# WINDOWS OF OPPORTUNITY: HISTORICAL AND ECOLOGICAL CONTROLS ON *BERBERIS THUNBERGII* INVASIONS

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*Abstract.* Attempts to determine characteristics that render habitats invasible to nonnative species have met with limited success. This may be because most studies focus on modern habitat conditions and do not consider invasibility in the context of a historically dynamic landscape in which both the abundance of a species and the invasibility of a site may change. We surveyed 159 currently forested sites for the occurrence and abundance of *Berberis thunbergii* (Japanese barberry), an invasive, nonnative shrub in forests of the northeastern United States, relative to modern environmental conditions, contemporary logging activity, and two periods of historical land use. *Berberis thunbergii* occurred more frequently and was more abundant in post-agricultural forests than in continuously wooded sites. This relationship was stronger for agricultural sites that were abandoned and reforested after *B. thunbergii* was introduced to the region than for sites that reforested prior to *B. thunbergii* introduction. In contrast, recent forest harvesting did not influence the occurrence or abundance of *B. thunbergii*. Modern soil fertility explained a significant portion of the variation in *B. thunbergii* occurrence, whereas site history considerably improved predictions of population density and helped evaluate potential invasion mechanisms. While land-use history covaries with soil fertility and distance to putative seed sources, the strong relationship between modern abundance patterns and historical agriculture suggests that *B. thunbergii* colonized recently abandoned agricultural lands in the early 20th century and then persisted and spread locally during subsequent reforestation. Our results indicate that interpretations of both native community composition and modern plant invasions must consider the importance of historical landscape changes and the timing of species introduction along with current environmental conditions.

*Key words: Berberis thunbergii; disturbance; forest harvesting; habitat invasibility; invasive plant species; land-use history; logging; propagule availability; Quabbin Reservoir Reservation, Massachusetts, USA.*

## INTRODUCTION

The spread of nonnative species into new habitats and landscapes presents a unique opportunity to understand controls on species distribution and abundance. Globally, few ecosystems remain unthreatened by nonnative biota (Vitousek et al. 1997). However, at the landscape scale, nonnative species are rarely ubiquitous, in part because habitats vary in their susceptibility to invasion (Elton 1958, Crawley 1987, Burke and Grime 1996, Lonsdale 1999, Davis et al. 2000). Despite considerable research on the determinants of invasibility, uncertainty remains regarding the relative importance of environmental factors and disturbances in rendering a landscape susceptible to the establishment and spread of exotic species.

Variation in invasibility among habitats is often attributed to the same factors that shape native plant communities. For example, richness or abundance of exotics may be correlated with soil nutrients, soil moisture, or light levels (Huenneke et al. 1990, Stohlgren et al. 1999, Parendes and Jones 2000, Meekins and McCarthy 2001). It is also widely recognized that disturbances, such as fire, grazing, or logging, may facilitate invasion by altering resource availability (Hobbs 1989, Hobbs and Huenneke 1992, Deferrari and Naiman 1994, Silveri et al. 2001). In addition to suitable conditions for germination and growth, successful invasions also require availability of viable propagules (Rejmanek 1989, Lonsdale 1999, Levine 2000, Foxcroft et al. 2004, Von Holle and Simberloff 2005).

While many studies document the effect of modern environmental characteristics, disturbances, and propagule availability on invasive species distributions, most ignore the temporal component of habitat invasibility. Few studies have evaluated the influences of past disturbance, changing landscape setting, or timing of species introduction (Aragon and Morales 2003, Lugo and Helmer 2004, Lundgren et al. 2004), despite the recognized importance of historical factors in controlling the modern distributions of many native plant species (Peterken and Game 1984, Matlack 1994, Motzkin et al. 1996, Donohue et al. 2000, Verheyen et

al. 2003). Invasion is an ongoing process that may span decades or centuries from the time of initial species introduction to a region. Consequently, an understanding of modern species distributions must incorporate changing landscape conditions and disturbances over time scales that are relevant to the history and process of invasion for individual species.

European settlement of eastern North America in the 17th–18th centuries resulted in rapid forest clearing, with 60–85% of the land cleared for agriculture by the mid-19th century. Subsequent abandonment of agricultural lands in the mid- to late-19th century led to widespread natural reforestation (Hall et al. 2002). Currently forested areas that were previously cleared for agriculture remain compositionally and biogeochemically distinct from adjacent areas that were continuously forested (Compton and Boone 2000, Eberhardt et al. 2003).

