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# Little impact of the invasive shrub Japanese barberry (*Berberis thunbergii* DC) on forest understory plant communities[1]

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FLINN, K. M., J. L. BECHHOFER, AND M. MALCOLM (Department of Biology, Franklin & Marshall College, Lancaster, PA 17604). Little impact of the invasive shrub Japanese barberry (*Berberis thunbergii* DC) on forest understory plant communities. J. Torrey Bot. Soc. 141: 217–224. 2014.—As exotic species invasions continue to transform patterns of biological diversity, it becomes increasingly urgent to understand invasions' full consequences. Woody exotics that colonize closed-canopy forests have the potential for strong effects on plant communities. *Berberis thunbergii* DC, one such species, has invaded forests throughout eastern North America. Here we quantified the impacts of *B. thunbergii* invasions on the diversity and composition of native plant communities, both directly and through possible modifications of nutrient, moisture, and light availability. Plots with and without *B. thunbergii* had similar species richness, evenness, and diversity. Only two species were less likely to occur in plots with *B. thunbergii*. We also found no effect of *B. thunbergii* on soil moisture or other key soil properties such as pH and organic matter content. Plots with *B. thunbergii* had lower light levels at 10 cm from the ground, as under any shrub. It is possible that the invasion we observed may develop into a dense thicket with more severe impacts; however, the effects of *B. thunbergii* were modest at this time.

Key words: alien species, diversity, exotic species, invasive species, light availability, nutrient availability, organic matter, pH, soil, soil moisture, species composition, species richness.

As exotic species invasions continue to transform patterns of biological diversity, it becomes increasingly urgent to understand invasions' full consequences. Invasive plants can have strong, far-reaching and sometimes unexpected effects on community structure and ecosystem function (Vitousek and Walker 1989, D'Antonio and Vitousek 1992, Gordon 1998, Mack et al. 2000). Besides directly displacing native vegetation, invasive plants may also alter resource availability (Ehrenfeld 2003). If these changes disadvantage native species or promote other exotics, "invasional meltdown" can result (Simberloff 2006).

One set of plant invaders with a particularly great potential for strong effects is the woody exotics that colonize closed-canopy forests. Though the majority of well-studied invasive plants have been herbaceous species invading herbaceous communities (Levine et al. 2004), ecologists have more recently recognized the potential threats posed to forests by invasive trees and shrubs (Webster et al. 2006, Martin et al. 2009). For example, European buckthorn (*Rhamnus cathartica* L.) has been shown to have multiple direct and indirect impacts on native plant communities (Knight et al. 2007), including reductions in the performance of native forbs (Klionsky et al. 2011), increases in soil nitrogen, pH and moisture availability (Heneghan et al. 2006), and facilitation of exotic earthworm invasion (Heneghan et al. 2007).

Less well-studied, Japanese barberry (*Berberis thunbergii* DC) is another woody forest invader that could have similarly far-reaching effects. First introduced to North America in 1875 and widely planted as an ornamental, *B. thunbergii* became increasingly common in undisturbed forests during the late 20$^{th}$ century (Ehrenfeld 1997). By the early 2000s, this species was widely recognized as invasive throughout eastern North America (Webster et al. 2006, Martin et al. 2009). Though *B. thunbergii* can form dense thickets, with obvious, concomitant losses of native plant diversity, the majority of *B. thunbergii* invasions involve moderately-sized populations of widely scattered individuals (Ehrenfeld 1997). The consequences of these much more common, moderate invasions remain much less clear. In New Jersey forests, Kourtev et al. (1998) found that areas invaded by *B. thunbergii* had fewer individuals of several *Quercus* L. and *Vaccinium* L. species, as well as higher soil pH and a thinner litter layer and

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organic horizon. They also advanced anecdotal evidence that the density of exotic earthworms was higher in invaded areas. In this study, we sought to quantify the impacts of moderate *B. thunbergii* invasions on the diversity and composition of native plant communities, both directly and through possible modifications of nutrient, moisture, and light availability.

