

# Invasive Japanese Barberry, *Berberis thunbergii* (Ranunculales: Berberidaceae) Is Associated With Simplified Branch-Dwelling and Leaf-Litter Arthropod Communities in a New York Forest

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## Abstract

Arthropod food webs can be indirectly impacted by woody plant invasions, with cascading consequences for higher trophic levels. There are multiple bottom-up pathways by which invasive plants can alter food webs: above-ground interactions based on plant-herbivore associations and below-ground at the interface of leaf-litter and soil food webs. We compared arthropod community composition in these two food web dimensions in a New York forest that has been heavily invaded by nonnative Japanese barberry. Using two sampling protocols, we compared arthropod community composition on Japanese barberry shrubs to multiple species of native host shrubs and then compared leaf-litter arthropod assemblages between forest patches with exceptionally high Japanese barberry densities and those with relatively little to no Japanese barberry present. Fitting with trends in other woody shrub invasions, arthropod species richness was significantly lower in the leaf litter around Japanese barberry and on Japanese barberry plants themselves. Although overall arthropod abundance was also significantly lower on and in the leaf litter around Japanese barberry than on and around native shrubs, total biomass did not differ due to the taxa associated with Japanese barberry tending to be larger-bodied. We observed a dramatic reduction in predatory arthropods in response to both bottom-up pathways, particularly among ants and spiders. Our results show that Japanese barberry-invaded habitats may be experiencing trophic downgrading as result of lower numbers of generalist predators like spiders and ants, which may have rippling effects up the food web to insectivorous animals and their predators.

**Key words:** invasive species, food webs, above-ground interaction, below-ground interaction, arthropod

Arthropod communities on plants form the foundation of terrestrial food webs, and these communities are becoming increasingly impacted by invasions of nonnative plant species (Mitchell et al. 2006). In forest food webs, nonnative invasive plants have two dominant trophic pathways through which they can influence arthropod communities: above-ground interactions arising from plant-feeding herbivores and soil food web interactions based around detritivory (Vestergård et al. 2015). Furthermore, invasive plants can impact below-ground or leaf litter food webs by altering soil chemistry, decomposition rates, and soil microbes, and these changes cascade up to arthropod communities by altering food resources (Elgersma and Ehrenfeld 2011, Elgersma et al. 2011, Wardle and Peltzer 2017). However, it is difficult to predict the consequences of invasion for food web interactions because invasive plants impact arthropod communities in a myriad of ways. In addition to reducing overall

arthropod abundance, invasions can reduce arthropod diversity (Mitchell et al. 2006, Schuh and Larsen 2015) and certain arthropod guilds differ in response to invasion depending on community context (Vilardo et al. 2018). Such changes to food web structure may cause trophic downgrading, which occurs when higher trophic levels are extirpated from food web interactions, and thereby reduce community stability (Britten et al. 2014).

For above-ground interactions, foliage-foraging arthropod communities are comprised of multiple guilds of insect herbivores, generalist and specialist predators, and plant parasites. Host-plant traits primarily determine the structure of these food web communities since insect herbivores, the foundation of this food web, depend entirely on host-plants for development and reproduction (Laigle et al. 2018). Insect herbivores have been found to exhibit reduced performance and avoid feeding, ovipositing, and reproducing on invasive

