



To manage or not? Successful native tree seedling restoration despite a dense, invasive shrub, *Berberis thunbergii*

Arthur F. Link III · Linda M. K. Johnson · Ryan M. Utz

Received: 4 January 2019 / Accepted: 8 April 2019
© Springer Nature B.V. 2019

Abstract Invasive plant species suppress native trees through a variety of mechanisms. A non-native shrub, *Berberis thunbergii*, has been shown to depress native tree seedling densities in eastern North American deciduous forests, but the mechanisms remain unclear. We attempted to identify the mechanisms leading to decreased native tree seedling densities in *Berberis*-invaded understories by experimentally measuring survivorship and growth of three common eastern deciduous tree seedlings, *Prunus serotina*, *Quercus alba*, and *Q. velutina*. First, we reared native tree seedlings in soil samples extracted from *Berberis*-invaded and control forest plots to determine if early growth and survival varied between medias. Then, we introduced surviving seedlings into three classes of in situ field subplots: control (outside *Berberis* invasion), invaded (*Berberis* present), and managed subplots where *Berberis* removal occurred following non-chemical best practice guidelines. Slight decrease of early-stage seedling survivorship and growth occurred in extracted soils from invaded plots. Seedling survival differed between field subplots, with seedlings either showing no differences between invaded subplots (*Q. alba*) or faring better (*P. serotina* and *Q.*

velutina) compared to managed subplots. Invaded subplots were about 1.18–1.30 °C cooler with 583–709 lumens m⁻² less light exposure compared to control or managed subplots. Additionally, managed and invaded subplots had increased moisture levels (12.0–14.9%) compared to control subplots. Seedling compromise was due to a legacy effect from *Berberis* disruption via soil sample extraction and/or management. Our findings contrast with other studies that show dense, invasive species outcompeting native tree seedlings and unsuccessful native restoration in *Berberis* stands.

Keywords Japanese barberry · Direct planting · Disruption legacy

Introduction

Invasive, non-native plant species spread aggressively (Grotkopp and Rejmánek 2007; Whitney and Gabler 2008; van Kleunen et al. 2010), grow in very dense populations (Ehrenfeld 1997; Silander and Klepeis 1999), and influence environmental conditions by inducing environmental stressors (Gordon 1998; Ehrenfeld 2010; Vilà et al. 2011) that dramatically alter native plant communities and associated ecosystem function (McDowell 2002; Daehler 2003; Graebner et al. 2012). Therefore, multiple mechanisms may

Communicated by Lori Biederman.

A. F. Link III (✉) · L. M. K. Johnson · R. M. Utz
Falk School of Sustainability, Chatham University, 6035
Ridge Road, Gibsonia, PA 15044, USA
e-mail: arthur.link6@gmail.com

separately or interactively lead to the loss of native floral biodiversity following infestation. But, identifying which mechanisms are most important to consider when managing an invasive can be exceedingly difficult due to potential mechanisms interacting concurrently (Vilà and Weiner 2004). Furthermore, management creates novel environmental conditions (Hobbs et al. 2009). Disturbances created through invasive removal can drastically revert some environmental conditions back to pre-infestation, whereas some aspects of infestation's influence linger and as a result may further alter ecosystem functions and inhibit native plant species through a legacy effect (Davis et al. 2000; Gurevitch and Padilla 2004; Kueffer et al. 2007).

One invasive, non-native species with particularly severe ecological consequences in eastern North American deciduous forests is *Berberis thunbergii* (Japanese barberry, hereafter referred to as *Berberis*; Ward et al. 2009, 2018). Drastic ecological changes occur in forests where *Berberis* invades, including altered soil characteristics, development of a recalcitrant understory, and microclimatic changes that may be unsuitable for native seedlings (Ehrenfeld 1997; Silander and Klepeis 1999; Kourtev et al. 2003; DeGasparis and Motzkin 2007). Reductions of native tree seedling densities (> 80%) were observed in invaded understories along varying density gradients of *Berberis* invasion (Link et al. 2018); however, the most important mechanisms leading to such effects have not been identified. Primary attributes that convey *Berberis*' competitive advantages over native understory species include increased soil pH and moisture, along with light limitation, and cooler understory conditions (Boyd et al. 2009; Williams and Ward 2010). *Berberis*-infested understories may further inhibit native tree densities and promote reinvasion, despite executing best practice management guidelines, due to lingering invasive-influenced environmental effects (Ehrenfeld et al. 2001; Kourtev et al. 2003; Coats et al. 2014; Sherry et al. 2016).

Common, best practice for managing *Berberis* has been population-based removal of its aboveground vegetation followed by flame treatment of the root stump (Ward et al. 2009, 2010), and not broader goals such as rejuvenation of natives and ecosystem processes (Reid and Ogden 2009; Prior et al. 2018). Even when using best practices to reduce infestations, outcomes are often unpredictable (D'Antonio and

Meyerson 2002; Reid and Ogden 2009; Bullock et al. 2011; Cordell et al. 2016) and dependent on land use (Foley et al. 2005; Mosher et al. 2009), historic disturbances (Daehler 2003), and invasion densities (D'Antonio and Meyerson 2002). When severe invasion negatively impacts native flora and critical ecosystem functions (Zavaleta et al. 2001), management actions require active post-management restoration efforts to promote native recovery (Gordon 1998). However, successful restoration efforts must still account for myriad factors (Didham et al. 2007; Chazdon 2008), such as land-use legacies that decrease overall native propagule densities (Clark et al. 2007), follow-up management required due to reinvasion (Cordell et al. 2009; Ward et al. 2009; Gabler and Siemann 2012), and unexpected effects post-management (Zarnetske et al. 2010).

Successful *Berberis* management is possible and post-management environmental conditions are desirable when compared to surrounding uninvaded sites, including warmer and less humid microclimatic conditions (Williams and Ward 2010) and removal of invasive competitive interference (Ward et al. 2018). However, even when following best management practices, environmental conditions rapidly and drastically change since areas were heavily conditioned by infestation (Aronson and Galatowitsch 2008). Post-management conditions may experience lingering invasive conditions and/or worsened conditions because of disturbances induced by invasive management (e.g. *Alliaria petiolata*, garlic mustard; Barto and Cipollini 2009; Lankau et al. 2014; *Solidago gigantea*, giant goldenrod; König et al. 2016). Native restoration is significantly more difficult if there are such unexpected outcomes as a legacy effect post-management (Corbin and D'Antonio 2012). Furthermore, novel environmental conditions created by management disturbances can be a determinant for unforeseen outcomes post-management (Hobbs et al. 2009; James et al. 2010) which may further hinder reestablishment of native plants and associated ecosystem functions (Renteria et al. 2012; Zeidler et al. 2018).

We explored possible seedling density impacts caused by *Berberis* using two experimental approaches. First, we planted native tree seeds in soils samples extracted from *Berberis*-invaded plots and uninvaded plots in a greenhouse study. Next, we introduced surviving seedlings into three classes of

in situ field subplots: control (outside *Berberis* invasion), invaded (*Berberis* present), and managed (*Berberis* removed/treated). Our goal was to explain the possible mechanistic advantages that may have caused > 80% reductions of native tree seedling densities observed in the same *Berberis*-infested forest stands by Link et al. (2018). Our objectives were to (1) identify potential mechanisms that link *Berberis* invasion with severely depressed native tree seedling densities and (2) assess how common, non-chemical control practices affect native tree seedlings success in post-management conditions. To our knowledge, no studies to date have experimentally assessed post-management survival of introduced native tree seedlings following the management of *Berberis* stands (Ehrenfeld 1997; Cassidy et al. 2004; Ward et al. 2013), and few studies have addressed the possibility of legacy effects post-management (Kourtev et al. 2002). We hypothesized that native seedlings reared in both *Berberis*-invaded soil samples and introduced into invaded in situ field subplots would experience decreased survivorship and growth. We also investigated the soil physiochemistry changes between subplots to determine how conditions changed post-management. Our aim was to provide information to land managers interested in restoration efforts through direct planting of native tree seedlings in forests where dense *Berberis* invasion presents a challenge.