Historical agriculture may facilitate plant invasions in two ways: (1) by creating a "window of opportunity" in which a locally present invasive species may establish prior to and during the reforestation process, and/or (2) through persistent alteration of environmental or biotic characteristics that favor nonnative species.

The first hypothesis suggests that current distributions of invasive species may be influenced by ephemeral biotic and abiotic conditions during or after local establishment of an exotic species. As most invasive plant species thrive in disturbed habitats (Elton 1958, Baker 1986, Orians 1986), those present during the period of agricultural abandonment may have capitalized on the opportunity to establish on open, resource-rich sites. Since many invasive plants in the eastern United States were initially introduced for horticulture (Mack and Lonsdale 2001, Reichard and White 2001), their cultivation in residential areas may have facilitated subsequent spread to adjoining agricultural fields. Current distributions of species that established on disturbed sites and persisted through subsequent environmental changes may thus reflect patterns related to historical conditions. If the historical processes of agricultural abandonment and reforestation are important, we would expect a strong relationship between current species distributions, time of species arrival, and the timing of abandonment of specific fields.

The second hypothesis assumes that modern invasive species distributions are strongly correlated with persistent environmental legacies of historical site modification. For instance, as a result of agricultural amendments, formerly cultivated sites may retain elevated levels of soil N and P and higher nitrification rates for many decades (Compton and Boone 2000). Enhancements of soil fertility, especially those involving N and P, can influence habitat invasibility (Hobbs 1989, Huenneke et al. 1990, Cassidy et al. 2004), suggesting that nonnative species may preferentially invade enriched former agricultural sites.

The two hypotheses presented here are not mutually exclusive. Species may preferentially establish on recently abandoned agricultural sites in proximity to source plants and progressively spread as a result of persistent site-quality enhancements (Wiser et al. 1998, Aragon and Morales 2003, Barton et al. 2004, Foxcroft et al. 2004). In addition, the factors influencing initial establishment and spread may differ from those influencing secondary dispersal and spread (Wiser et al. 1998). Therefore, historical land-use changes have the potential to influence various stages of the invasion process via different mechanisms.

In this study, we assessed the relative importance of modern environmental characteristics, contemporary forest harvesting, and historical land use (both pre- and post-species introduction) as determinants of Japanese barberry (Berberis thunbergii DC.) distribution and abundance. Specifically, we addressed the following questions: (1) Do patterns of historical land use influence modern B. thunbergii distribution and abundance? (2) Does disturbance type and timing relative to B. thunbergii introduction influence current distribution and abundance? (3) Which historical and modern factors best predict current B. thunbergii distribution and abundance?

## METHODS

### Berberis thunbergii in the northeastern United States

Berberis thunbergii is a dense, spiny, perennial shrub native to central and southern Japan (Ohwi 1965). While recruitment is predominantly from seed (Ehrenfeld 1999), B. thunbergii also spreads vegetatively via rhizomes and layering. Berberis thunbergii may persist under dense canopies (<1–2% full sun) and tolerates a wide range of soil moistures (<10% to >40% of bulk mass). Aboveground biomass varies as a function of light availability, soil moisture, and nitrogen availability (Silander and Klepeis 1999, Cassidy et al. 2004). Fruit production varies with light level, but even in low light (≤4% full sun), some seeds are produced (Silander and Klepeis 1999). Cassidy et al. (2004) suggest that sites with higher rates of nitrification may be more susceptible to B. thunbergii invasion.

Silander and Klepeis (1999) compiled historical background on B. thunbergii in the northeastern United States. Berberis thunbergii was first introduced to Boston's Arnold Arboretum in 1875 (Steffey 1985). By the late 1800s, B. thunbergii was commonly marketed as a decorative shrub or low hedge plant by nurseries throughout eastern Massachusetts (Sargent 1889), although there is little evidence of it having naturalized in the region prior to 1910 (Silander and Klepeis 1999). Since then, it has become a prominent understory species in many forests and natural areas across the region.