**Materials and Methods.** Field Methods. We conducted this study in the Theodore A. Parker III Natural Area, a 40-hectare preserve in southern Lancaster County, Pennsylvania. Apparently logged in the early 20$^{th}$ century but never cleared for agriculture (K.M. Flinn, personal observation; Marks and Gardescu 2001), this forest has a canopy dominated by *Liriodendron tulipifera* L. It is possible that the site was once grazed. The timing of the *B. thunbergii* invasion at this site is unknown. The soil is a Newark silt loam, a floodplain soil that is deep, level, and somewhat poorly drained (Custer 1985).

Along a ~1.6 km north-south transect on the east side of Stewart Run, we walked until we encountered *B. thunbergii* and established a 1 × 1 m plot with *B. thunbergii* and a 1 × 1 m plot 5 m away in an arbitrary direction without *B. thunbergii*. All established *B. thunbergii* shrubs we encountered were included, regardless of size. All plots occurred in similar topographic positions, on the nearly level land adjacent to Stewart Run. In 50 pairs of plots, we recorded the percentage cover of all vascular plant species $<$ 1 m high, using the classes 0 to $<$ 1, 1 to $<$ 5, 5 to $<$ 25, 25 to $<$ 75, and 75 to 100. Nomenclature follows the PLANTS database (USDA Natural Resources Conservation Service 2013).

From each plot, we collected a 10-cm-deep soil sample with a soil corer, and we measured the volumetric water content of the soil to 7.5 cm with a Field Scout TDR 300 soil moisture meter (Spectrum Technologies, Aurora, IL). We measured light availability at both 1 m and 10 cm from the ground with a LI-COR LI-250 light meter (LI-COR Biosciences, Lincoln, NE). Light measurements were taken on clear afternoons. All paired measurements of light and soil moisture were taken at the same time. A random subset of 20 pairs of soil samples was selected for analysis. Soils were analyzed by the Cornell Nutrient Analysis Laboratory, Ithaca, NY for pH in water, loss on ignition (LOI), total C, total N, and modified Morgan extractable Al, Ca, Cu, Fe, K, Mg, Mn, P and Zn.

Statistical Methods. We compared plots with and without *B. thunbergii* in species richness, evenness and Shannon and Simpson diversity indices using paired t-tests. We used G-tests to ask whether individual species were more or less likely to occur in plots with *B. thunbergii*, considering only species with at least ten occurrences. For species with at least ten occurrences in plots with *B. thunbergii*, we assessed correlations between the species' cover and the cover of *B. thunbergii*.

We also used G-tests to ask whether plots with *B. thunbergii* were more or less likely to contain other exotic plants. Among plots with other exotics, we asked whether the proportion of non-*B. thunbergii* cover comprised of exotics differed between plots with and without *B. thunbergii* using a t-test. Proportions were square-root transformed. Where *B. thunbergii* and other exotic plants were both present, we tested the correlation between the cover of *B. thunbergii* and the cover of other exotics.

We used canonical correspondence analysis (CCA) to quantify the percentage of the variance in species composition explained by the cover of *B. thunbergii*, and a Monte Carlo randomization test to assess whether species composition was significantly related to the cover of *B. thunbergii* (PC-ORD 5.31, MjM Software, Gleneden Beach, OR). In the CCA, the main community matrix consisted of the cover of all species except *B. thunbergii* in all plots, and the second, explanatory matrix consisted of the cover of *B. thunbergii* in all plots.