Methods

Site selection

We conducted our study in two temperate deciduous forest stands in southwestern Pennsylvania, USA: Eden Hall Campus (40°39'49.68"N, 79°57'21.23"W; 157 ha) and Irwin Run Conservation Area (40°37'27.12"N, 80°0'19.08"W; 30 ha). These stands were located within 6 km of one another. Agricultural land use legacies and forest fragmentation due to urban expansion influenced both sites. Environmental stressors in both forests' stands included herbivore over-abundance due to a lack of apex predators, multiple exotic plant invasions (sensu Royo and Carson 2006; Royo et al. 2010; Ward et al. 2018), and low native tree seed availability (sensu Labatore et al. 2017), all of which likely led both sites to be dominated by tolerant species of *Acer* (particularly *A.*

rubrum; red maple). Such conditions are typical for forested areas within proximity to urban areas in the region. Other dominant tree species included *Prunus serotina* (black cherry) and *Quercus* spp. (oak) with the most mature individuals between 50 and 100 years old. Canopy cover was consistently thick between sites ($\bar{x} = 84.9 \pm 1.5\%$; ± 1 standard error; Cierra Snyder, Chatham University, unpublished data). Other invasive plant species found in the sites included *Microstegium vimineum* (Japanese stiltgrass), *Rosa multiflora* (multiflora rose), *Celastrus orbiculatus* (oriental bittersweet), and *Elaeagnus umbellata* (autumn olive), though populations of these species were not nearly as dense as those of *Berberis*. Soil compositions were similar between sites and included Hazelton (Typic Dystrudepts), Clymer (Typic Hapludults), and Wharton (Aquic Hapludults) silt loam soil series (Andrasko 2011). Such soil series drain well, have moderately slow to rapid permeability, and moderate to high water capacity (National Cooperative Soil Survey 1981). Additionally, soil slopes were 3–15% with strong acidity ranging 4–5 pH (Andrasko 2011; Soil Survey Staff 2017).

Greenhouse study

We conducted greenhouse experiments to test if native seedlings exhibited reduced survivorship and growth in *Berberis*-invaded soil samples. Between July and August 2016, invaded *Berberis* plots and uninvaded (control) plots were randomly selected from Eden Hall Campus and Irwin Run Conservation Area. All major understory patches of *Berberis* that exceeded 90% aerial coverage were mapped prior to soil collection by walking the perimeter of invasion patches with a GPS unit (Link et al. 2018; Utz et al. 2018). We used GIS to overlay two grids of 400, 1 × 1 m plots throughout the forested land at Eden Hall and Irwin Run. Fourteen sites were randomly selected within (“invaded”) and outside (“control”) of the *Berberis* patches to serve as locations for soil collection. Control sites were within 60 m of the invaded plots to ensure similar environmental conditions (Cordell et al. 2009). Within each of these sites we randomly selected three mature *A. rubrum* or *Quercus* spp. with a diameter at breast height (DBH) between 5 and 15 cm as a center point of the soil collection sites. Six soil cores to a depth of 30 cm and diameter of 10 cm were retrieved in July 2016 from the critical root zone of each tree (Oliveira

et al. 2000; Georgia Forestry Commission 2005). We combined the six core samples collected per tree. Plots and soil core samples were also used in additional *Berberis*-related projects investigating how native tree seedling densities and mycorrhizal fungi abundance varies between invaded and uninvaded forest plots (Link et al. 2018).

From the 84 possible combined soil core samples, we randomly selected 46 cores to provide substrate for experimental growth of native trees. Cores were sifted with a 2.5 mm sieve to remove clumps of roots and rocks. Soil samples were refrigerated at 1.6 °C for approximately 5 months until greenhouse trials were ready. In February 2017, we planted seeds of three common, abundant, and shade-intolerant forest tree species common to the region, *P. serotina*, *Q. alba* (white oak), and *Q. velutina* (black oak), in control and invaded soil samples (Tirmenstein 1991; Uchytel 1991). We retrieved the seed stock for each species from the same surrounding deciduous forests as the soil cores in the autumn of 2016 and cold-stratified at 1.6 °C for four months in plastic Ziploc® bags containing moistened commercial peat moss until initial seedling germination occurred.

We initiated greenhouse trials once seeds showed initial signs of taproot formation in February 2017. Each seed free of mold and/or noticeable defects was transferred into a randomly selected pot/cell that contained either control or invaded soil samples (Dreesen 2013). *Q. alba* ($n = 251$) and *Q. velutina* seeds ($n = 202$) were introduced to pots that were 10 cm wide \times 10 cm long \times 8 cm deep. *P. serotina* seeds ($n = 605$) were introduced into six-celled seedling starter trays with each cell being 4 \times 4 \times 6 cm. Pots were filled approximately 2 cm from the top, while cells were filled only 1 cm from the top. After planting, locally collected rainwater was applied until soil reached saturation. Oven-dried *Q. alba* leaf litter was applied to the top of the soil to assist in retaining moisture. Rainwater was provided as necessary and equally among replicates throughout the trial period (Silander and Klepeis 1999; Kourtev et al. 2003; Dreesen 2013). We rotated seedling trays every other week to evenly distribute solar exposure.

After the first month, once seedlings were established and before introduction to the field, plant survivorship was assessed, and plant growth was measured. Plant growth metrics included leaf count, total height, height to first petiole, and largest leaf

length (Royo and Carson 2006; Waller and Mass 2013). We collected temperature ($\bar{x} = 13.0$ °C), humidity ($\bar{x} = 70.3\%$), and light ($\bar{x} = 321$ lumens m^{-2}) data throughout the greenhouse process with an ONSET, HOBO solar intensity/temperature pendant and a HOBO U23 Pro v.2 temperature/relative humidity data logger.

Field study

Following the greenhouse studies, we conducted field experiments that tested native tree seedling survivorship and growth in different *Berberis* environments at the Eden Hall site. We used the same GIS overlay for soil sampling to randomly select three field trial sites that were at least 75 m from one another. The field trial sites consisted of three random, replicate 2.5 \times 2.5 subplots: control (outside *Berberis* invasion), invaded (*Berberis* present), and managed (*Berberis* removed and heat-treated) (Fig. 1a). Control subplots for each site were located ≤ 50 m from the invaded and managed subplots to maximize environmental homogeneity (Cordell et al. 2009). Invaded subplots were located 2.5 m away from managed subplots. Managed subplots were subjected to mechanical cutting of aboveground stems and subsequent burning with a propane-fueled weed torch (Ward and Williams 2011).

We chose mechanical removal and direct burning due to local herbicide restrictions, to limit damage to non-target plants, and since it is a common management method among land managers (Flory and Clay 2009; Ward et al. 2009). Management occurred before leaf-out and *Berberis* seedling production as outlined by best practices (Ward and Williams 2011). A buffer zone of 2.5 m was created around all subplots treated by mechanical removal and direct burning of present *Berberis* (Cordell et al. 2009). We applied heat treatment by a propane weed torch (500,000 BTU) to remaining crowns until blackened, a process that required more than 90 s for some clump treatments due to invasion density. Ward and Williams (2011) suggest that bigger clumps require 40 s per treatment and a second application later in the summer, but since juvenile plants were present in subplots, a two-tiered burn would have been impractical. We removed the aboveground biomass from the subplot vicinity to prevent cut stems from rooting.

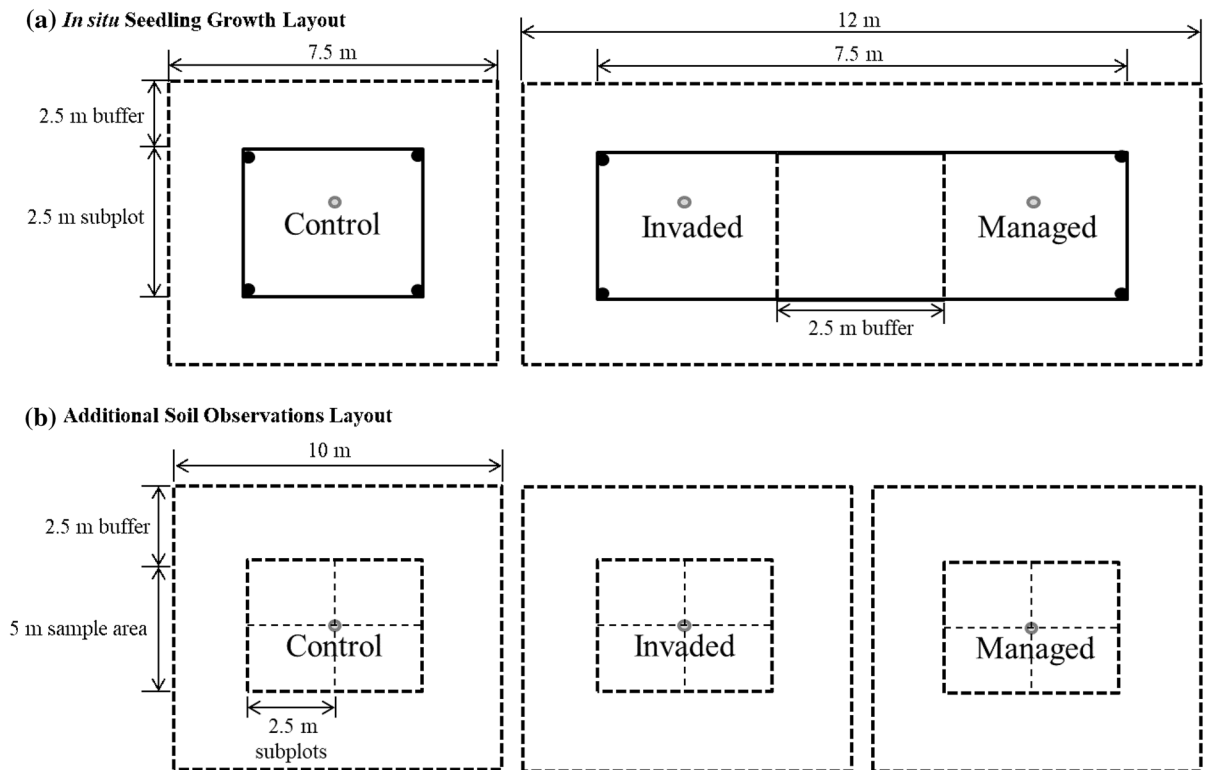


Fig. 1 **a** Layout for in situ seedling growth trials. Seedlings were introduced to the 2.5×2.5 m subplots. Soil tests were taken within and outside the perimeters of the subplots. **b** Layout for additional soil observations. Soil tests were conducted in the