### Study area

This study was conducted on the Quabbin Reservation's Prescott Peninsula (~5000 ha) in central Massa-

chusetts, USA (42°23′ N, 72°21′ W). Topography is characterized by rolling hills, with slopes rarely exceeding 30%. Upland soils are acidic sandy loams derived from glacial till, with smaller areas of outwash sands (Barten et al. 1998). Annual precipitation averages 114 cm and mean annual temperatures range from −3°C in January to 21°C in July. The area is 96% forested with <1% open fields. The vegetation is typical of the transition hardwoods–white pine–hemlock region (Westveld et al. 1956) with the addition of red pine (*Pinus resinosa*), white pine (*Pinus strobus*), and Norway spruce (*Picea abies*) plantations on some abandoned agricultural sites.

The Quabbin Reservoir Reservation (21 450 ha) was created in 1939 to provide a drinking water supply for metropolitan Boston by damming and flooding the Swift River Valley. All inhabitants were forced to relocate and their homes were either moved or razed to the foundations. While the lowest elevations of the reservation were inundated, a large area remained above the waterline, forming the Prescott Peninsula. The history of the Quabbin region prior to the creation of the reservoir is typical of much of the northeastern United States. Prior to widespread abandonment of agricultural land in the second half of the 19th century, ~68% of the peninsula was cleared for agriculture (Fig. 1a). By 1927, 60% of the peninsula was sproutland (young, regenerating forests) with only 21% remaining in agriculture (Fig. 1b). While much of the surrounding landscape subsequently experienced substantial residential and commercial development, the Prescott Peninsula has remained protected from development and closed to general public access since 1939. Timber harvesting has been the primary form of anthropogenic disturbance in the study area for the past 50 years. Since 1984, 19% of the peninsula has been harvested (Fig. 1c).

### Site selection

Currently forested areas were selected following a fully stratified random sampling design, with sample sites stratified by pre-introduction (1830) land use, post-introduction (1927) land use, and recent harvesting activity (harvested vs. unharvested since 1984). Pre-introduction land-cover (open vs. wooded) was digitized from surveyed municipal maps from the 1830s (Hall et al. 2002). The open category included areas that were tilled, pastured, hayed, or residential. The 1927 real estate maps from the Quabbin Reservoir watershed were digitized to provide post-introduction land-cover data. These maps classified land use into arable, pasture, sproutland, and woodland categories, and indicated the location of buildings, roads, and land-use boundaries (fences and stone walls; Fig. 1d). All forest harvests from 1984 to 2003 were digitized based on information collected under the Massachusetts Forest Cutting Practices Act (Kittredge et al. 2003, McDonald et al. 2006), which includes data on the size of harvested areas

and the species and volume of timber removed. Depending on the availability of suitable sites, we randomly sampled 9–11 polygons ≥0.5 ha in each of the resulting strata (Appendix A). Polygons dominated by hemlock (*Tsuga canadensis*) and spruce were excluded as these stand types were uncommon and rarely support *B. thunbergii*.

### Field sampling

In the summer of 2005, 159 polygons were sampled for *B. thunbergii* abundance and environmental characteristics. Within each polygon, a series of $2 \times 2$ m plots (10/ha), separated from each other and the polygon boundary by at least 20 m, were sampled along transects oriented based on polygon shape. Within each plot, the percent cover of *B. thunbergii* was estimated using a modified Braun-Blaunquet scale (0%, <1%, 1–3%, 3–5%, 5–15%, 15–25%, 25–50%, 50–75%, >75%) and the number of *B. thunbergii* stems was recorded. The percentage frequency, percent cover, and stem density (number of stems/m$^2$) were combined into a synthetic measure of *B. thunbergii* abundance as follows:

$$[\text{Abundance} = \text{percentage frequency} + \text{mean percent cover} + \text{mean relative density}]$$

where relative density equals the density of *B. thunbergii* stems in a plot divided by the maximum-recorded stem density (39.5 stems/m$^2$) multiplied by 100. Mean percent cover was calculated using cover class maximums. Abundance values were log-transformed prior to analysis to achieve normality. If *B. thunbergii* occurred within a polygon but did not fall into any of the sampled plots, its presence was noted and included in subsequent analyses of occurrence data.