Also in PC-ORD, we conducted a principal components analysis (PCA) to summarize the variation in the many soil properties we measured (pH, LOI, total C, total N, and extractable Al, Ca, Cu, Fe, K, Mg, Mn, P, and Zn) onto two composite axes. We interpreted the axes by calculating distance-based biplot scores for the soil properties (Legendre and Legendre 1998). We then asked whether each of the axes differed between plots with and without *B. thunbergii* using paired t-tests. Paired t-tests also evaluated whether plots with and without *B. thunbergii* differed in soil moisture, light availability at 1 m and 10 cm, and the proportion of the light available at 1 m

Table 1. Species comprising understory plant communities in the Theodore A. Parker III Natural Area in Lancaster County, Pennsylvania. Species are listed in order of their frequency (number of plots where the species occurred, of 100 plots). By design, 50 plots contained *Berberis thunbergii*. All vascular plant species < 1 m high were included. Nomenclature follows the PLANTS database (USDA Natural Resources Conservation Service 2013).

| Species | Origin | Frequency |
|---|---|---|
| *Glechoma hederacea* L. | Exotic | 44 |
| *Lindera benzoin* (L.) Blume | Native | 40 |
| *Polystichum acrostichoides* (Michx.) Schott | Native | 30 |
| *Toxicodendron radicans* (L.) Kuntze | Native | 27 |
| *Polygonum persicaria* (L.) | Exotic | 23 |
| *Arisaema triphyllum* (L.) Schott | Native | 22 |
| *Duchesnea indica* (Andrews) Focke | Exotic | 21 |
| *Lonicera japonica* Thunb. | Exotic | 19 |
| *Deparia acrostichoides* (Sw.) M. Kato | Native | 16 |
| *Athyrium filix-femina* (L.) Roth | Native | 14 |
| *Parthenocissus quinquefolia* (L.) Planch. | Native | 11 |
| *Rosa multiflora* Thunb. | Exotic | 11 |
| *Viburnum acerifolium* L. | Native | 11 |
| *Carex* L. species | Native | 10 |
| *Dryopteris intermedia* (Muhl. ex Willd.) A. Gray | Native | 8 |
| *Maianthemum canadense* Desf. | Native | 8 |
| *Circaea lutetiana* L. | Native | 6 |
| *Pilea pumila* (L.) A. Gray | Native | 6 |
| *Ligustrum vulgare* L. | Exotic | 5 |
| *Betula lenta* L. | Native | 4 |
| *Cornus florida* L. | Native | 4 |
| *Dennstaedtia punctilobula* (Michx.) T. Moore | Native | 4 |
| *Rubus allegheniensis* Porter | Native | 4 |
| *Rubus idaeus* L. | Native | 4 |
| *Smilax rotundifolia* L. | Native | 4 |
| *Thelypteris noveboracensis* (L.) Nieuwl. | Native | 4 |
| *Viola* L. species | Native | 4 |
| *Carya cordiformis* (Wangenh.) K. Koch | Native | 3 |
| *Hemerocallis fulva* (L.) L. | Exotic | 3 |
| *Microstegium vimineum* (Trin.) A. Camus | Exotic | 3 |
| *Osmunda cinnamomea* L. | Native | 3 |
| *Acer rubrum* L. | Native | 2 |
| *Carpinus caroliniana* Walter | Native | 2 |
| *Hamamelis virginiana* L. | Native | 2 |
| *Huperzia lucidula* (Michx.) Trevis | Native | 2 |
| *Phytolacca americana* L. | Native | 2 |
| *Ailanthus altissima* (Mill.) Swingle | Exotic | 1 |
| *Alliaria petiolata* (M. Bieb.) Cavara & Grande | Exotic | 1 |
| *Commelina communis* L. | Exotic | 1 |
| *Eurybia divaricata* (L.) G.L. Nesom | Native | 1 |
| *Fagus grandifolia* Ehrh. | Native | 1 |
| *Fraxinus americana* L. | Native | 1 |
| *Glyceria striata* (Lam.) Hitchc. | Native | 1 |
| *Hydrophyllum virginianum* L. | Native | 1 |
| *Polygonum perfoliatum* L. | Exotic | 1 |
| *Polygonatum pubescens* (Willd.) Pursh | Native | 1 |
| *Sambucus nigra* L. | Native | 1 |
| *Sanicula marilandica* L. | Native | 1 |

reaching 10 cm. Light availability at 1 m and 10 cm were natural-log transformed, and three outliers were removed.