sampling area that consisted of four 2.5×2.5 m subplots. Solid-black lines represent fencing, dashed lines are perimeters, black dots are fence posts, and the gray dot inside the subplot(s) is an ONSET, HOBO solar intensity/temperature pendant

In mid-April 2017, a total of 293 *P. serotina*, 52 *Q. alba*, and 186 *Q. velutina* seedlings that survived from the greenhouse experiments were removed from the pot/cell medias and randomly planted among subplots to assess native plant survivorship and growth between the three subplot treatments. To exclude *Odocoileus virginianus* (white-tailed deer) and thereby prevent browsing of seedlings, a 1.5 m high polypropylene fence was constructed around the subplots and anchored by ground stakes. The fence mesh was 0.8 mm thick with 2.54×2.54 cm openings. Seedlings were provided a 25 cm buffer zone from the fence to limit growth interference and herbivory (Waller and Maas 2013). The 2×2 m planting area within each subplot was divided into a grid layout and species were randomly planted at 25 cm spacing to limit competition. We measured seedling survivorship and growth metrics three times in the field setting: during planting (May), mid-summer (July), and early autumn (September).

To identify any potential invasive legacy *Berberis* effects in soils, we managed six additional replicate sites for *Berberis* at Eden Hall Campus ($n = 4$) and Irwin Run Conservation Area ($n = 2$). These sites were monitored for physiochemistry properties over the same growing season as the in situ seedling growth trials (e.g. Silander and Klepeis 1999). We selected additional sites using the same criteria as the other field sites, but we heat-treated twice over the growing season as suggested by Ward and Williams (2011). Each subplot type was 10×10 m (e.g. Cordell et al. 2009), and less than 25 m away from each other (Fig. 1b). We monitored soil conditions within all nine sites to determine the degree to which management changed soil physiochemistry. Parameters included soil electroconductivity (EC), temperature, pH, volumetric water content, and water saturation. For the in situ seedling growth plot layout, soil measurements were taken in the center of the subplots and outside the surrounding fence. In the additional soil observations

layout, we took measurements in the center of each of the four subplots. EC and temperature were collected at soil depths of 8–15 cm, 20–30 cm, and 35–45 cm with the Field Scout Direct Soil EC Meter, by Spectrum Technologies, Inc. Saturation and pH were measured by a Kelway soil pH and moisture meter. Volumetric water content was taken by a METER/Decagon GS1 soil moisture sensor. Soil tests were conducted from late May until early July, every other week, and only on days with clement weather.

Berberis stem counts and diameters were measured 5 cm aboveground in each of the subplots for the field trials (area: 2.5 × 2.5 m) and in the *Berberis* soil legacy trials (area: 5 × 5 m). Differences in plot sizes were accounted for by dividing by the respective areas to provide a relative subplot size of 1 × 1 m. Diameters were then used to predict whole plant dry mass (see Link et al. 2018 for the allometric equation). These measurements were recorded to evaluate *Berberis* invasion density. Controls subplots had a mean of 4.8 *Berberis* stems/m² and dry mass of 4.2 g/m², whereas invaded and managed subplots (prior to treatment) had 66.8 stems/m² and predicted dry mass of 172.2 g/m². Additionally, an ONSET HOBO solar intensity/temperature pendant was placed in the center of all the subplots 10 cm from the ground that recorded temperature and light every 30 min over the field season. We deployed a total of 18 sensors.

Statistical analyses

We determined if the three individual native seedlings' survivorship varied between the soil and subplot types in both the greenhouse and field experiments using a χ^2 test for independence. Pearson's χ^2 post hoc comparisons were conducted on tests that were statistically significant at $\alpha = 0.05$. Native seedling growth was analyzed using factorial one-way analysis of variance (ANOVA) models with dependent variables of either leaf count, total plant height, height of first petiole, or largest leaf. For all models we included an interaction term between the independent variables of treatment types (soil or subplots) and plant species. Tukey's post hoc mean comparisons were executed on models where the interaction terms were statistically significant.

To identify light and microclimatic changes associated with *Berberis* invasion, which could possibly explain differing native seedling success or growth,

we conducted a comparison of sensor-recorded data between subplots. Daily mean light intensities and temperatures of control and managed subplots were compared to invaded subplots by calculating the difference between sensors from either control or managed subplots to those from invaded subplots and calculated the mean pairwise difference for each parameter for all possible subplot × subplot comparison. We used the mean difference among each subplot comparison rather than comparing temperature or light directly so that the 24-h variability of each parameter did not distort differences between subplots, since the differences were the variable of interest. Each parameter consisted of 36 comparisons due to the six-by-six subplot design: six control and/or managed sensors compared to six invaded sensors. Differences in light were only assessed during daylight hours; readings recorded after dusk and pre-dawn were omitted from pairwise comparisons. We conducted a single one-sample t test on each subplots' mean temperature and light comparison differences and we tested against the null assumption that the mean difference between subplot categories was zero. We did a Bonferroni correction ($\alpha = 0.001$) to account for experiment-wise error.

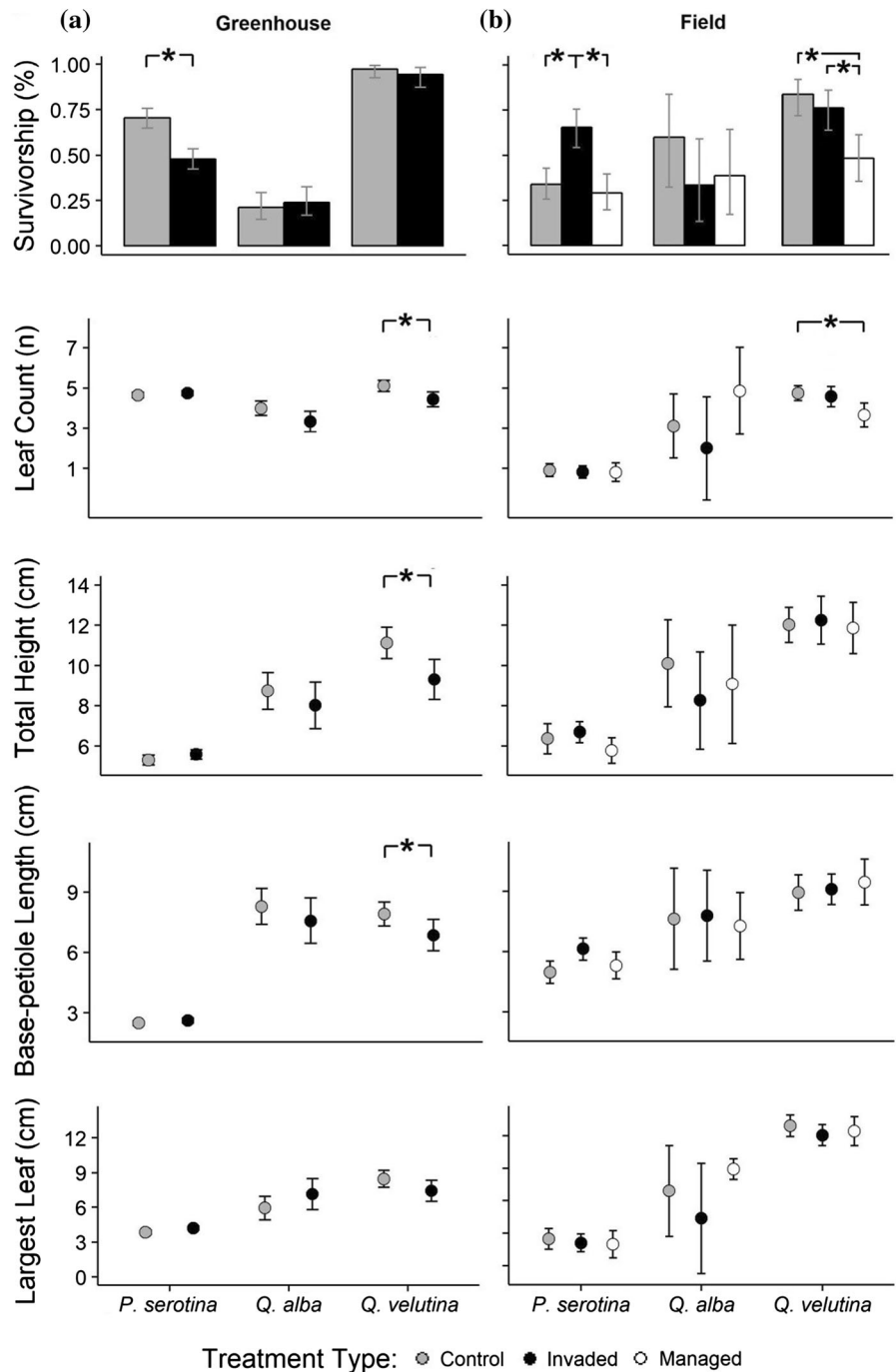
One-way ANOVAs were conducted to detect differences in soil parameters between subplots. Dependent variables included all soil parameters with subplot type as the independent variable and a random block factor of site location. Tukey's post hoc comparisons were performed on models found to be statistically significant. All models were tested for statistical assumptions through graphical means by plotting the residuals.

