

Are native plants always better for wildlife than invasives? Insights from a community-level bird-exclusion experiment

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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 more nuanced, 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). In the United States alone, invasive species are estimated to also cause a yearly average of \$19.9 billion in economic losses (Fantle-Lepczyk et al. 2021) and \$120 billion is annually spent on their management (Pimentel et al. 2007). Invasive plants are particularly challenging to manage in terrestrial ecosystems, with the cost of removal efforts still being difficult to estimate accurately for the U.S. or globally (Rai et al. 2022). 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 is still not a consensus on whether such practices actually 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). Since conservation resources are severely limited relative to the impact of invasive species, prioritization 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 will provide more food resources to wildlife. Such practice is justified since removal of particularly aggressive invasive plant species can drive recovery of arthropod assemblages, which are an important food source for songbirds (Gratton and Denno, 2005, Hopfensperger et al. 2017). Native plants are recommended as replacements for exotic shrubs to provide more insect prey for birds (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, negatively impacting native animals indirectly (McCary et al. 2016, Fletcher et al. 2019). Some studies have 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 are many: compounds released from invasive plants through roots and decaying leaves can impact detritus-based food webs (Robison et al. 2021), while the atypical architecture of invasive plants modifies the behavior of arthropod communities (Pearson 2009, Lind and Parker 2010, Landsman et al. 2021).

In managed forests, invasive plant removal is typically conducted without active restoration of native plants and relies on local native plants to move into recently cleared areas on their own (Flory and Clay 2009, Shields et al. 2015, Farmer et al. 2016, Cutway 2017). Removal is suggested since habitats dominated by invasive plants often have lower abundances of plant-feeding arthropods which could be prey for birds, particularly caterpillars or spiders (Richard et al. 2019, Clark and Seewagen 2019). A critical gap in regional management of invasive plants is establishing whether a target invasive species indeed provides lower quality food resources to birds compared to the alternative native woody plants in the same habitat patch.

Our study involved a comparison of invasive and native members of a plant community within a Connecticut, USA mature forest. We tested three hypotheses: (1) the 'weaker predatory effects hypothesis', (2) the 'low food quantity hypothesis', and (3) the 'low food quality hypothesis'. 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. 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 (Lieurance and Cipollini 2013, Haan et al. 2021, Lampert et al. 2022). We tested all three hypotheses through a predator exclusion experiment on four intensively managed invasive woody plant species of the northeastern, U.S., using a set of six common, 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 (*Eunonymus 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 co-occur with these invasive shrubs 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*). Performing our experiment across these 10 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 (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”). Each of these branches was paired with a nearby (< 10 m away) unmanipulated control branch of the same species. We set up 12 treatment pairs for each of the 10 focal plant species, resulting in a total of 240 individual host plants in the study. 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 -80° 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 -80° 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 was fitted as a normally distributed GLMM after log-transformation and included both host plant species and bird exclusion treatment as fixed effects, and branch as a random effect. All abundance models were fitted with a negative binomial GLMM. In abundance models, invasive status (yes or no) was a fixed effect along with bird-exclusion treatment, and branch and host-plant species were included as random effects. Samples taken across the three sampling periods were pooled together in arthropod models to avoid pseudoreplication (Clark et al. 2016). Nitrogen content models were fit with a normal distribution, but since all arthropod samples were pooled across sampling periods and only taken from exclusion branches, only 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 χ^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). LRRs, 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, Wootton 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. LRR 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 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 biomass than the three other invasive plant species (Fig. 1D). Native plants varied in biomass, with musclewood, sweet birch and witch-hazel exhibiting relatively higher 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 LRR 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).

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: $P = 0.88$, Fig. 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: $P = 0.98$, Fig. 4, Table S4).

Discussion

The prevailing paradigm in habitat management and restoration assumes that all invasive plants are of little value or harmful to native wildlife. However, this broad-brush approach 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 plants that are major components of northeastern U.S. forests. Our results suggest that it should first be demonstrated, not assumed, that a given non-native, invasive plant is of inferior quality to 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 some invasive plants should be prioritized over others depending on the habitat in question.