**Results.** PLANT COMMUNITIES. Besides *B. thunbergii*, the understory plant community contained 48 species (Table 1). The most frequent species were the exotic herb *Glechoma hederacea* L., the native shrub *Lindera benzoin* (L.) Blume, the native fern *Polystichum acrostichoides* (Michx.) Schott, and the native vine *Toxicodendron radicans* (L.) Kuntze (Table 1).

Plots with and without *B. thunbergii* had similar species richness ($t = -0.81$, d.f. = 49, $P = 0.422$), with means of 4.4 and 4.6 species

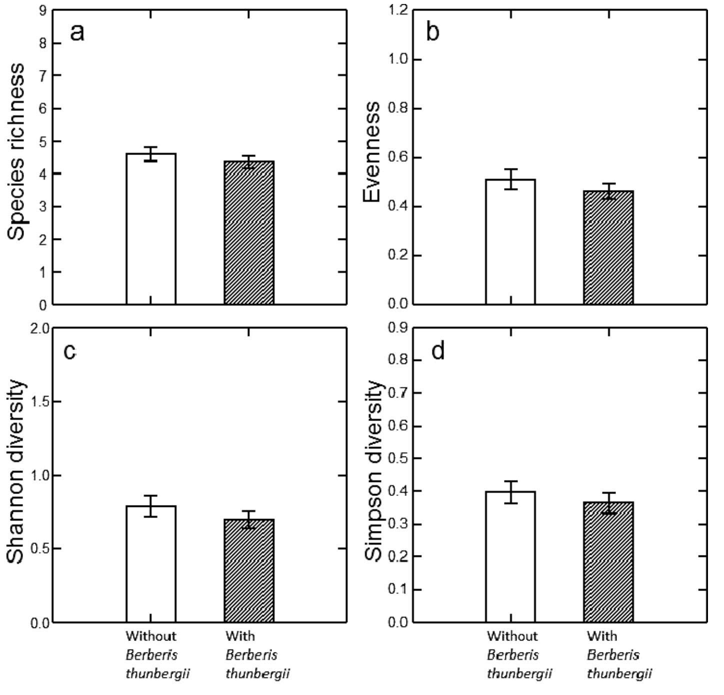


FIG. 1. Diversity of understory plant communities in the Theodore A. Parker III Natural Area in Lancaster County, Pennsylvania, including (a) species richness, (b) evenness, (c) Shannon's diversity index, and (d) Simpson's diversity index. Diversity was measured in 1 $m^2$ plots, 50 with and 50 without *Berberis thunbergii.*

per meter squared, respectively (Fig. 1a). Evenness was also similar between plots with and without *B. thunbergii* ($t = -0.85$, d.f. = 49, $P = 0.400$; Fig. 1b). Shannon and Simpson diversity indices were similar between the plots as well (Shannon, $t = -0.96$, d.f. = 49, $P = 0.340$; Simpson, $t = -0.63$, d.f. = 49, $P = 0.531$; Fig. 1c, d).

Of 14 species with at least ten occurrences, only two had significant associations with the presence of *B. thunbergii*. Both the native herb *Arisaema triphyllum* (L.) Schott and the invasive vine *Lonicera japonica* Thunb. were less likely to occur in plots with *B. thunbergii* (*A. triphyllum*, $G = 6.00$, d.f. = 1, $P = 0.014$; *L. japonica*, $G = 5.44$, d.f. = 1, $P = 0.020$). Of five species with at least ten occurrences in plots with *B. thunbergii*, none had cover values that were positively or negatively correlated with the cover of *B. thunbergii*.