All statistical analyses were conducted in R v.1.0.136. χ^2 post hoc analyses were executed through 'fifer' (Fife 2017). All figure artwork was created through 'ggplot2' (Wickham 2016).

Results

In the greenhouse trials, we detected mixed results between tested species in survivorship and growth between soil types. Plant survivorship for *P. serotina* was significantly different between soil sample types when grown in a greenhouse setting ($\chi^2 = 30.72$, $df = 1$, $p < 0.05$), with individuals 23% less likely to survive in invaded soils (Fig. 2a). However, the two

Fig. 2 Survivorship and growth measurements of seedlings in the **a** greenhouse setting and in the **b** field setting. χ^2 and Tukey's HSD post hoc of significance at p values < 0.05 are indicated by '*'. Error bars identify $\pm 95\%$ confidence intervals (CI)



Quercus spp. did not differ in survivorship between soil types ($p > 0.05$). Growth metrics for each model were different for at least one factor (Table 1). Measurements of leaf count, total height, and base-petiole length (3:4 metrics) for *Q. velutina* were different between soil types ($p < 0.05$; Fig. 2a), with

all growth metrics lower in *Berberis*-invaded soils in the greenhouse setting. No differences in growth (0:4 metrics) were detected between soil types in the other two tree species (Fig. 2a).

In the in situ field trials, plant survivorship for *P. serotina* ($\chi^2 = 28.3$, $df = 2$, $p < 0.05$) and *Q. velutina*

Table 1 Results of factorial ANOVAs on metrics relating to model terms of treatments, tree seedling species, and the interaction between them in the greenhouse and field setting

Setting	Metric	Model terms	Statistical parameter	
			<i>F</i>	<i>p</i>
Greenhouse	Leaf count (<i>n</i>)	Soil	$F_{1,2,2,601} = 7.25$	< 0.05*
		Species	= 21.64	< 0.05*
		Soil × species	= 7.37	< 0.05*
	Total height (cm)	Soil	= 3.51	= 0.06
		Species	= 185.78	< 0.05*
		Soil × species	= 8.25	< 0.05*
	Base-petiole length (cm)	Soil	= 1.41	= 0.24
		Species	= 399.60	< 0.05*
		Soil × species	= 4.90	< 0.05*
	Largest leaf (cm)	Soil	= 0.05	= 0.83
		Species	= 151.22	< 0.05*
		Soil × species	= 6.01	< 0.05*
In situ field	Leaf count (<i>n</i>)	Subplot	$F_{2,2,4,264} = 3.43$	< 0.05*
		Species	= 199.78	< 0.05*
		Subplot × species	= 5.65	< 0.05*
	Total height (cm)	Subplot	= 0.48	= 0.62
		Species	= 119.28	< 0.05*
		Subplot × species	= 0.53	= 0.72
	Base-petiole length (cm)	Subplot	= 0.59	= 0.55
		Species	= 65.21	< 0.05*
		Subplot × species	= 0.80	= 0.53
	Largest leaf (cm)	Subplot	= 5.60	< 0.05*
		Species	= 288.92	< 0.05*
		Subplot × species	= 1.39	= 0.24

Significant model terms at *p* values < 0.05 are indicated by ‘*’

($\chi^2 = 20.04$, $df = 2$, $p < 0.05$) was found to differ between subplot treatments, with the greatest survivorship observed in invaded subplots (Fig. 2b). *P. serotina* had higher survival in invaded subplots (65%) compared to control (34%) or managed (29%) subplots. Additionally, *Q. velutina* was less likely to survive in managed subplots (48%) compared to invaded (76%) or control (83%) subplot treatments. *Q. velutina*'s leaf count (1:4 metrics) was the only different growth metric in the field setting (Table 1; Fig. 2b), where fewer leaves were observed on managed subplots. Growth metrics of *Q. alba* and *P. serotina* showed no differences between subplots.

Control and managed subplots experienced significantly more light exposure ($\bar{x} = 583.06$, $t_{35} = 7.91$, $p < 0.05$; Fig. 3a, $\bar{x} = 708.69$, $t_{35} = 16.36$, $p < 0.05$; Fig. 3c) and exhibited warmer temperatures ($\bar{x} = 1.30$,

$t_{35} = 11.92$, $p < 0.05$; Fig. 3b, $\bar{x} = 1.18$, $t_{35} = 14.13$, $p < 0.05$; Fig. 3d) compared to invaded subplots. In contrast, EC and temperature at soil depths of 8–15 cm, 20–30 cm, and 35–45 cm did not differ between subplots (Table 2; Fig. 4). Furthermore, soil pH and volumetric water content did not differ between subplots (Table 2; Fig. 5). But soil moisture differed between subplots, with higher water percentages observed in managed and invaded subplots (12.0–14.9%; Table 2; Fig. 5).

Discussion

Contrary to our expectations, we detected limited evidence for reduced native tree seedling survivorship or growth in understories heavily invaded by *Berberis*.