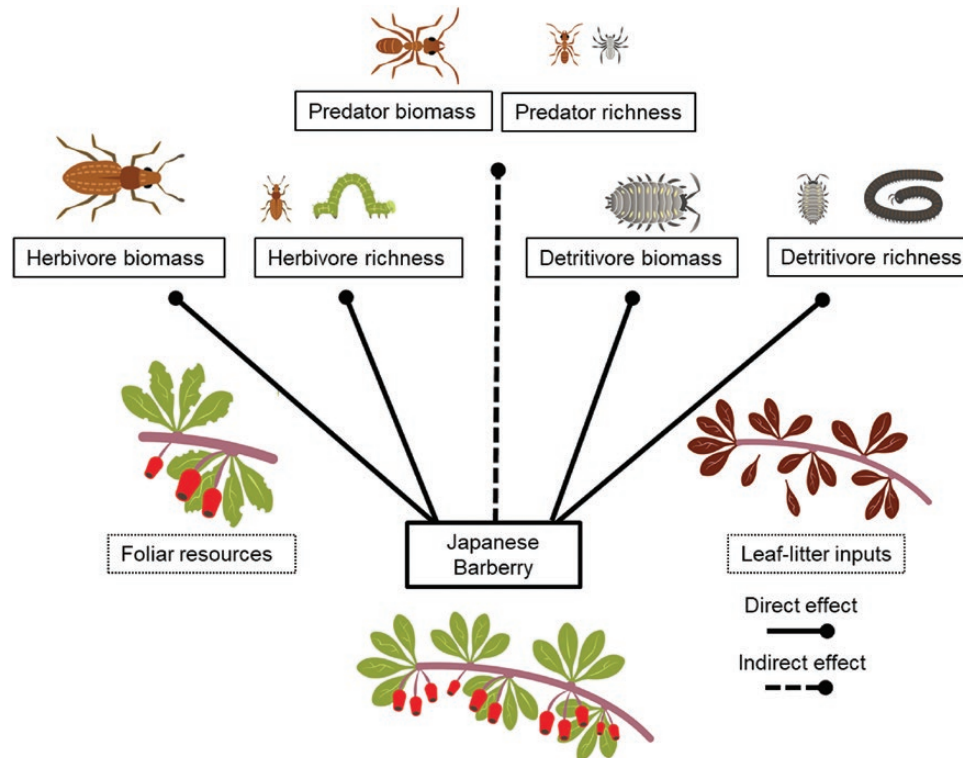
plants (Harvey et al. 2010, Yoon and Reed 2016). Consequently, these changes to the structure of herbivore communities cascade up through forest food webs, with nonnative invasive shrubs frequently having a lower abundance, biomass, and species richness of arthropods compared to native plants in the same habitat (e.g., Liu et al. 2006).

Below the canopy and shrub layer, arthropod food webs are impacted by nonnative plant invasions because leaf-litter and decomposition processes become restructured (Suseela et al. 2016). While the trophic mechanisms are not direct, root exudates from invasive plants often also indirectly mediate soil pH, detrital decomposition rates, and micronutrients available, with each process impacting decomposer food webs (reviewed by McCary et al. 2016). Because of this, plant invasions can simultaneously impact soil arthropod abundance, biomass, species richness, and food web structure in addition to above-ground communities (Motard et al. 2015, Vilardo et al. 2018). We expect predatory arthropod abundance to be indirectly susceptible due to changes in food availability on branches and in leaf litter.

We examined above- and below-ground changes to arthropod communities associated with the invasion by Japanese barberry (DC. Ranunculales: Berberidaceae) in a temperate forest in New York State. Japanese barberry was first introduced to North America from Asia in the late 1800s as an ornamental plant and has since become one of the most widespread nonnative woody plants in the forests of the northeastern United States (Ehrenfeld 1997, Silander and Klepeis 1999). Japanese barberry is able to suppress the establishment and growth of co-occurring woody plant species and is largely unpalatable to white-tailed deer (*Odocoileus virginianus*), which give it strong competitive advantages over native species and contribute to its ability to overtake understory plant communities (Harrington et al. 2004, Williams et al. 2009, but see Flinn et al. 2014). Forests with high white-tailed deer densities have

been observed to have virtually no tree regeneration and no shrub layer other than that created by dense clusters of Japanese barberry (Williams et al. 2009). In invaded areas, Japanese barberry can affect soil structure, function, and nutrient cycling (Kourtev et al. 1999, 2003; Ehrenfeld 1997), and thereby alter soil biota (Kourtev et al. 1999, 2003). Japanese barberry may benefit nonnative earthworms, which can have detrimental effects on leaf-litter fauna, or conversely, it may be that nonnative earthworms are what create the conditions that then favor the colonization and proliferation of Japanese barberry (Maerz et al. 2009, Nuzzo et al. 2009). Notably, invasion of Japanese barberry is associated with an increased abundance of black-legged ticks (*Ixodes scapularis*), the primary vector of the causative agent of Lyme disease (Williams et al. 2009, Linske et al. 2018). Otherwise, despite the extreme prevalence of this highly invasive plant throughout much of the northeastern United States and the suspected impact it is having on native biodiversity, we are not aware of any other investigations of the effects of Japanese barberry on North American invertebrates.