Plots with *B. thunbergii* were no more or less likely to contain other exotic plants ($G = 0.41$, d.f. = 1, $P = 0.523$). Among plots with other exotics, plots with and without *B. thunbergii* had similar proportions of non-*B. thunbergii* cover comprised of exotics ($t = -1.22$, d.f. = 65, $P = 0.227$). Where *B. thunbergii* and other exotic plants were both present, there was no correlation between the cover of *B. thunbergii* and the cover of other exotics (Pearson correlation = $-0.03$, $P = 0.852$).

In CCA, the cover of *B. thunbergii* explained only 1.4% of the variance in species composition. The proportion of 999 randomized runs with correlations between species composition and the cover of *B. thunbergii* that were greater than or equal to the observed correlation was 0.432, indicating no significant relationship between species composition and the cover of *B. thunbergii*.

ENVIRONMENTAL CONDITIONS AND RESOURCES. In the PCA of soil properties, the first axis evidently represented a gradient of organic matter content, with the strongest biplot scores for LOI, total C, and total N (Fig. 2a). This organic matter axis explained 45% of the variation in soil properties. The second axis represented the pH gradient, with strong biplot scores for Ca, Mg, Zn, and pH (Fig. 2a), and it explained an additional 28% of the variation in soil properties. Plots with and without *B.*

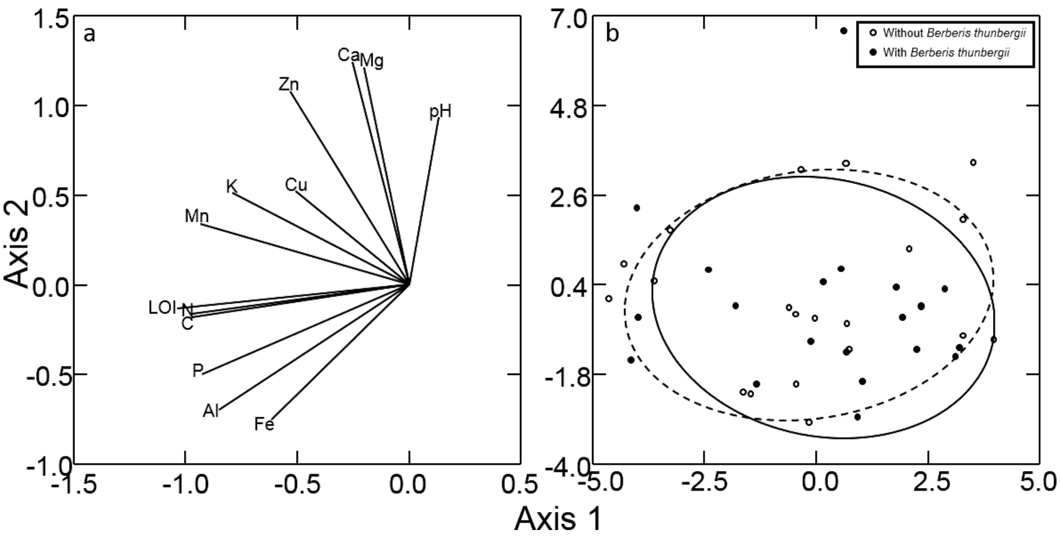


FIG. 2. Principal components analysis of soil properties in the Theodore A. Parker III Natural Area in Lancaster County, Pennsylvania. Soil properties were measured in 1 $m^2$ plots, 20 with and 20 without *Berberis thunbergii*. (a) Distance-based biplot scores showing the relationships between the individual soil properties and the composite axes. Soil properties included pH, LOI, total C, total N, and extractable Al, Ca, Cu, Fe, K, Mg, Mn, P and Zn. (b) A scatterplot of the plots has 68% confidence ellipses for plots with *Berberis thunbergii* (black circles, solid line) and plots without *Berberis thunbergii* (white circles, dashed line). Axis 1 explained 45% of the variation in soil properties, and Axis 2 explained 28%.