To characterize overstory vegetation and light conditions, basal area was determined using an angle gauge (10 factor) and canopy cover was measured using a convex spherical densiometer (Forestry Suppliers, Jackson, Mississippi, USA). Basal area and canopy cover measurements (5/ha) were recorded in transect plots separated by at least 30 m. We measured organic soil (O horizon) depth and collected composite samples of 0–15 cm mineral soil from five locations in each polygon. Mineral soils were sampled with a $5 \times 15$ cm cylindrical steel corer. In the laboratory, samples were air-dried and sieved to <2.0 mm. Mineral samples were analyzed for pH, percentage of organic matter, exchangeable Ca, Mg, K, and Na, total exchange capacity, and Mehlich III extractable P, Mn, Zn, B, Cu, Fe, and Al (Brookside Laboratories, New Knoxville, Ohio, USA). Soil texture (percentage sand, silt, and clay) was determined using a hydrometer (ASTM D422; Barnstead International, Dubuque, Iowa, USA). Subsamples were ground to <250 μm, oven-dried at 80°C for 24 h, and analyzed for total C and N at the University of Georgia's Stable Isotope Laboratory (Athens, Georgia, USA).

a) Pre-introduction land use

b) Post-introduction land use

c) Modern harvesting activity
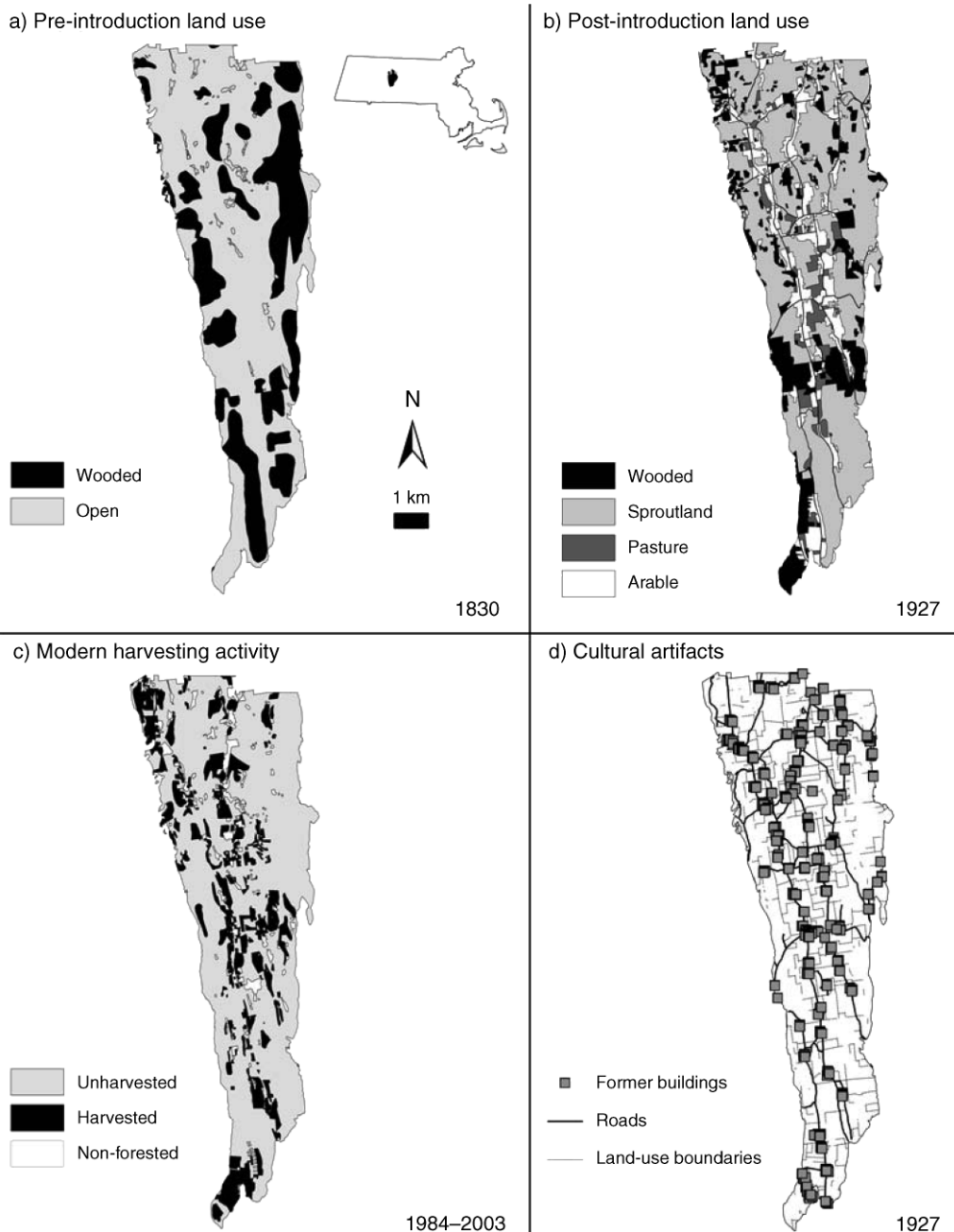
d) Cultural artifacts