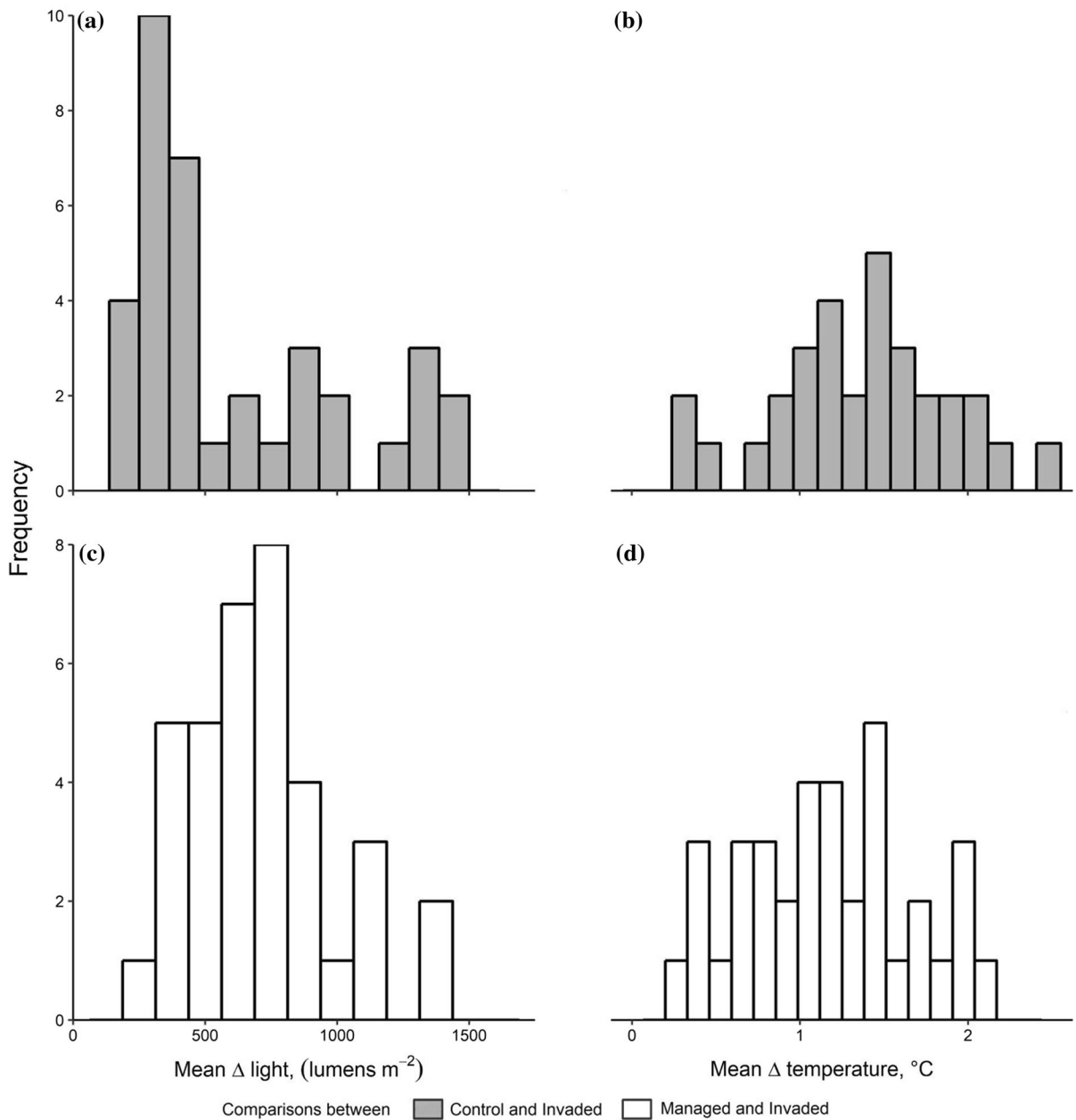


Fig. 3 Mean difference comparisons between control (a, b) and managed (c, d) subplots' daily light (lumens m⁻²) and temperature (°C) compared to invaded subplots

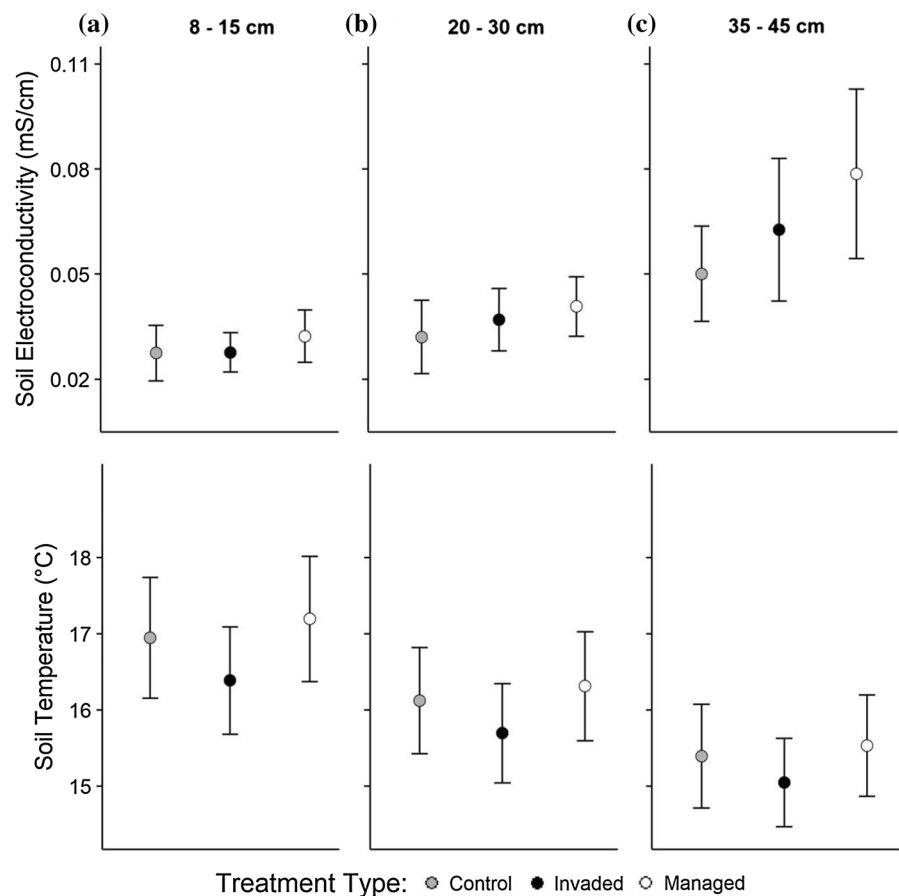
In the greenhouse setting, *P. serotina* was less likely to survive and *Q. velutina* grew less on *Berberis*-invaded soils, yet, when introduced to invaded in situ subplots, seedlings performed just as well (*Q. alba*) or better (*P. serotina* and *Q. velutina*) compared to managed subplots. Negative effects observed in the greenhouse setting could be due to disturbances caused by soil

core extraction. Furthermore, when significant disturbances occurred via mechanical removal/heat treatment of *Berberis*, in in situ managed subplots, native seedlings also experienced compromises. Thus, dense *Berberis* presence may be modifying environmental conditions, such as light exposure, microclimatic understory temperature, and soil moisture, in

Table 2 Results of ANOVAs of soil measurements of in situ field subplots

Metric	Depths	Statistical parameter	
		<i>F</i>	<i>p</i>
Electroconductivity (mS/cm)	8–15 cm	$F_{2,85} = 0.63$	= 0.54
	20–30 cm	$F_{2,85} = 0.91$	= 0.41
	35–45 cm	$F_{2,81} = 2.12$	= 0.13
Temperature (°C)	8–15 cm	$F_{2,85} = 1.19$	= 0.31
	20–30 cm	$F_{2,85} = 0.88$	= 0.42
	35–45 cm	$F_{2,81} = 0.64$	= 0.53
pH	Surface	$F_{2,37} = 1.00$	= 0.38
Volumetric water content (m ³ m ⁻³)	Surface	$F_{2,42} = 0.76$	= 0.48
Moisture (%)	Surface	$F_{2,85} = 15.5$	< 0.05*

Significant models at *p* values < 0.05 are indicated by ‘*’

Fig. 4 Electroconductivity (mS/cm) and temperature (°C) of subplot soil depths: **a** 8–15 cm, **b** 20–30 cm, and **c** 35–45 cm. Error bars identify ± 95% CI

favorable ways for some native seedlings whereas disturbing this invasive through management may not be. The original intention of this study was to explain the association of decreased native tree seedling densities observed by Link et al. (2018); however,

the causal agent continues to remain unclear. Even with observed *Berberis*-induced mechanistic changes, our results offered very limited support to the assertion that such environmental conditions suppress native seedling survivorship or growth, at least for the three-

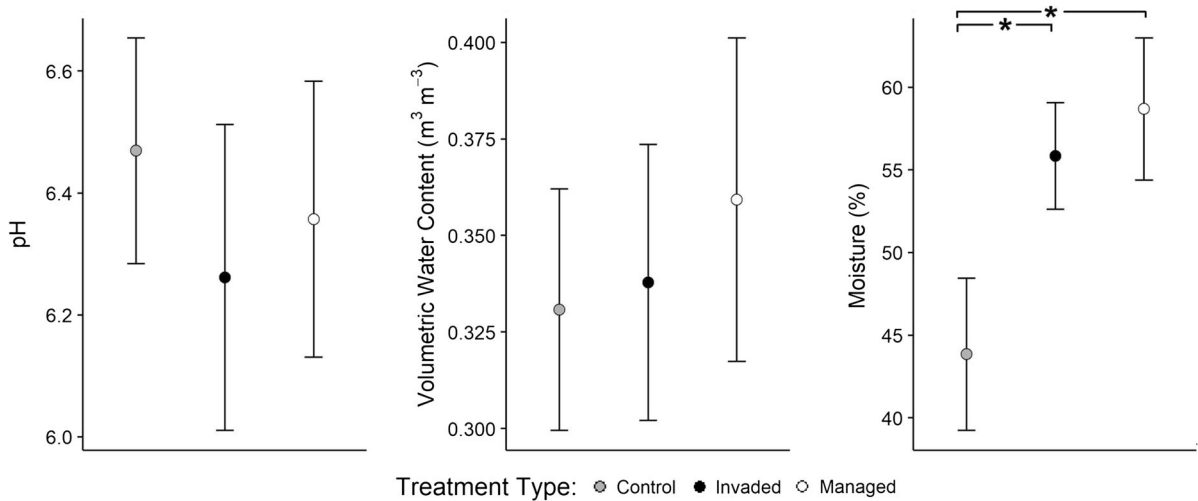


Fig. 5 Soil pH, volumetric water content ($\text{m}^3 \text{m}^{-3}$), and moisture/saturation percent of subplots. Tukey's HSD post hoc of significance at p values < 0.05 are indicated by '*'. Error bars identify $\pm 95\%$ CI

focal species during their first year of growth. Our findings represent the importance of testing assumptions associated with an invasive plant species, specifically those connected with outcompeting native tree species.