*thunbergii* were similar along both axes (Axis 1, $t = 0.65$, d.f. = 19, $P = 0.523$; Axis 2, $t = -0.76$, d.f. = 19, $P = 0.454$; Fig. 2b).

Soil moisture was similar between plots with and without *B. thunbergii* ($t = -0.93$, d.f. = 49, $P = 0.355$; Fig. 3a). Plots with and without *B. thunbergii* had similar light levels at 1 m from the ground ($t = 0.39$, d.f. = 46, $P = 0.697$; Fig. 3b), but plots with *B. thunbergii* had lower light levels at 10 cm ($t = -2.11$, d.f. = 46, $P = 0.040$; Fig. 3c). The proportion of the light available at 1 m reaching 10 cm did not differ between plots with and without *B. thunbergii* ($t = -1.02$, d.f. = 46, $P = 0.311$; Fig. 3d).

**Discussion.** The presence of *B. thunbergii* had little measurable impact, whether direct or indirect, on understory plant communities in the forests we studied. By any measure, *B. thunbergii* did not affect plant diversity or composition in its immediate surroundings. Only two species were less likely to occur in plots with *B. thunbergii*. We also found no effect of *B. thunbergii* on soil moisture or other key soil properties such as pH and organic matter content. This lack of impact was unexpected given previous results. Areas invaded by *B. thunbergii* had fewer *Quercus* and *Vaccinium* plants and higher soil pH in New Jersey (Kourtev et al. 1998). At the same sites, Ehrenfeld et al. (2001) also found higher soil pH and higher nitrification and N mineralization rates under *B. thunbergii* than under native *Vaccinium* shrubs. They suggest that these changes result from the large masses of N-rich fine roots and N-rich leaf litter that *B. thunbergii* produces (again relative to native *Vaccinium*; Ehrenfeld et al. 2001). One possible reason for the discrepancy between these results and ours is that both previous studies involved "very dense populations" of *B. thunbergii* (Kourtev et al. 1998, p. 494), whereas we studied scattered individuals. In addition, because *Vaccinium* is strongly associated with acidic soils (e.g. Coudun and Gegout 2007), it might seem that many types of vegetation would appear to raise soil pH when compared to *Vaccinium* patches. However, mean soil pH of uninvaded, *Vaccinium*-dominated areas at Kourtev et al.'s (1998) and Ehrenfeld et al.'s (2001) sites ranged from 4.4 to 4.9, and our site had a comparable mean soil pH of 4.8. It appears that the scattered individuals of *B. thunbergii* at our site simply did not elevate soil pH as did dense