FIG. 1.   Maps of the Prescott Peninsula (Quabbin Reservation, central Massachusetts, USA) depicting (a) land use prior to the introduction of *Berberis thunbergii* (1830), (b) post-introduction (1927) land use, (c) modern land cover and harvesting activity (1984–2003), and (d) the distribution of buildings, roads, and land-use boundaries in 1927.

*Additional GIS data*

Mean distances to historical buildings, roads, and land-use boundaries were calculated for each polygon using 1927 real estate maps. An area-weighted average was used to calculate mean soil drainage class in each polygon. Drainage classes were based on standard NRCS soils classification (USDA 1993). Mean distance to streams was determined using a Massachusetts Department of Environmental Protection wetland data layer (*available online*).[2] A digital elevation model (DEM) with 30-m horizontal resolution from the National Elevation Dataset (*available online*),[3] was used to calculate slope and aspect using ArcView GIS 3.2

[2] ⟨http://www.mass.gov/mgis/⟩
[3] ⟨http://ned.usgs.gov/⟩

(ESRI, Redlands, California, USA). Transformed radiative aspect (Roberts and Cooper 1989) was then calculated using the following formula:

$$\text{TRASAP} = \frac{\left[1 - \cos\left(\frac{\pi}{180}\right)\right] \times (\text{aspect} - 30)}{2}.$$

This formula transforms the circular aspect variable into a biologically relevant radiation index ranging from 0 to 1. Aspects receiving low incident radiation (NNE) are assigned a value of 0 while SSW aspects receive a value of 1.

### Data analyses

Analyses were performed separately for: (1) *B. thunbergii* presence/absence in each polygon, and (2) the log-transformed abundance of *B. thunbergii* in those polygons where it was present in sample plots. By separately modeling the probability of presence and abundance when present, we investigated the possibility that different factors influence these two measures of invasion.

### Effects of disturbance on Berberis thunbergii distribution and abundance

Single-step stepwise logistic and linear regressions were used to determine which of the three main disturbance variables (pre-introduction land use, post-introduction land use, and recent harvesting activity) was the single best predictor of *B. thunbergii* presence/absence and log-abundance. Prior to stepwise selection, we fit a full model to test for significant interaction terms. *G* tests of independence were used to determine whether the frequency of occurrence of *B. thunbergii* varied with the three main effects (Gotelli and Ellison 2004). Fixed effect one-way analysis of variance (ANOVA) was used to test for differences in log-abundance as a function of historical land use and harvesting. A posteriori comparisons of abundance data between post-introduction land use categories were made using Tukey-Kramer hsd tests. To determine if *B. thunbergii* presence and abundance varied as a function of harvest intensity and years since harvest, we used logistic and linear regressions, respectively. We elected not to perform Bonferroni corrections for multiple tests (Rice 1989), accepting that some mistakes may be made while most of the conclusions should be sound (Moran 2003).

### Relationships between disturbance and environmental variables

Environmental variables (edaphic and non-edaphic) with non-normal distributions were normalized using logarithmic or square-root transformations prior to analysis. Environmental differences among historical land use and harvesting categories were tested using Kruskal-Wallis tests. To reduce the dimensionality and characterize the variation in these data, edaphic and non-edaphic environmental variables were separately ordinated using principal component analysis (PCA; Gotelli and Ellison 2004). We selected the first three edaphic principal axes and the first three non-edaphic principal axes for use in multiple regression analyses. To ensure that assumptions of multicollinearity were met, we calculated correlations between edaphic and non-edaphic principal axes prior to their inclusion in multiple regression analyses. Differences in principal axes between pre- and post-invasion land-use categories were tested using post hoc Tukey-Kramer hsd tests. Prior to these post hoc comparisons, post-introduction arable and pastureland cover, and sproutland and woodland cover, were lumped into their equivalent pre-introduction land-use categories of "open" and "wooded," respectively.