In this study, we examined the association between Japanese barberry density and the composition of a forest food web base by comparing the abundance, biomass, and species richness of foliage-dwelling and leaf-litter invertebrates between heavily and sparsely invaded portions of a forest preserve in New York State (Fig. 1). We predicted that Japanese barberry is associated with reductions in overall arthropod abundance and species richness, which may lead to trophic downgrading (e.g., reduced abundance of higher trophic levels within arthropod food webs). The prediction of this hypothesis is that Japanese barberry is of poorer quality as a host, which will have cascading effects up the above-ground arthropod food web and result in lower abundance, richness, and fewer members of higher trophic levels compared to native host-plants. For the



**Fig. 1.** Schematic diagram of Japanese barberry's potential effects on arthropod food webs and community attributes considered in this study. Solid boxes indicate trophic relationships (herbivory, detritivory, predation), while dotted boxes indicate mechanisms by which Japanese barberry might alter arthropod food webs.

soil food web, we predicted that Japanese barberry's impacts on soil and leaf litter reduces food availability to soil-foraging arthropods. In all, we expected a lower abundance, biomass, and species richness of arthropods in the leaf litter around Japanese barberry than around native shrubs, in addition to changes in the abundance of arthropods at higher trophic levels (Fig. 1).

## Methods

### Study Site

We conducted our study from 18 May to 26 May 2017 at the Pawling Nature Reserve, which lies along the Hammersly Ridge in the towns of Dover and Pawling, New York (41.616669, -73.563227). Pawling Nature Reserve is approximately 429 ha and dominated by second-growth oak and mixed hardwood forest, along with stands of red pine (*Pinus resinosa*) and eastern hemlock (*Tsuga canadensis*), old fields, and red maple swamps. Other surface waters include several vernal pools and two freshwater streams that feed into Quaker Lake, which occupies much of the southern end of the reserve. The northern end of the reserve is characterized by steep slopes of predominantly American beech (*Fagus grandifolia*) that transition down into yellow birch (*Betula alleghaniensis*) forest to the east. The timing of arthropod collections coincides with other studies examining bird predator effects on arthropod communities in northeastern U.S. forests (i.e., Singer et al. 2012).

Like many woodlands invaded by Japanese barberry (e.g., Maerz et al. 2009, Kourtev et al. 2003, Brand et al. 2012), some forested portions of Pawling Nature Reserve show invasion fronts, where Japanese barberry occurs in dense clusters from the edges inward, up to a point beyond which there is little to no Japanese barberry present. Additionally, stone walls that are a legacy of past agricultural uses intersect the forest and divide areas that have greatly different densities of Japanese barberry on one side and the other, likely depending on the form of past agricultural use (e.g., livestock pasture vs crops) and the time when that activity was last abandoned relative to the arrival and establishment of Japanese barberry in the region (DeGasperi and Motzkin 2007). This natural variation in Japanese barberry density and distribution that is commonly found within the same forests provides opportunities to non-experimentally compare biotic and abiotic attributes among areas with differing levels of invasion intensity (sensu Maerz et al. 2009, Nuzzo et al. 2009).

### Plot Selection and Vegetation Surveys

As part of a separate study of the effects of Japanese barberry on the physiological condition of breeding male ovenbirds (*Seiurus aurocapilla*), we selected forest patches that we visually estimated to have either little to no Japanese barberry (<10% of ground cover) or a relatively high density of Japanese barberry (>25% of ground cover) over an area of at least 0.5 ha, had a singing male ovenbird present (indicating breeding territory establishment), and were at least 50 m in from the nearest road, house, or other sharp edge. At each such location, we captured the ovenbird using a mist-net and playback recording to collect morphological measurements and other data from the bird before releasing it. We then used the midpoint of the mist-net to represent the center of a 0.02 ha circular plot in which we surveyed vegetation. We surveyed shrubs by walking perpendicular east-west and north-south transects across the plot, while identifying and counting each shrub (defined as a woody plant <7.6 cm DBH) either intercepted by the observer's outstretched arms or occurring at a height between the observer's outstretched arms and knees (adapted

from James and Shugart 1970). We later converted shrub counts to density (shrubs per ha) by adapting the formula for circular plots in James and Shugart (1970) to our plot size. We also calculated percentage of ground cover from observations that were made through an ocular tube at 10 locations along both of the two transects within the plot (James and Shugart 1970) and scored as one of the following categories: Japanese barberry, other nonnative shrub, native shrub, or no shrub (i.e., herbaceous vegetation or non-vegetated ground).