In both study settings, a disturbance legacy effect explained native tree seedling compromise (Corbin and D'Antonio 2012). When disturbing *Berberis* through soil sample extraction for the greenhouse study, *P. serotina*'s survivorship and *Q. velutina*'s growth (3:4 metrics) was slightly compromised compared to control soils. Slightly more compromises occurred through *Berberis* management. Both *P. serotina*'s and *Q. velutina*'s survivorship was less likely when compared to invaded subplots. Anecdotally, throughout monitoring in both settings, seedlings exhibited signs of elevated stress such as leaf browning or loss. We believe soil moisture and ambient temperature were significant factors that ultimately led to compromised seedlings, especially in environmental conditions heavily influenced by infestation. Managed and invaded subplots shared soil physicochemistry: greater soil moisture levels (12.0–14.9%) than control subplots, potentially due to a shading effect that kept soils cooler and less prone to evaporation. In the greenhouse setting, invaded soil samples dried out quickly since the composition was no longer reliant on *Berberis*' recalcitrant understory, cooler microclimate, and root mass to retain water moisture, and in the field setting managed subplot

soils—already high in moisture—were splashed up under seedling leaves by rainfall. Such conditions accompanied by higher temperature/light exposure in both settings surely enhanced stressors, along with additional seedling decapitation by small rodents/birds in the field setting.

Positive facilitative interactions between non-native and native plant species, although commonly overlooked in most studies, are most frequently shown by mechanistic changes through habitat modification and belowground soil processes (Rodriguez 2006; Molina-Montenegro et al. 2015; French et al. 2017). Dense *Berberis* facilitated native seedling success by alleviating stressful abiotic factors, specifically by providing coverage from solar exposure, temperature, moisture, and rain-fall soil splash (Gómez-Aparicio et al. 2008; Zarnetske et al. 2013). Additionally, belowground soil processes such as elevated arbuscular mycorrhizal fungi levels could be assisting introduced seedling success (Sarah Daugherty, Chatham University, unpublished data). We believe our results represent the value of directly planting natives in intact, dense *Berberis* stands that perform as a shrub “nurse” plant (although typically identified in literature as a native in Mediterranean habitats) which can greatly benefit restorative efforts, specifically for woody seedling success (Gómez-Aparicio et al. 2004; Castro et al. 2004; Padilla and Pugnaire 2006; Jordan et al. 2011). Lastly, *Berberis* management facilitates further invasion of other plant species (C.

orbiculatus and *R. multiflora*) that might not have been an issue otherwise and would still require additional revegetation techniques, such as native seedling introduction (Kettenring and Adams 2011; Ward et al. 2013; Flory and Bauer 2014; REDW-SAMO 2017). Before *Berberis* management initiates and when pursuing restorative efforts, we suggest that land managers consider possible consequences from disturbing dense *Berberis* infestation which has been shown by our study to cause drastic and stressful environmental conditions that negatively influence native plant and ecosystem restoration. If management of *Berberis* occurs after tree seedlings establish, those trees can in turn become nurse plants which shape canopy composition, provide a local source of seeds and limit environmental over-exposure to future native seedlings, but additional observations would

be needed to assess the long-term success of these seedlings in the canopy class.

Although our study has not identified a significant compromise to native tree seedling growth or survivorship associated with *Berberis* invasion, consideration should be given to the study limitations. Since our study was temporally limited to a single-field season, not all life history stages were included in these experiments: the initial germination of native seedlings was performed in store-bought media to make sure root formation occurred. However, despite such a limitation, significant seedling inhibition would have occurred given that the seedling stage is most vulnerable to environmental stressors and herbivory (Boege and Marquis 2005). In addition, severe *Berberis* density observed in our study site, limited cohabitating invasive species such as *M. vimineum*



Fig. 6 Visual illustrations at Eden Hall Campus (top) and Irwin Run (bottom) before (left panels) and after (right panels) removal of *Berberis*

and *R. multiflora*, and recorded subplot measurements, i.e. soil moisture, microclimatic temperature, and light exposure, corresponded with other notable studies (Silander and Klepeis 1999; D'Appollonio 2006). Other recognizable studies on *Berberis* and studies that shared the same forest stand observed altered pH levels (Kourtev et al. 2003; Utz et al. 2018), whereas, in this study, soil pH, electroconductivity, temperature, and volumetric water content were similar between subplots. Such measurements, although associated with *Berberis*, may not be indicative to all *Berberis* infestation. Other limitations to our findings could be that introduced seedling species were not representative of the full diversity of the woodland. However, the three-focal species represented common, desirable species for timbering and ecosystem services in eastern temperate deciduous forests (Axelrod 1966). Furthermore, despite such limited representation, our results compliment another account which has reported little to no impact on understory plant communities (Flinn et al. 2014).

Additional methodological caveats may be that in the greenhouse experiments, the soil microbial composition almost certainly changed once soils were extracted from the field (Waldrop and Firestone 2006). Other studies have executed similar tests of native plant performance in extracted invaded soils (Zubek et al. 2016) and the in situ stages of our experiment likely did maintain the microbial differences (Batten et al. 2006). Lastly, seedlings experienced no herbivory in the controlled greenhouse setting and the presence of field personnel, fencing, and buffer zones free of *Berberis* surely influenced herbivore behavior in the field which constrained or deterred seedling predators' interaction with introduced seedlings. Yet, woodland rodents (i.e. chipmunks and mice) could access subplots despite fencing which could explain decreased *P. serotina* survival in control subplots that anecdotally contained dense fern populations which may have provided a groundcover habitat for rodents (Royo and Carson 2006; Labatore et al. 2017). In addition, other studies have shown that introduced seedlings within invaded areas experience less herbivory (e.g. Bauer and Reynolds 2016; Shen et al. 2016) and open-area sites free from shrub coverage have less seedling regeneration/success (e.g. Gómez-Aparicio et al. 2004, 2008; Elgar et al. 2014).

As *Berberis* invasion continues, its density in both our forests' understories (Fig. 6) is likely to be or

become shared by other forest stands (e.g. Vilà et al. 2011; Labatore et al. 2017). Even though *Berberis* management can be successful and most desirable at the initial stages of infestation to limit any effects on native plant communities (Link et al. 2018) and/or soil conditions (Kourtev et al. 1999), populations become dense quickly—completely covering a forest understory within as little as three years in some cases (Matson 2011). Due to *Berberis*' varying density gradients and management's disturbance legacy effect, current management practices are inadequate for reestablishing native communities and ecosystem functions (Lichstein et al. 2004; Bauer and Reynolds 2016; Schuster et al. 2018). Myriad factors influence native tree densities which include decreased overall native propagule availability, post-management legacy effects, and native performance due to environmental over-exposure (Cordell et al. 2009; Labatore et al. 2017). We accounted for these factors through active restoration management by directly planting tree seedlings to *Berberis*-invaded subplots (Beasley and McCarthy 2011) and monitoring introduced native plants and environmental conditions post-*Berberis* management (D'Antonio and Meyerson 2002; Marchante et al. 2009) which plays a crucial role when managing severe non-native, invasive plant densities, as observed by *Berberis*.

Conclusion

Many non-native, invasive plant species outcompete natives and alter ecosystem functions. In the hopes of successfully managing an invasive species, it is crucial to test such an assumption, especially when native plant restoration is the goal. Studies have shown that dense *Berberis* populations support lower densities of native tree seedlings compared to uninvaded areas, a phenomenon observed with severity in our study location. However, our results show little support for the assumption that inhibited native tree seedling densities are due to *Berberis*-induced environmental changes such as, decreased solar exposure, decreased ambient understory temperature, and increased soil moisture. Although there were mechanistic changes observed by *Berberis*, such factors benefited some native tree species. Lastly, when disturbing environments heavily influenced by *Berberis* caused via extracting soil cores and managing the species,

introduced native seedling survivorship and growth were compromised through a disturbance legacy effect. For future research, we recommend testing assumptions of additional non-native plant species associated with outcompeting natives, accounting for post-management legacy effects for native restoration efforts and conducting experiments on native seedling predation in *Berberis* which may explain the association of lower tree seedling densities observed in former studies.

Acknowledgements This research would not have been possible without the assistance, guidance, and suggestions from many individuals: V. Kefeli, K. Phillips, J. Mason, C. Snyder, A. Bennett, S. Daugherty, T. Rice, M. Fetsko, T. Turnblacer, C. Feagins, C. Hausner, J. Mannino, Students in SUS 404 – Quantitative Ecology class of spring 2017, T. Macagno, H. Jensen, R. Weitzell, T. Miga, and L. Baldarelli. Land-use was possible due to Eden Hall’s Land Use Committee and the Allegheny Land Trust. We received funding through Chatham’s Falk School Graduate Assistantship, The Falk Foundation, the Falk School of Sustainability, and the Fine Foundation. Lastly, we thank the multiple reviewers that provided ample comments and suggestions which significantly built upon this manuscript.