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'. Furthermore, support for the '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 a major group of forest insectivores, birds, 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 of lower quality or more highly defended than on native plants, reducing biomass of arthropods on invasive plants (van Hengstum et al. 2014). 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). Spider abundance was higher on low-lying Japanese barberry, similar to 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 site did not include *Prunus* (cherries) and *Quercus* (oaks), which are known to be high-quality food plants for forest insects like caterpillars (Wagner 2005), because they are regenerating poorly and declining in many northeastern forests (including our study site) due to a variety of factors (e.g., deer over-browsing). 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 dominant or becoming dominant in our region's forests. Our study suggests 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.

Declarations

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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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Figures

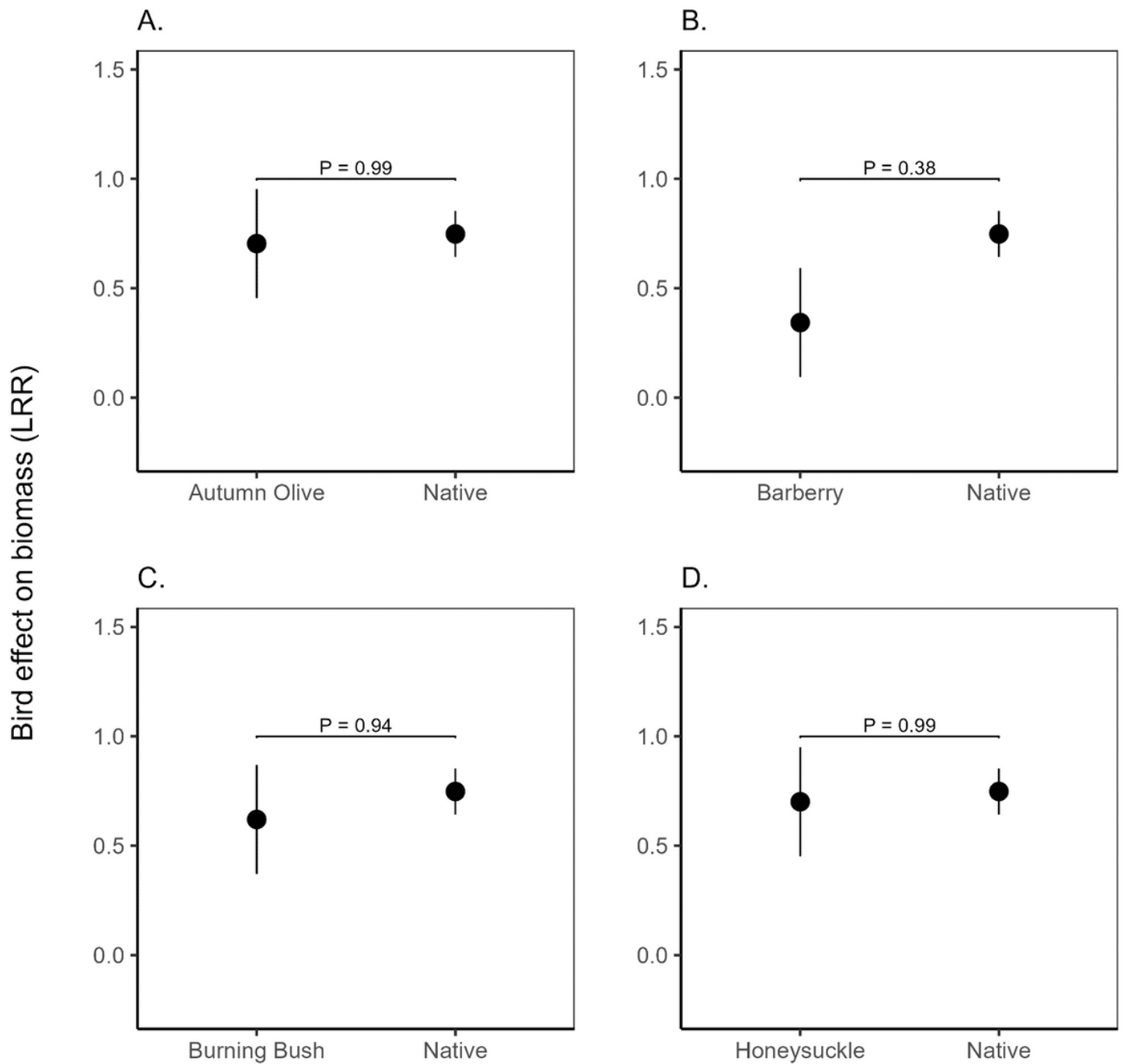


Figure 1

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

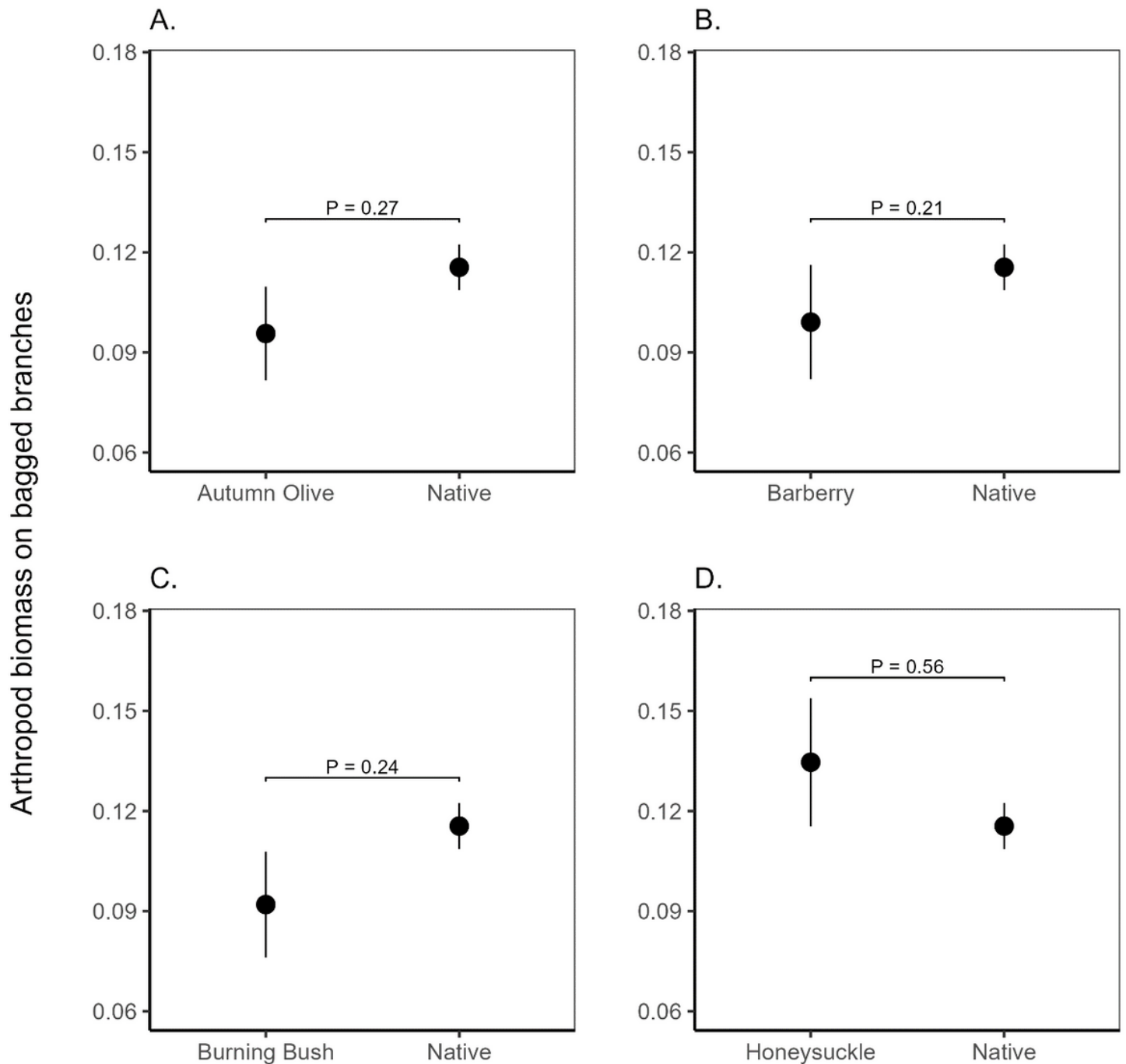


Figure 2

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 $\pm$ SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts.