### Invertebrate Collection

To sample leaf-litter invertebrates, we collected 0.04 m<sup>2</sup> of leaf litter down to the hummus layer at the centerpoint of each plot and again 10 m to the east and west of that centerpoint for a total of 0.12 m<sup>2</sup> samples of leaf litter per plot. The leaf litter samples were stored in the field in inflated plastic bags for up to 6 h and immediately taken to a laboratory for processing. Foliage-dwelling invertebrates were sampled from Japanese barberry in high-density plots and from native woody understory plants in low-density plots using a beat-sheet technique (Cooper and Whitmore 1990) in which shrubs were struck with a wooden dowel five times to dislodge invertebrates from the foliage and branches while holding a white canvas sheet underneath. We sampled the first three Japanese barberry shrubs encountered while walking the transects across the high-density plots and the first three native shrubs encountered while walking the transects across the low-density plots. The invertebrates were collected from the canvas sheet with aspirator or forceps and transferred to plastic vials containing a piece of cotton soaked in acetone.

### Invertebrate Processing

On the day of collection, invertebrates were extracted from the leaf litter samples using Berlese funnels that were operated with a 40-W light bulb for 12–18 h. The extracted invertebrates were identified to taxonomic order or family under a dissecting scope and then oven-dried to a constant mass at 60°C. All individuals in the same taxonomic group from a given plot were then combined and weighed together on an analytical balance to the nearest 0.1 mg.

Invertebrates collected from the shrubs were identified to family under a dissecting scope and given a morphospecies designation for estimating species richness. Morphospecies were tagged to order (e.g., Hymenoptera-1) or family (e.g., Formicidae-1). If a specimen could be readily identified to species (such as ants), we would code it appropriately (e.g., *Aphaenogaster rudis*). To estimate carnivore abundance, we used two arthropod families as indicators of relative abundance of predators: spiders (Araneae) and ants (Hymenoptera: Formicidae). These two guilds are dominant generalist predators in both food webs examined (e.g., Moya-Laraño and Wise 2007, Dehart et al. 2017), and therefore were used as indicators of changes in food web interactions resulting from either pathway. While ants can occupy other functional positions in food webs, such as scavengers and hemipteran mutualists (Lach et al. 2010), we primarily observed ant species implicated as predators in northeastern forest food webs. The most common genera observed were *Aphaenogaster*, *Tetramorium*, and *Camponotus*. We pooled counts of Collembola, Isopoda, Pauropoda, Symphyla, and Diplopoda together as an estimate of detritivore abundance. The arthropods were then oven-dried and weighed as described above.

### Statistical Analyses

We assigned plots with a density of fewer than 3460 Japanese barberry bushes per hectare to a 'low density' category ( $N = 17$ ) and plots with a density of greater than 4940 Japanese barberry bushes

**Table 1.** Description of density, % shrub community, and % cover for high-density and low-density Japanese barberry plots, including native and nonnative plants

Plant species	Low-density plots			High-density plots		
	Density (per ha)	% shrub community	% ground cover	Density (per ha)	% shrub community	% ground cover
Japanese barberry	1322 ( $\pm$ 1389)	12.3 ( $\pm$ 14.4)	3.1 ( $\pm$ 4.0)	7690 ( $\pm$ 2409)	52.0 ( $\pm$ 18.3)	30.9 ( $\pm$ 17.3)
Other nonnative shrubs	843 ( $\pm$ 1359)	8.5 ( $\pm$ 13.5)	3.1 ( $\pm$ 7.0)	3837 ( $\pm$ 4785)	14.5 ( $\pm$ 15.3)	7.2 ( $\pm$ 9.1)
Native shrubs	11246 ( $\pm$ 7010)	78.3 ( $\pm$ 25.4)	16.6 ( $\pm$ 13.5)	28899 ( $\pm$ 22833)	33.5 ( $\pm$ 20.5)	12.2 ( $\pm$ 11.7)

Native shrubs across both groups included American beech (*Fagus grandifolia*), ash (*Fraxinus* spp.), black birch (*Betula lenta*), blueberry (*Vaccinium* spp.), black cherry (*Prunus serotina*), grape (*Vitis riparia*), hickory (*Carya* spp.), hophornbeam (*Ostrya virginiana*), mapleleaf viburnum (*Viburnum acerifolium*), musclewood (*Carpinus caroliniana*), northern red oak (*Quercus rubra*), raspberry (*Rubus* spp.), spicebush (*Lindera benzoin*), striped maple (*Acer pensylvanicum*), sugar maple (*Acer saccharum*), white oak (*Quercus alba*), and witch-hazel (*Hamamelis virginiana*). Values are means  $\pm$  SD.

per hectare to a ‘high density’ category ( $N = 15$ ); those with intermediate levels of Japanese barberry density were omitted from our analyses. We selected these thresholds because they provided nearly balanced sample sizes, allowed most plots to be included in the analyses, and provided a substantial difference in Japanese barberry density between the two categories (see Results). Analyses were performed using R version 3.5.1 (2018-7-02). Invertebrate abundance and biomass were compared between treatment groups using generalized linear models (Poisson-fit for count-data and Gaussian-fit for biomass). Estimated predicted marginal means and SEs were obtained using the lsmeans package (Lenth 2016). Significance tests were completed with the car package (Fox and Weisberg 2018). Species accumulation curves were fitted using the vegan package, and first-order jackknife procedure was used to extrapolate species richness and CIs based on collection effort (Oksanen et al. 2019).