Compliance with ethical standards

Conflict of interest Authors declare that they have no conflicts of interest.

References

- Andrasko II RR (2011) Summary of soil and hydrogeological investigations supporting a program for soil infiltration of treated sewage effluent at Chatham University Eden Hall Campus Richland Township, Allegheny County, Pennsylvania. Civil and Environmental Consultants, Inc. Project: 092-033.0002
- Aronson MFJ, Galatowitsch S (2008) Long-term vegetation development of restored prairie pothole wetlands. *Wetlands* 28:883–895
- Axelrod DI (1966) Origin of deciduous and evergreen habits in temperate forests. *Evolution* 20(1):1–15
- Barto EK, Cipollini D (2009) Garlic mustard (*Alliaria petiolata*) removal method affects native establishment. *Invasive Plant Sci Manag* 2(03):230–236
- Batten KM, Scow KM, Davies KF, Harrison SP (2006) Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biol Invasions* 8(2):217–230
- Bauer JT, Reynolds HL (2016) Restoring native understory to a woodland invaded by *Euonymus fortunei* multiple factors affect success: setbacks to restoring an invaded understory. *Restor Ecol* 24(1):45–52
- Beasley RR, McCarthy BC (2011) Effects of *Microstegium vimineum* (Trin) A. Camus (Japanese Stiltgrass) on native hardwood survival and growth Implications for restoration. *Nat Areas J* 31(3):246–255
- Boege K, Marquis RJ (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends Ecol Evolut* 20(8):441–448
- Boyd JN, Xu C-Y, Griffin KL (2009) Cost-effectiveness of leaf energy and resource investment of invasive *Berberis thunbergii* and co-occurring native shrubs. *Can J For Res* 39(11):2109–2118
- Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM (2011) Restoration of ecosystem services and biodiversity: conflicts and opportunities. *Trends Ecol Evol* 26(10):541–549
- Cassidy TM, Fownes JH, Harrington RA (2004) Nitrogen limits an invasive perennial shrub in forest understory. *Biol Invasions* 6(1):113–121
- Castro J, Zamora R, Hódar JA, Gómez JM, Gómez-Aparicio L (2004) Benefits of using shrubs as nurse plants for reforestation in mediterranean mountains: a 4-year study. *Restor Ecol* 12(3):352–358
- Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320(5882):1458–1460
- Clark CJ, Poulsen JR, Levey DJ, Osenberg CW (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. *Am Nat* 170(1):128–142
- Coats VC, Pelletreau KN, Rumpho ME (2014) Amplicon pyrosequencing reveals the soil microbial diversity associated with invasive Japanese barberry (*Berberis thunbergii* DC.). *Mol Ecol* 23(6):1318–1332
- Corbin JD, D’Antonio CM (2012) Gone but not forgotten Invasive plants’ legacies on community and ecosystem properties. *Invasive Plant Sci Manag* 5(1):117–124
- Cordell S, Ostertag R, Rowe B, Sweinhart L, Vasquez-Radonic L, Michaud J, Colleen Cole T, Schulten JR (2009) Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. *Biol Conserv* 142(12):2997–3004
- Cordell S, Ostertag R, Michaud J, Warman L (2016) Quandaries of a decade-long restoration experiment trying to reduce invasive species: beat them, join them, give up, or start over? Quandaries of a decade-long restoration experiment. *Restor Ecol* 24(2):139–144
- D’Antonio C, Meyerson LA (2002) Exotic plant species as problems and solutions in ecological restoration: a synthesis. *Restor Ecol* 10(4):703–713
- D’Appollonio J (2006) Regeneration strategies of Japanese barberry (*Berberis thunbergii* DC.) in coastal forests of Maine. Electronic Theses and Dissertations. <https://digitalcommons.library.umaine.edu/etd/433>
- Daehler CC (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Ann Rev Ecol Evol Syst* 34(1):183–211
- Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *J Ecol* 88(3):528–534
- DeGasperis BG, Motzkin G (2007) Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. *Ecology* 88(12):3115–3125

- Didham R, Tylanakis J, Gemmell N, Rand T, Ewers R (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol Evol* 22(9):489–496
- Dreesen D (2013) Raising native plants in nurseries: basic concepts by R. Kasten Dumroese, Thomas D. Landis, Tara Luna. *Nativ Plants J* 14(1):71
- Ehrenfeld JG (1997) Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC). *J Torrey Bot Soc* 124(2):210–215
- Ehrenfeld JG (2010) Ecosystem consequences of biological invasions. *Ann Rev Ecol Evol Syst* 41(1):59–80
- Ehrenfeld JG, Kourtev P, Huang W (2001) Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol Appl* 11(5):1287–1300
- Elgar AT, Freebody K, Pohlman CL, Shoo LP, Catterall CP (2014) Overcoming barriers to seedling regeneration during forest restoration on tropical pasture land and the potential value of woody weeds. *Front Plant Sci* 5:1–10
- Fife D (2017) *fifer*: a biostatisticians toolbox for various activities, including plotting, data cleanup, and data analysis. R package version 1.1. <https://CRAN.R-project.org/package=fifer>.
- Flinn KM, Bechhofer JL, Malcolm M (2014) Little impact of the invasive shrub Japanese barberry (*Berberis thunbergii* DC) on forest understory plant communities I. *J Torrey Bot Soc* 141(3):217–224
- Flory SL, Bauer JT (2014) Experimental evidence for indirect facilitation among invasive plants. *J Ecol* 102(1):12–18
- Flory SL, Clay K (2009) Invasive plant removal method determines native plant community responses. *J Appl Ecol* 46(2):434–442
- Foley JA, DeFries R, Asner GP, Barford C, Bonan G, Carpenter SR, Chapin FS, Coe MT, Daily GC, Gibbs HK, Helkowski JK, Holloway T, Howard EA, Kucharik CJ, Monfreda C, Patz JA, Prentice IC, Ramankutty N, Snyder PK (2005) Global consequences of land use. *Science* 309:570–574
- French K, Robinson S, Smith L, Watts E (2017) Facilitation, competition and parasitic facilitation amongst invasive and native liana seedlings and a native tree seedling. *NeoBiota* 36:17–38
- Gabler CA, Siemann E (2012) Environmental variability and ontogenetic niche shifts in exotic plants may govern reinvasion pressure in restorations of invaded ecosystems: predicting variation in reinvasion pressure. *Restor Ecol* 20(5):545–550
- Georgia Forestry Commission (2005) Where are my trees' roots? <https://www.gatrees.org/community-forests/ask-the-arborist/ask-the-arborist-resources.cfm>. Accessed 09 May 2017
- Gómez-Aparicio L, Zamora R, Gómez JM, Hódar JA, Castro J, Baraza E (2004) Applying plant facilitation to forest restoration: a meta-analysis of the use of shrubs as nurse plants. *Ecol Appl* 14(4):1128–1138
- Gómez-Aparicio L, Zamora R, Castro J, Hódar JA (2008) Facilitation of tree saplings by nurse plants: Microhabitat amelioration or protection against herbivores? *J Veg Sci* 19(2):161–172
- Gordon DR (1998) Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecol Appl* 8:975–989
- Graebner RC, Callaway RM, Montesinos D (2012) Invasive species grows faster, competes better, and shows greater evolution toward increased seed size and growth than exotic non-invasive congeners. *Plant Ecol* 213(4):545–553
- Grotkopp E, Rejmánek M (2007) High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. *Am J Bot* 94(4):526–532
- Gurevitch J, Padilla D (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19(9):470–474
- Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends Ecol Evol* 24(11):599–605
- James JJ, Smith BS, Vasquez EA, Sheley RL (2010) Principles for ecologically based invasive plant management. *Invasive Plant Sci Manag* 3(3):229–239
- Jordan NR, Larson DL, Huerd SC (2011) Evidence of qualitative differences between soil-occupancy effects of invasive vs native grassland plant species. *Invasive Plant Sci Manag* 4(1):11–21
- Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis: invasive plant control experiments. *J Appl Ecol* 48(4):970–979
- König J, van Kleunen M, Dawson W (2016) No consistent legacy effects of invasion by giant goldenrod (*Solidago gigantea*) via soil biota on native plant growth. *J Plant Ecol* 9(3):320–327
- Kourtev PS, Huang WZ, Ehrenfeld JG (1999) Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. *Biol Invasions* 1:237–245
- Kourtev PS, Ehrenfeld JG, Häggblom M (2002) Exotic plant species alter the microbial community structure and function in the soil. *Ecology* 83(11):3152
- Kourtev PS, Ehrenfeld JG, Häggblom M (2003) Experimental analysis of the effect of exotic and native plant species on the structure and function of soil microbial communities. *Soil Biol Biochem* 35(7):895–905
- Kueffer C, Schumacher E, Fleischmann K, Edwards PJ, Dietz H (2007) Strong below-ground competition shapes tree regeneration in invasive *Cinnamomum verum* forests. *J Ecol* 95(2):273–282
- Labatore AC, Spiering DJ, Potts DL, Warren RJ (2017) Canopy trees in an urban landscape—viable forests or long-lived gardens? *Urban Ecosyst* 20(2):393–401
- Lankau RA, Bauer JT, Anderson MR, Anderson RC (2014) Long-term legacies and partial recovery of mycorrhizal communities after invasive plant removal. *Biol Invasions* 16(9):1979–1990
- Lichstein JJ, Grau HR, Aragón R (2004) Recruitment limitation in secondary forests dominated by an exotic tree. *J Veg Sci* 15:721–728
- Link AF, Turnblacer T, Snyder CK, Daugherty SE, Utz RM (2018) Low recruitment of native trees in a deciduous forest associated with Japanese barberry (*Berberis thunbergii* DC) invasion. *Invasive Plant Sci Manag* 11(1):20–26