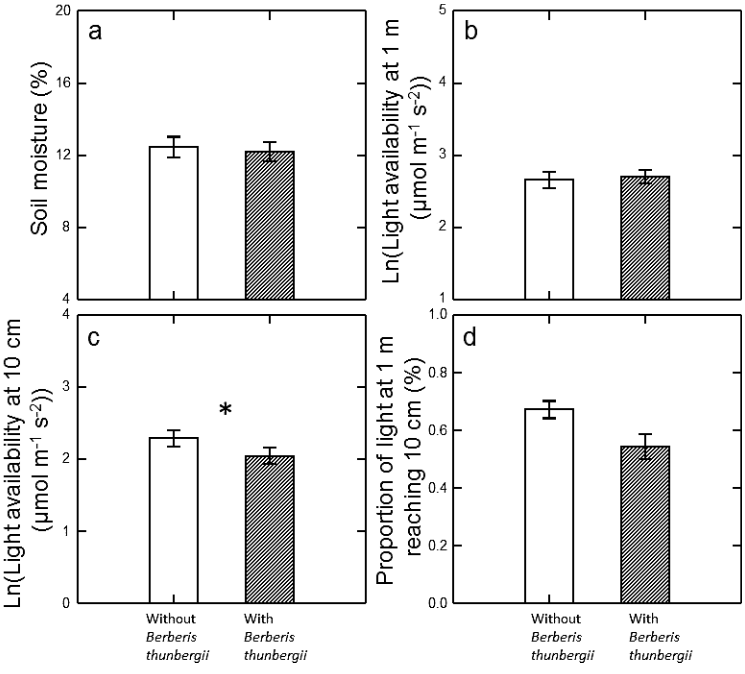


FIG. 3. Soil moisture and light availability in 50 plots with and 50 plots without *Berberis thunbergii* in the Theodore A. Parker III Natural Area in Lancaster County, Pennsylvania. Measures include (a) soil volumetric water content, (b) light availability at 1 m from the ground, (c) light availability at 10 cm from the ground, and (d) the proportion of light at 1 m reaching 10 cm. A significant difference according to a paired t-test is indicated with an asterisk.

populations in a *Vaccinium*-dominated forest understory.

At 10 cm, light levels were reduced beneath *B. thunbergii*, as beneath any shrub. In fact, the apparent lack of impact of *B. thunbergii* on this community could result from its similarity to the native shrubs that were also frequent throughout the forest understory, especially *L. benzoin* (Table 1). Similarly, if the many other exotic species in the community were having similar impacts to those of *B. thunbergii*, then this would make impacts of *B. thunbergii* difficult to detect. The lack of impact we observed could also depend on the current closed-canopy conditions of this forest; if the canopy were opened, *B. thunbergii* might respond more strongly than native species. Of course, the environmental conditions and resources measured here could have been more thoroughly quantified. It is also possible that the invasion of this forest is relatively recent, and more severe impacts may develop over time. This study may have missed impacts that could only be documented by long-term studies (Blossey 1999, Strayer et al. 2006).

Future research should include both experimental and longitudinal studies of this species' impacts. Depending on the likelihood that moderate invasions develop into dense thickets, it may be worthwhile to control any invasion before severe effects appear. However, our results demonstrate that at least several key attributes of this forest community and ecosystem currently seem unaffected by *B. thunbergii* invasion.

Another factor that could affect the severity of *B. thunbergii*'s impacts is deer herbivory. Some invasive shrubs like *Lonicera maackii* can afford native plants some protection from deer herbivory (Gorchov and Trisel 2003, Cipollini et al. 2009). If *B. thunbergii* acts similarly, then we may have found relatively small impacts on native plant cover in part due to heavy deer browse. On the other hand, the abundance of *B. thunbergii* has been shown to increase more in areas with higher deer densities (Eschtruth and Battles 2008), which would lead to greater impacts in the presence of heavy deer browse. The interactions among *B. thunbergii*, native plants, and deer herbivory merit further research.

**Conclusions.** *Berberis thunbergii*'s apparent lack of impact on forest understory plant communities suggests that it may only become "invasive" in some contexts. If, as some suggest, a plant is considered invasive when it "produce[s] reproductive offspring in areas distant from sites of introduction" (Richardson et al. 2000, p. 93), then *B. thunbergii* is unambiguously invasive (Ehrenfeld 1997, Ehrenfeld 1999, Silander and Klepeis 1999). If, however, we follow the common practice of considering species invasive only when they cause ecological or economic damage (Cronk and Fuller 1995, Mack 1997, IUCN 1999), then *B. thunbergii* may not always warrant the distinction. In situations where this species forms dense thickets, its negative effects seem clear. However, these effects may be context-dependent. In the common situation documented here, where populations are less dense (Ehrenfeld 1997), *B. thunbergii* may join many other exotic species in adding to overall diversity without causing loss of native species (Sax and Brown 2000, Moore et al. 2001, Dupré et al. 2002, Ricklefs 2004). A critical goal for further research is to identify the factors that allow low-density populations to become dense thickets. For now, if we consider *B. thunbergii* undesirable in many North American forests, we must find reasons other than its impacts on plant species diversity and composition.

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