

Lieurance D, Cipollini D (2013) Exotic Lonicera Species Both Escape and Resist Specialist And Generalist Herbivores In The Introduced Range In North America. Biol Invasions 15:1713–1724.

Lind EM, Parker JD (2010) Novel Weapons Testing: Are Invasive Plants More Chemically Defended than Native Plants? PLOS ONE 5:e10429.

McCary MA, Mores R, Farfan MA, Wise DH (2016) Invasive Plants Have Different Effects on Trophic Structure Of Green And Brown Food Webs In Terrestrial Ecosystems: A Meta-Analysis. Ecol Lett 19:328–335.

McDonald P, Edwards RA, Greenhalgh JFD, Morgan CA, Sinclair LA, Wilkinson RG (2011) Animal Nutrition, 7th edn. Pearson, Harlow, UK.

Midway S, Robertson M, Flinn S, Kaller M (2020) Comparing Multiple Comparisons: Practical Guidance for Choosing the Best Multiple Comparisons Test. PeerJ 8:e10387.

Mosher ES, Silander JA, Latimer AM (2009) The Role of Land-Use History In Major Invasions By Woody Plant Species In The Northeastern North American Landscape. Biol Invasions 11:2317.

Narango DL, Tallamy DW, Marra PP (2018) Nonnative Plants Reduce Population Growth of An Insectivorous Bird. Proc Natl Acad Sci USA 115:11549–11554.

Nelson, S.B., Coon, J.J., Duchardt, C.J., Fischer, J.D., Halsey, S.J., Kranz, A.J., Parker, C.M., Schneider, S.C., Swartz, T.M. and Miller, J.R., 2017. Patterns and mechanisms of invasive plant impacts on North American birds: a systematic review. Biological Invasions, 19, pp.1547-1563.

Peracchio, D. 2020. Connecticut’s 2020 Forest Action Plan. Connecticut Department of Energy and Environmental Protection. https://portal.ct.gov/-/media/DEEP/forestry/2020-Approved-CT-Forest-Action-Plan.pdf

Pearson DE (2009) Invasive Plant Architecture Alters Trophic Interactions By Changing Predator Abundance And Behavior. Oecologia 159:549–558.

Pimentel D, Pimentel M, Wilson A (2007) Plant, Animal, and Microbe Invasive Species in the United States and World. In: Nentwig W (ed) Biological Invasions. Springer, Berlin, Heidelberg, pp 315–330.

R Development Core Team (2022) *R version 4.1.2. R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria.

Rai RK, Shrestha L, Joshi S, Clements DR (2022) Biotic and Economic Impacts of Plant Invasions. In: Clements DR, Upadhyaya MK, Joshi S, Shrestha A (eds) Global Plant Invasions. Springer International Publishing, Cham, pp 301–315.

Razeng E, Watson DM (2015) Nutritional Composition of The Preferred Prey Of Insectivorous Birds: Popularity Reflects Quality. J Avian Biol 46:89–96.

Reeves JT, Fuhlendorf SD, Davis CA, Wilder SM (2021) Arthropod Prey Vary Among Orders in Their Nutrient and Exoskeleton Content. Ecol Evol 11:17774–17785.

Ricciardi A, Iacarella JC, Aldridge DC, Blackburn TM, Carlton JT, Catford JA, Dick JTA, Hulme PE, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, Meyerson LA, Pyšek P, Richardson DM, Ruiz GM, Simberloff D, Vilà M, Wardle DA (2021) Four Priority Areas to Advance Invasion Science In The Face Of Rapid Environmental Change. Environ Rev 29:119–141.

Richard M, Tallamy DW, Mitchell AB (2019) Introduced Plants Reduce Species Interactions. Biol Invasions 21:983–992.

Riedl HL, Stinson L, Pejchar L, Clements WH (2018) An Introduced Plant Affects Aquatic-Derived Carbon in The Diets Of Riparian Birds. PLOS ONE 13:e0207389.

Robichaud CD, Basso JV, Rooney RC (2022) Control of Invasive Phragmites australis (European Common Reed) Alters Macroinvertebrate Communities. Restor Ecol 30:e13548.

Robison AL, Berta JL, Mott CL, Register KJ (2021) Impacts of Invasive Amur Honeysuckle, *Lonicera Maackii*, Leaf Litter On Multiple Trophic Levels Of Detritus‐Based Experimental Wetlands. Freshw Biol 66:1464–1474.

Robbins CT, Felicetti LA, Sponheimer M (2005) The Effect of Dietary Protein Quality on Nitrogen Isotope Discrimination In Mammals And Birds. Oecologia 144:534–540.