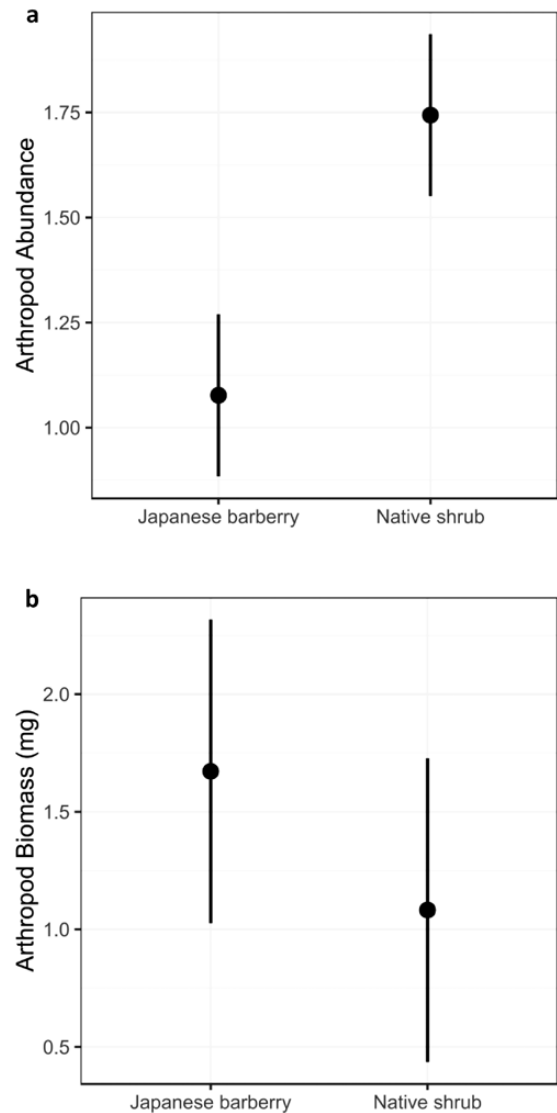
## Results

### Vegetation Composition

Japanese barberry density averaged 1322 plants per hectare and represented only 12% of the shrub community in the low-density plots while averaging 7690 plants per hectare and representing 52% of the shrub community in the high-density plots (Table 1). Other nonnative shrub species, which included multiflora rose (*Rosa multiflora*) along with lesser amounts of Oriental bitter-sweet (*Celastrus orbiculatus*) and burning bush (*Euonymus alatus*), were also more prevalent in the high-density plots than the low-density plots, but considerably less abundant than Japanese barberry in both treatments (Table 1). Native shrubs, in contrast, represented an average of 78.3% of the shrub community in the low-density plots and only 33.5% of the shrub community in the high-density plots (Table 1).

### Foliage-Dwelling Invertebrates

Arthropod abundance was lower on Japanese barberry than on native shrubs (Fig. 2a,  $P = 0.016$ ). This was largely driven by ants, which were 10 times more abundant on native shrubs than on Japanese barberry (0.53 ants per native shrub sample vs 0.05 ants per Japanese barberry sample;  $P = 0.001$ ). There was a marginally significant reduction in spider abundance on Japanese barberry ( $P = 0.083$ ). Despite the difference in arthropod abundance, total biomass was similar between Japanese barberry and the native shrubs (Fig. 2b;  $P = 0.518$ ). Species richness was significantly lower on Japanese barberry than on native shrubs, with an estimated 22 species occurring on the native shrubs and only



**Fig. 2.** (a) Arthropod abundance on Japanese barberry and native shrubs (# individuals per shrub sample). Height of points indicates predicted marginal mean, and error bars SE of the mean. (b) Arthropod biomass on Japanese barberry and native shrubs (milligrams per shrub sample). Height of points indicates predicted marginal mean, and error bars SE of the mean.