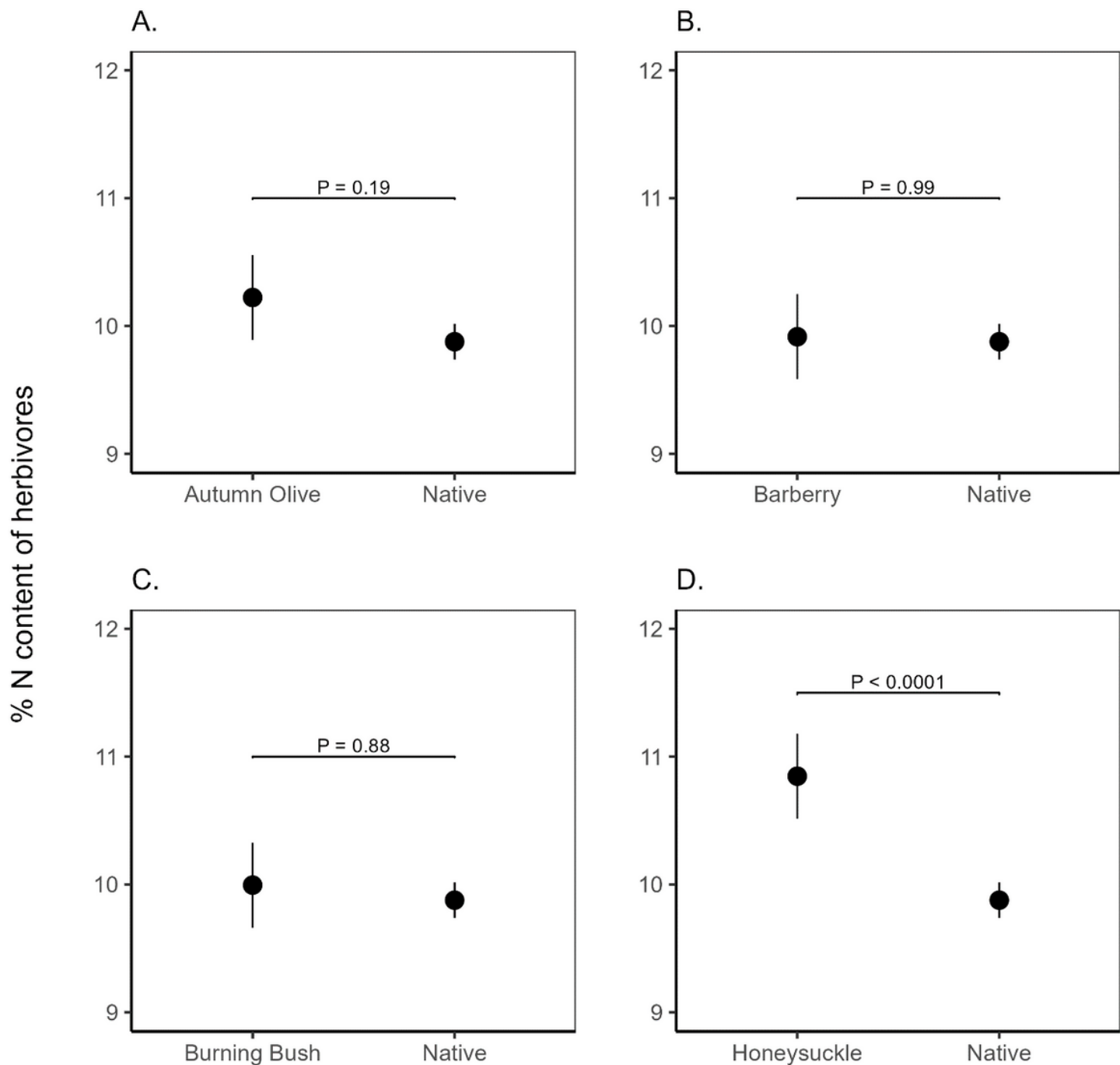


Figure 3

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 $\pm$ SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts.