Schlaepfer MA (2018) Do non-native species contribute to biodiversity? PLOS Biol 16:e2005568.

Schneider SC, Miller JR (2014) Response of Avian Communities to Invasive Vegetation in Urban Forest Fragments. The Condor 116:459–471.

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, M Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No Saturation in The Accumulation Of Alien Species Worldwide. Nat Commun 8:14435.

Serniak, L.T., Rohloff, P. and Agnew, C.C., 2023. Amur Honeysuckle (Lonicera maackii) increases abundance and diversity of shrub-dwelling arthropods and birds in forest edge habitat. Journal of Ornithology, 164:943-951

Shackleton RT, Vimercati G, Probert AF, Bacher S, Kull CA, Novoa A (2022) Consensus and Controversy in the Discipline of Invasion Science. Conserv Biol 36:e13931.

Shields J, Saunders M, Gibson K, Zollner P, Dunning J, Jenkins M (2015) Short-Term Response of Native Flora to the Removal of Non-Native Shrubs in Mixed-Hardwood Forests of Indiana, USA. Forests 6:1878–1896.

Singer MS, Farkas TE, Skorik CM., Mooney KA (2012) Tritrophic Interactions at A Community Level: Effects Of Host Plant Species Quality On Bird Predation Of Caterpillars. Am Nat 179:363–374.

Smets R, Claes J, Van Der Borght M (2021) On the Nitrogen Content and a Robust Nitrogen-To-Protein Conversion Factor Of Black Soldier Fly Larvae (Hermetia illucens). Anal Bioanal Chem 413:6365–6377.

Smith, S.B., DeSando, S.A. and Pagano, T., 2013. The value of native and invasive fruit-bearing shrubs for migrating songbirds. Northeastern Naturalist, 20(1), pp.171-184.

Tallamy DW, Narango DL, Mitchell AB (2021) Do Non-Native Plants Contribute to Insect Declines? Ecol Entomol 46:729–742.

Tarr MD (2022) Effects of Non-native Shrubs on Caterpillars and Shrubland-Dependent Passerines Within Three Transmission Line Rights-of-Way in Southeastern New Hampshire. Northeast Nat 29:1–43.

Traylor C, Ulyshen M, Wallace D, Loudermilk L, Ross C, Hawley C, Atchison RA, Williams JL, McHugh J (2022) Compositional Attributes of Invaded Forests Drive the Diversity of Insect Functional Groups. Glob Ecol Conserv 35:e02092.

Wagner DL (2005) Caterpillars of Eastern North America: A Guide to Identification and Natural History, 1st edn. Princeton University Press, Princeton, N.J.

Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D (2021) Insect Decline in The Anthropocene: Death by A Thousand Cuts. Proc Natl Acad Sci USA 118:e2023989118.

Wang W, Zhang C, Allen J, Li W, Boyer M, Segerson K, Silander J (2016) Analysis and Prediction of Land Use Changes Related to Invasive Species and Major Driving Forces in the State of Connecticut. Land 5:25.

Weidlich EWA, Flórido FG, Sorrini TB, Brancalion PHS (2020) Controlling Invasive Plant Species in Ecological Restoration: A Global Review. J Appl Ecol 57:1806–1817.

Westman WE (1990) Park Management of Exotic Plant Species: Problems and Issues. Conserv Biol 4:251–260.

Wootton JT (1997) Estimates and Tests of Per Capita Interaction Strength: Diet, Abundance, and Impact of Intertidally Foraging Birds. Ecol Monogr 67:45–64.

Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing Invasive Species Removal in a Whole-Ecosystem Context. Trends Ecol Evol 16:454–459.

Statements and Declarations:

Funding: Funding for this research was provided by Great Hollow Nature Preserve & Ecological Research Center.

Acknowledgements:

The bird exclusion experiment and taxonomic identification of insects were completed by three dedicated and talented summer technicians at Great Hollow: Max Kirsch, Chris Tait, and Joan Tremblay. Volunteers Joe McLaughlin, Ethan Mackenzi, and Alexa Dattner provided valued support for fieldwork in 2021. Helen Poulos and Paul Kraut provided help on elemental analysis in 2022. We thank Tim Farkas and Ian Cranston for advice on statistical analyses and data manipulation over the course of this project.

Competing interests: The authors have no conflicts of interest to declare.

Author contributions: RC, WC, CS completed fieldwork. TK completed elemental analysis. RC completed data analysis. All authors wrote and revised the manuscript.

Data availability statement: All data and R Code for this manuscript are available through Open Science Framework (osf.io) at DOI 10.17605/OSF.IO/BVFNA.