### Modeling of Berberis thunbergii occurrence and abundance

In order to determine the factors controlling *B. thunbergii* distribution and abundance, we modeled *B. thunbergii* occurrence and log-abundance as a function of anthropogenic disturbance and environmental variables using logistic and linear regressions, respectively. The following variables were entered into the multiple regression models: pre-introduction land use, post-introduction land use, recent harvesting activity, and values along six principal component axes (three edaphic and three non-edaphic). Stepwise selection was used to determine the subset of independent variables that best explained the observed occurrence and abundance patterns. The most parsimonious model was selected based on Akaike Information Criterion (AIC; Gotelli and Ellison 2004). All statistical analyses were performed using JMP 5.0.1.2 (SAS Institute, Cary, North Carolina, USA).

### RESULTS

#### Influence of historical and modern disturbances

Of the three disturbance effects tested, post-introduction land use was the single strongest predictor of *B. thunbergii* occurrence ($R^2 = 0.15$, $P < 0.001$). Sites that remained in agriculture (i.e., arable and pasture land) after *B. thunbergii* introduction are more likely to have *B. thunbergii* today than sites that were wooded or sproutlands at the time. *Berberis thunbergii* was found at 88% of early-20th century arable sites vs. 36% of sites that were wooded at the time (Fig. 2b). Agricultural land use after *B. thunbergii* introduction had a stronger influence on the modern distribution of *B. thunbergii* than agricultural use pre-dating introduction. *Berberis thunbergii* occurred in 72% of sites that were open in the early 19th century vs. 58% of wooded sites, but the difference was only marginally significant (Fig. 2a). In contrast, recent harvesting did not influence *B. thunbergii* distribution with *B. thunbergii* occurring in 60% of harvested vs. 70% of unharvested sites (Fig. 2c). Similarly, harvest intensity ($m^3$/ha) and time since harvest were unimportant ($P = 0.72$ and $P = 0.25$,
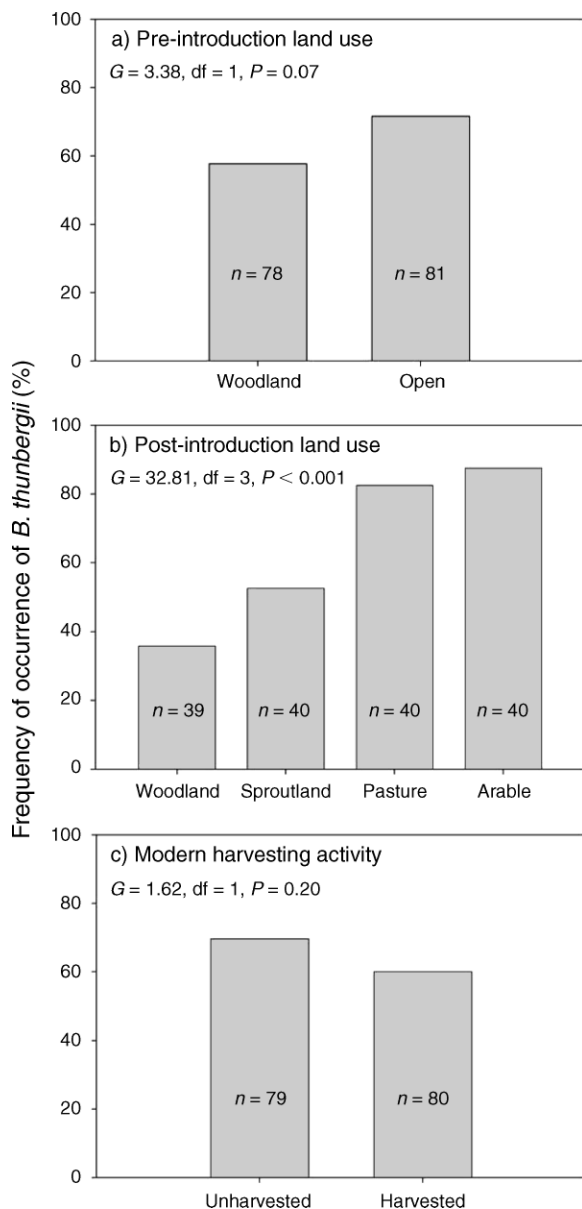
FIG. 2. Frequency of occurrence of *Berberis thunbergii* relative to: (a) pre-introduction land use, (b) post-introduction land use, and (c) modern harvesting activity. *G* tests of independence were used to determine whether the frequency of occurrence of *B. thunbergii* differed among historical land-use and modern harvesting categories. Sample sizes represent the number of sites sampled.

respectively). Since there were no significant interactions between historical and modern disturbance variables, results are presented by treatment.