17 species occurring on Japanese barberry (Fig. 3; Jackknife estimated species richness based on sampling effort is  $33.6 \pm 4.59$  for native plants, and  $24.7 \pm 3.08$  for Japanese barberry). Arthropod

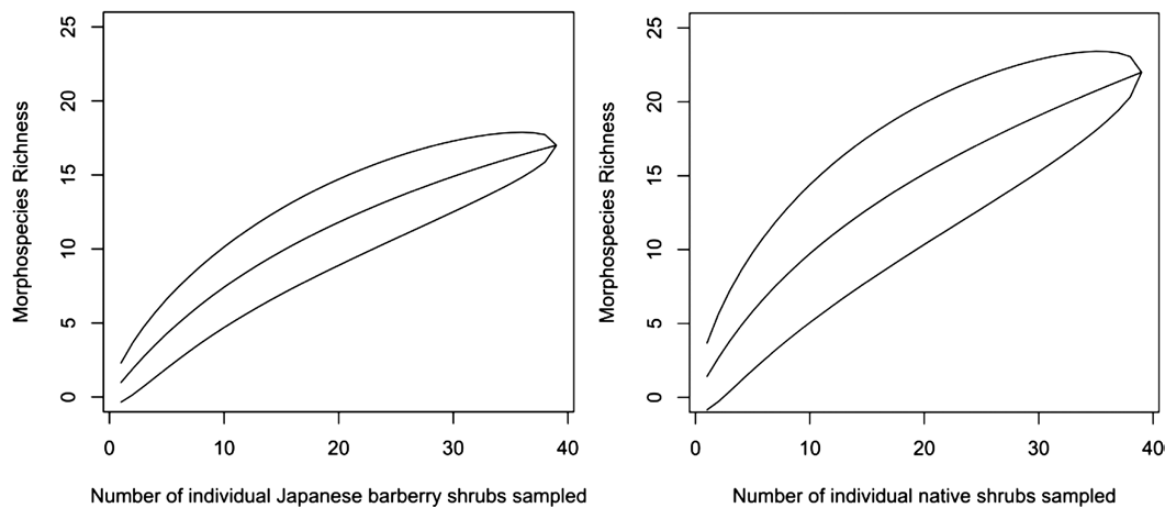


Fig. 3. Species accumulation curve for native shrubs and Japanese barberry based on sampling effort (# of shrubs).

Table 2. Abundance of arthropods in branch and leaf-litter sampled communities

Taxonomic group	Abundance			
	Foliage		Leaf litter (barberry density)	
	Barberry	Native	High	Low
Non-insects				
Acari	4.4%	12.5%	1.6%	0.3%
Araneae	35.6%	10.9%	8.4%	3.4%
Chilopoda	2.2%		2.4%	1.6%
Collembola			7.3%	4.7%
Diplopoda	4.4%		3.4%	1.6%
Isopoda			2.6%	1.5%
Opiliones				0.1%
Pauropoda				0.1%
Psuedoscorpiones			1.8%	1.6%
Symphyla				0.6%
Insects				
Blattodea		1.6%	0.8%	
Coleoptera	8.9%	12.5%	36.1%	17.1%
Coleoptera (Elateridae)			1.3%	1.6%
Diptera	6.7%	7.8%	2.9%	2.8%
Ephemeroptera		1.6%		
Hemiptera	4.4%	4.7%	4.7%	1.0%
Hymenoptera		1.6%	1.8%	0.7%
Hymenoptera (Formicidae)	4.4%	34.4%	18.6%	56.6%
Lepidoptera	4.4%	3.1%	6.3%	4.8%
Orthoptera	11.1%	4.7%		
Psocoptera	13.3%	4.7%		