- Marchante E, Kjølner A, Struwe S, Freitas H (2009) Soil recovery after removal of the N₂-fixing invasive *Acacia longifolia*: consequences for ecosystem restoration. *Biol Invasions* 11(4):813–823
- Matson E (2011) Wisconsin DNR: *Berberis thunbergii* DC. https://dnr.wi.gov/topic/Invasives/documents/classification/LR_Berberis_thunbergii.pdf Accessed 05 Sept 2017
- McDowell SC (2002) Photosynthetic characteristics of invasive and noninvasive species of *Rubus* (Rosaceae). *Am J Bot* 89(9):1431–1438
- Molina-Montenegro MA, Osés R, Torres-Díaz C, Atala C, Núñez MA, Armas C (2015) Fungal endophytes associated with roots of nurse cushion species have positive effects on native and invasive beneficiary plants in an alpine ecosystem. *Perspect Plant Ecol Evol Syst* 17(3):218–226
- 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(10):2317–2328
- Oliveira M, Noordwijk M, Gaze SR, Brouwer G, Bona S, Mosca G, Hairiah K (2000) Auger sampling, ingrowth cores and pinboard methods. In: *Root methods: a handbook*. Springer, Berlin, pp 175–210.
- Padilla FM, Pugnaire FI (2006) The role of nurse plants in the restoration of degraded environments. *Front Ecol Environ* 4(4):196–202
- Prior KM, Adams DC, Klepzig KD, Hulcr J (2018) When does invasive species removal lead to ecological recovery? Implications for management success. *Biol Invasions* 20(2):267–283
- REDW-SAMO (2017) Invasive plant management plan and environmental assessment for redwood national park and Santa Monica mountains national recreation area. <https://parkplanning.nps.gov/document.cfm?parkID=341&projectID=44351&documentID=83505>. Accessed 09 Sept 2018
- Reid MA, Ogden RW (2009) The importance of habitat, biogeography and hydrology as drivers of diatom distributions in floodplain lakes of the southeast Murray Basin (Australia) and implications for palaeolimnological studies. *J Paleolimnol* 41(3):453–470
- Renteria JL, Gardener MR, Panetta FD, Crawley MJ (2012) Management of the invasive hill raspberry (*Rubus niveus*) on Santiago Island, Galapagos: eradication or indefinite control? *Invasive Plant Sci Manag* 5(1):37–46
- Rodriguez LF (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol Invasions* 8(4):927–939
- Royo AA, Carson WP (2006) On the formation of dense understory layers in forests worldwide: consequences and implications for forest dynamics, biodiversity, and succession. *Can J For Res* 36(6):1345–1362
- Royo AA, Collins R, Adams MB, Kirschbaum C, Carson WP (2010) Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91(1):93–105
- Schuster MJ, Wragg PD, Reich PB (2018) Using revegetation to suppress invasive plants in grasslands and forests. *J Appl Ecol* 55(5):2362–2373
- Shen X, Bourg NA, McShea WJ, Turner BL (2016) Long-term effects of white-tailed deer exclusion on the invasion of exotic plants: a case study in a Mid-Atlantic temperate forest. *PLoS ONE* 11(3):e0151825
- Sherry RA, Shafroth PB, Belnap J, Ostoja S, Reed SC (2016) Germination and growth of native and invasive plants on soil associated with biological control of tamarisk (*Tamarix* spp). *Invasive Plant Sci Manag* 9(4):290–307
- Silander JA, Klepeis DM (1999) The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. *Biol Invasions* 1(2):189–201
- Soil Survey Staff (2017) Natural Resources Conservation Service, United States Department of Agriculture. Web Soil Survey. <https://websoilsurvey.sc.egov.usda.gov/>. Accessed 31 Oct 2017.
- Survey National Cooperative Soil (1981) Soil survey of Allegheny County. Pennsylvania, The Natural Resources Conservation Service
- Tirmenstein DA (1991) *Quercus alba*. In: Fire effects information system, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/>. Accessed 4 Oct 2017.
- Uchytel RJ (1991) *Prunus serotina*. In: Fire effects information system, [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). <https://www.fs.fed.us/database/feis/>. Accessed 4 Oct 2017.
- Utz RM, Pearce TA, Lewis DL, Mannino JC (2018) Elevated native terrestrial snail abundance and diversity in association with an invasive understory shrub, *Berberis thunbergii*, in a North American deciduous forest. *Acta Oecol* 86:66–71
- van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol Lett* 13(2):235–245
- Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species?—evidence from pair-wise experiments. *Oikos* 105(2):229–238
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems: ecological impacts of invasive alien plants. *Ecol Lett* 14(7):702–708
- Waldrop MP, Firestone MK (2006) Response of microbial community composition and function to soil climate change. *Microb Ecol* 52(4):716–724
- Waller DM, Maas LI (2013) Do white-tailed deer and the exotic plant garlic mustard interact to affect the growth and persistence of native forest plants? *For Ecol Manag* 304:296–302
- Ward JS, Williams SC (2011) Controlling an invasive shrub, Japanese barberry (*Berberis thunbergii* DC), using directed heating with propane torches. *Nat Areas J* 31(2):156–162
- Ward JS, Worthley TE, Williams SC (2009) Controlling Japanese barberry (*Berberis thunbergii* DC) in southern New England, USA. *For Ecol Manag* 257(2):561–566
- Ward JS, Williams SC, Worthley TE (2010) Effectiveness of two-stage control strategies for Japanese barberry

- (*Berberis thunbergii*) varies by initial clump size. *Invasive Plant Sci Manag* 3(1):60–69
- Ward JS, Williams SC, Worthley TE (2013) Comparing effectiveness and impacts of Japanese barberry (*Berberis thunbergii*) control treatments and herbivory on plant communities. *Invasive Plant Sci Manag* 6(4):459–469
- Ward JS, Williams SC, Linske MA (2018) Influence of invasive shrubs and deer browsing on regeneration in temperate deciduous forests. *Can J For Res* 48(1):58–67
- Whitney KD, Gabler CA (2008) Rapid evolution in introduced species, “invasive traits” and recipient communities: challenges for predicting invasive potential: evolution and invasion predictions. *Divers Distrib* 14(4):569–580
- Wickham H (2016) ggplot2: elegant graphics for data analysis. <https://ggplot2.org>.
- Williams SC, Ward JS (2010) Effects of Japanese barberry (Ranunculales: Berberidaceae) removal and resulting microclimatic changes on *Ixodes scapularis* (Acari: Ixodidae) abundances in Connecticut, USA. *Environ Entomol* 39(6):1911–1921
- Zarnetske PL, Seabloom EW, Hacker SD (2010) Non-target effects of invasive species management: beachgrass, birds, and bulldozers in coastal dunes. *Ecosphere* 1(5):1–20
- Zarnetske PL, Gouhier TC, Hacker SD, Seabloom EW, Bokil VA (2013) Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. *J Ecol* 101(4):905–915
- Zavaleta ES, Hobbs RJ, Mooney HA (2001) Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol Evol* 16(8):454–459
- Zeidler M, Hertlová B, Banaš M, Zahradník D (2018) Vegetation shift after a clear-cut of non-native dwarf pine (*Pinus mugo*). *Biologia* 73:113–119
- Zubek S, Majewska ML, Błaszczkowski J, Stefanowicz AM, Nobis M, Kapusta P (2016) Invasive plants affect arbuscular mycorrhizal fungi abundance and species richness as well as the performance of native plants grown in invaded soils. *Biol Fertil Soils* 52(6):879–893

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.