Early-20th century land use was also the single strongest predictor of *B. thunbergii* log-abundance ($R^2 = 0.20$; $P < 0.001$). *Berberis thunbergii* was more abundant in early-20th century arable sites than in former sproutlands (Fig. 3b). Mean abundance of *B. thunbergii* was three times greater in arable sites than in

early-20th century wooded sites, although the difference was not significant. The abundance of *B. thunbergii* did not differ between sites that were open or wooded in the early 19th century (Fig. 3a). Whether or not a site was harvested in the past 21 years did not influence *B. thunbergii* abundance (Fig. 3c). Furthermore, harvest intensity and time since harvest had no discernible influence on *B. thunbergii* log-abundance ($P = 0.93$ and $P = 0.73$, respectively).

### Interrelationships of disturbance and environmental variables

Sites that were open in the early 19th century were generally flatter and were associated with lower incident radiation than wooded sites (Appendix B). Pastures in the early 20th century had lower incident radiation and were closer to roads than sites that were wooded at the time. Early-20th century arable sites were closer to streams, buildings, and roads than wooded sites. Harvested sites had less canopy cover and basal area and were flatter and farther from streams than unharvested sites.

Sites that were open in the early 19th century had finer textured and less well-drained soils, with higher pH, percent base saturation, percent nitrogen, and zinc concentrations than sites that were wooded (Appendix C). Sites that were used for agriculture in the early 20th century had more poorly drained and siltier soils with thinner organic layers, higher pH, percentage base saturation and nitrogen, and lower percentage of carbon and C:N ratios than wooded sites. Early-20th century agricultural sites also had higher concentrations of phosphorus, boron, manganese, and copper and lower concentrations of iron than other land-use categories. Sites that were harvested had higher C:N ratios and percentage nitrogen, and lower pH, percentage base saturation, potassium, and soluble sulfur concentrations than did unharvested sites.

### Interrelationships of principal components and disturbance variables

Non-edaphic axis 1, constructed mainly from distance to buildings, roads, and land-use boundaries, was named "seed sources" since these factors are likely to have influenced the locations of *B. thunbergii* source populations at the time of agricultural abandonment (Appendix D). Non-edaphic axis 2 ("overstory") was constructed mainly from canopy cover and total basal area, which were positively correlated ($r = 0.62$, $P < 0.001$). Non-edaphic axis 3, primarily loaded by slope, aspect, and distance to streams, was named "topography."

Edaphic axis 1 ("soil nutrients") was constructed primarily from macronutrients including nitrogen, magnesium, and potassium (Appendix E). Edaphic axis 2 ("soil acidity") was primarily loaded by pH and percent base saturation, which were positively correlated ($r = 0.99$, $P < 0.001$). Edaphic axis 3 ("soil texture") was

constructed mainly from percentage sand and silt, which were negatively correlated ($r = -0.87$, $P < 0.001$).

Several edaphic and non-edaphic principal components were correlated. Seed sources was negatively correlated with soil nutrients ($r = -0.33$, $P < 0.001$) and positively correlated with soil acidity ($r = 0.32$, $P < 0.001$). Overstory was positively correlated with soil nutrients ($r = 0.19$, $P < 0.05$) and negatively correlated with soil acidity ($r = -0.19$, $P < 0.05$). Sites cleared for agriculture in the early 20th century had lower values for the seed sources and soil acidity factors than sites cleared for agriculture in the early 19th century according to Tukey-Kramer pairwise comparisons ($\alpha = 0.05$).