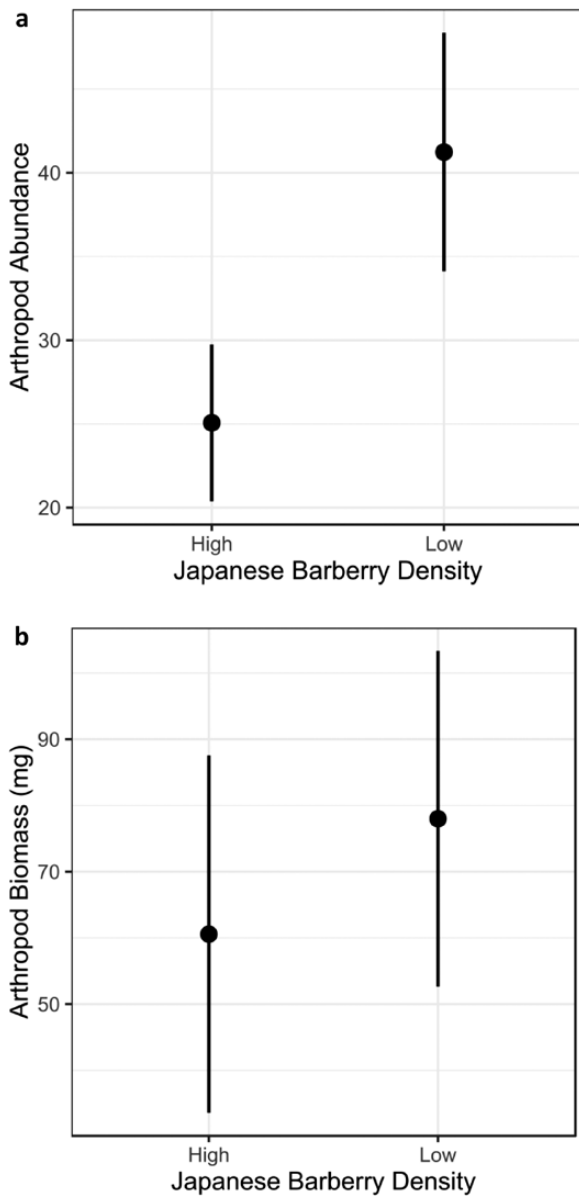
% abundance is out of total arthropods under each sampling protocol and plant invasion category (native vs nonnative, high vs low density, respectively).

communities on foliage were predominately mites (Acari), spiders (Araneae), beetles (Coleoptera), and ants (Hymenoptera: Formicidae) (Table 2).

#### Leaf-Litter Invertebrates

Leaf-litter arthropod abundance was lower in the high Japanese barberry density plots (Fig. 4a,  $P = 0.052$ ). This was also largely driven by ants, which were five times more abundant in the leaf litter in plots with little to no Japanese barberry than in those

with a high density of Japanese barberry ( $P = 0.005$ ). Spider abundance in the leaf litter, however, did not differ between treatment groups ( $P = 0.288$ ). Detritivore abundance was also similar between the high and low Japanese barberry density plots ( $P = 0.763$ ). Total arthropod biomass was not significantly different between treatment groups (Fig. 4b,  $P = 0.637$ ). Leaf-litter arthropod richness was significantly lower in the high Japanese barberry density plots than in those with little to no Japanese barberry, with an estimated 29 species occurring



**Fig. 4.** (a) Arthropod abundance in plots with high Japanese barberry density compared to low Japanese barberry density (# individuals per 0.04m<sup>2</sup> leaf-litter area sampled). Height of points indicates predicted marginal mean, and error bars SE of the mean. (b) Arthropod biomass in plots with high Japanese barberry density compared to low Japanese barberry density (mg per 0.12m<sup>2</sup> leaf-litter area sampled). Height of points indicates predicted marginal mean, and error bars SE of the mean.

around the native shrubs and only 21 species occurring around Japanese barberry (Fig. 5; Jackknife estimated species richness based on sampling effort is  $37.4 \pm 3.4$  for low barberry density, and  $25.7 \pm 2.1$  for high barberry density). Arthropod abundance in leaf litter had a more even distribution of non-insect arthropods, but beetles (Coleoptera) and ants (Hymenoptera: Formicidae) were numerically dominant (Table 2).

## Discussion

Japanese barberry is one of the most prevalent nonnative invasive plants in northeastern U.S. forests, and yet almost nothing is known about its effects on invertebrates or other wildlife communities.