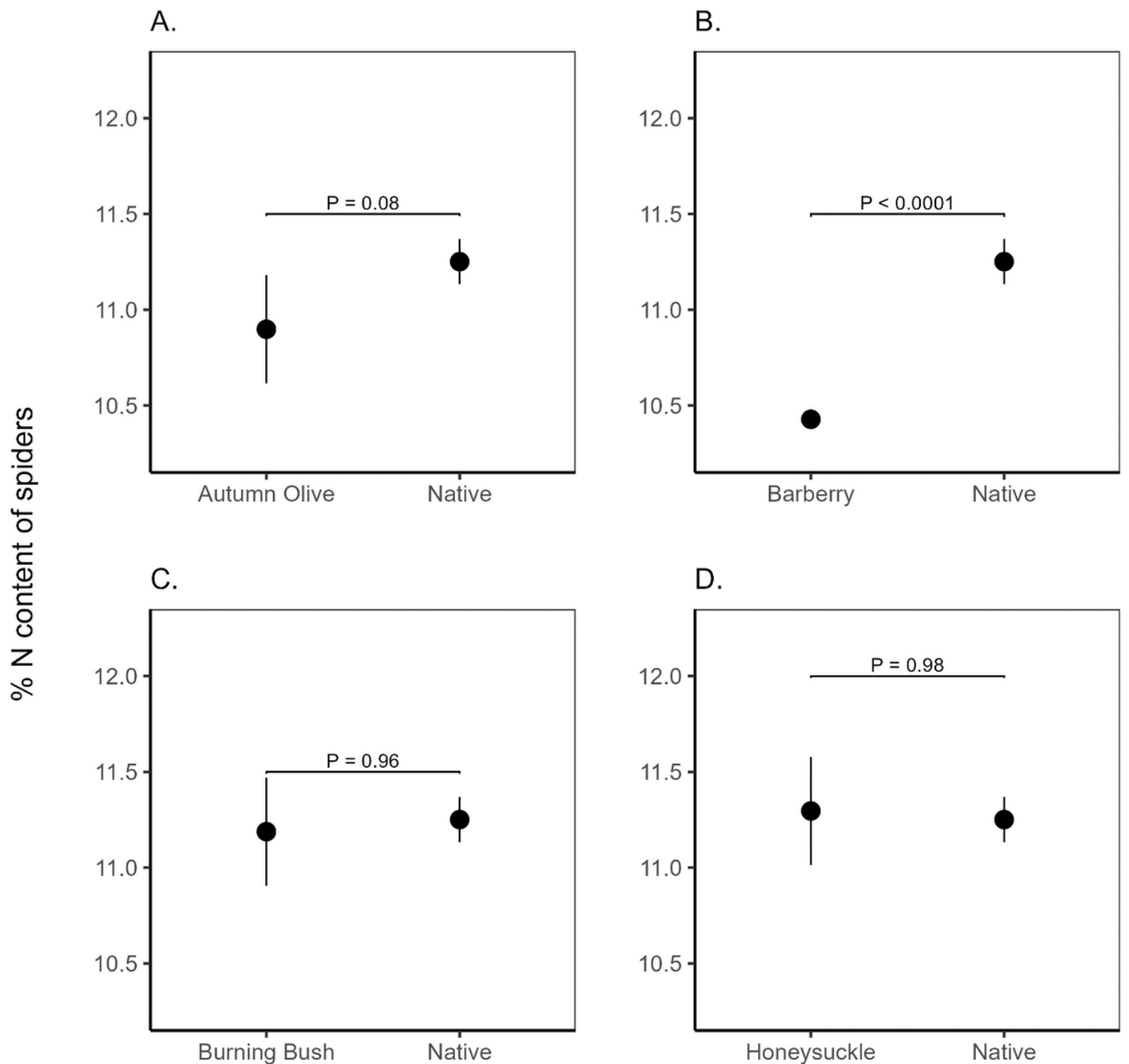


Figure 4

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 $\pm$ SEM is plotted, with levels of significance illustrated for natives versus invasive plant species using grouped, planned contrasts.

Supplementary Files

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