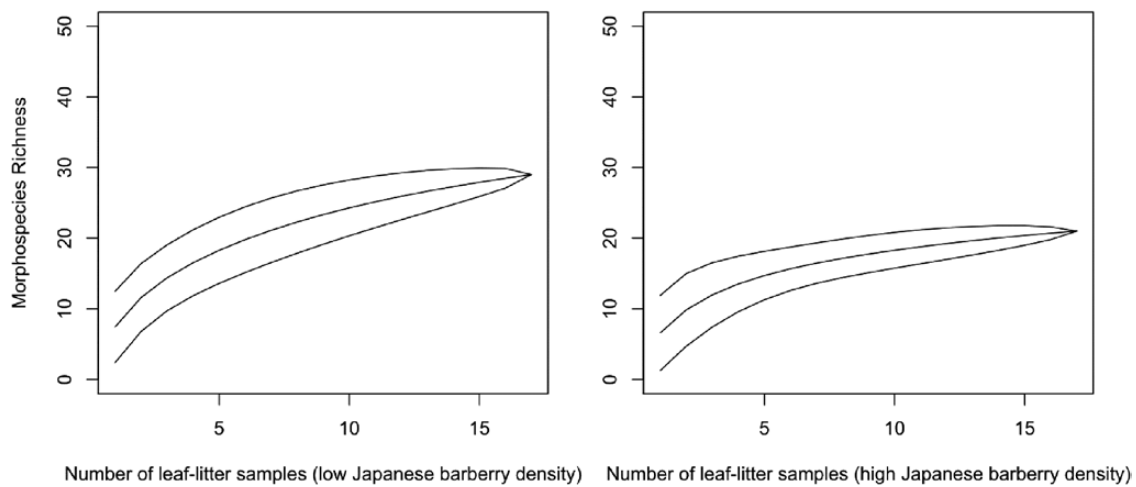
Here, we found Japanese barberry to be associated with substantial changes in arthropod community composition as a result of significant reductions in arthropod species richness and abundance in both the forest understory and leaf-litter layer. Our results indicate that Japanese barberry-invaded habitats experience trophic downgrading as result of lower numbers of generalist predators like spiders, which may have rippling effects up the food web to insectivorous animals and their predators. These patterns match other studies on plant invasion in which displacement of native plants has cascading consequences for arthropod communities beyond changes to herbivore abundance (Wardle and Peltzer 2017).

Fitting with predictions that herbivore diversity is lower on non-native plants, we saw fewer species of arthropods on Japanese barberry than on native shrubs. This was expected given the wealth of observations that native foliage-feeding herbivores perform poorly on exotic host-plant species (Liebhold et al. 2017). However, there was not a concomitant reduction in arthropod biomass, suggesting that the body-size composition of the community had changed. Additionally, ant abundance was dramatically lower on Japanese barberry than native plants, and to some degree spider abundance was as well, suggesting some loss of top-down control that would typically be seen on native plants. In the leaf-litter food web, we also observed lower arthropod diversity along with lower abundance in areas heavily invaded by Japanese barberry. Ants were dramatically reduced in abundance in the leaf litter around Japanese barberry as well as on the Japanese barberry itself, demonstrating that ant communities are heavily impacted in both dimensions where this invasive plant is prevalent.

Soil food webs, and leaf-litter and foliage-foraging arthropod communities are intrinsically linked (McCary et al. 2016). Our study design and analysis attempted to compartmentalize the two pathways in which Japanese barberry could impact arthropod communities, but these are not entirely separate. For example, leaf litter in areas with high densities of Japanese barberry was found to have fewer ants, and this could reflect changes in foliage-foraging ants on Japanese barberry given that most ant species in northeastern U.S. forests nest in soil (Ellison et al. 2012). However, because we sampled leaf litter in addition to foliage, our study indicates that woody plants can impact arthropod communities at the level of individual plants and habitat patches. Further work could examine the underlying mechanisms, such as reduced host-plant quality or changes to leaf-litter structure in response to Japanese barberry invasion.

By altering species richness and food web complexity, plant invasions frequently lead to more simplified communities and weakened top-down control (Estes et al. 2011). Our observed changes to arthropod communities in response to invasion may have arisen from loss of top-down control of some insect populations (e.g., Suseela et al. 2016). For example, given the reduction in generalists predators we observed, this may explain why Japanese barberry is associated with increased abundances of black-legged ticks (e.g., Williams and Ward 2009) as opposed to previous interpretations that Japanese barberry creates favorable environmental conditions for the ticks and/or their common host, the white-footed mouse (*Peromyscus leucopus*) (Williams et al. 2009, Linske et al. 2018). If so, this suggests that simplified food webs on invasive plants can have consequences for human health by disrupting trophic interactions that suppress vectors for diseases.

Our results show that Japanese barberry is associated with simplified leaf-litter and foliage-dwelling arthropod communities that represent an important part of the foundation of forest food webs. Although our study was limited to one forest, we consider



**Fig. 5.** Species accumulation curve for high Japanese barberry density plots and low Japanese barberry density plots based on sampling effort (# of litter samples).

it likely that the patterns that we observed are largely consistent throughout other northeastern U.S. forests that have also been heavily invaded by Japanese barberry. Such disruptions of invertebrate food webs can have detrimental consequences for wildlife in higher trophic positions, even at the population level (Narango et al. 2018). Much more work on the cascading effects of nonnative invasive plants throughout ecosystem food webs is needed before the full breadth of their ecological impact can be appreciated and managed.

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