### Predictors of *Berberis thunbergii* occurrence and abundance

Edaphic characteristics ("soil acidity" and "soil nutrients") were the best overall predictors of *B. thunbergii* occurrence ($R^2 = 0.42$; Appendix F). The ability to explain the distribution of *B. thunbergii* improved only slightly by adding "soil texture" ($R^2 = 0.43$). No significant explanatory power was gained by including disturbance variables or non-edaphic environmental axes in the model of *B. thunbergii* occurrence. The strongest predictors of *B. thunbergii* log-abundance were "seed sources" and post-introduction land use ($R^2 = 0.40$; Appendix G). Adding edaphic characteristics ("soil nutrients" and "soil acidity") further improved the accuracy of the model ($R^2 = 0.49$).

### DISCUSSION

#### Importance of the timing of disturbance

*Berberis thunbergii* distribution and abundance are more strongly correlated with patterns of historical land use than with modern forest harvesting activity, indicating that the influences of significant land-use changes can persist for many decades. However, the influence of historical land use on the modern occurrence and abundance of *B. thunbergii* varies depending on the timing of agriculture relative to species introduction. Post-introduction land use had a significantly greater influence on *B. thunbergii* invasion patterns than pre-introduction land use, suggesting that current distribution and abundance patterns largely reflect: (1) historical establishment in agricultural fields abandoned after local introduction, and/or (2) modern environmental differences between pre- and post-introduction agricultural sites. In order to differentiate between these two factors, we assessed current environmental variation between sites cleared for agriculture at different times.

Although simply knowing whether a site was cleared for agriculture in the past helps to explain current biotic and abiotic conditions (Peterken and Game 1984, Motzkin et al. 1996, Koerner et al. 1997, Compton and Boone 2000), we documented two potentially important differences between pre- and post-introduction agricultural sites. Sites cleared for agriculture in the
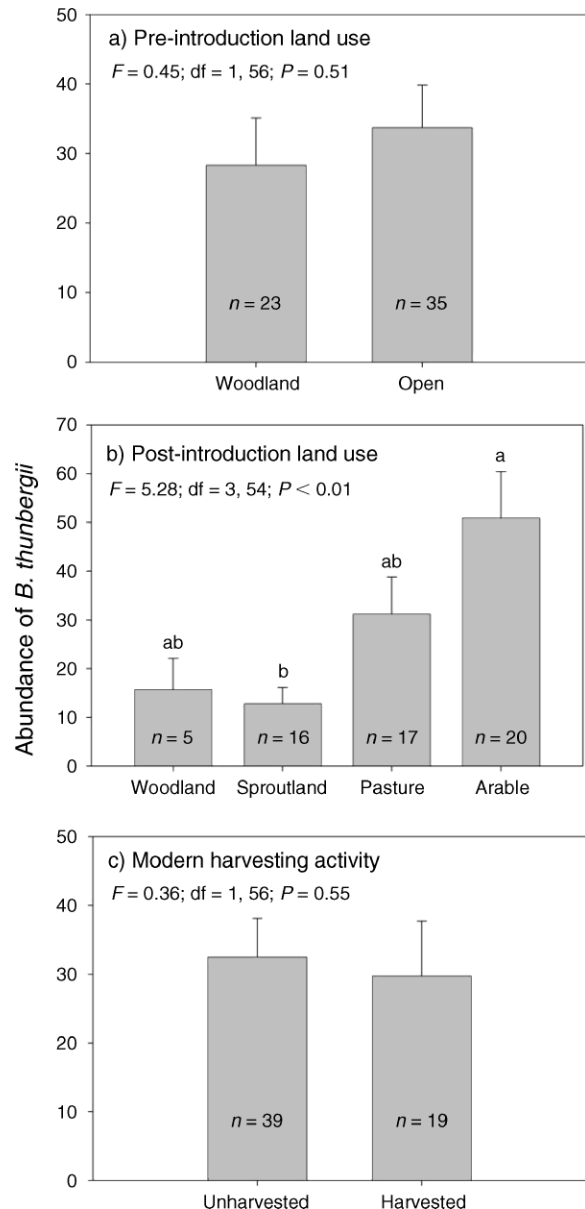


FIG. 3. Abundance (mean + SE) of *Berberis thunbergii* relative to: (a) pre-introduction land-use, (b) post-introduction land-use, and (c) modern harvesting activity. Abundance is a synthetic measure of percentage frequency, percent cover, and stem density. See the *Methods* for more information. Means with different letters are significantly different ($\alpha = 0.05$) according to Tukey-Kramer hsd pairwise comparisons. Sample sizes represent the number of sites sampled.

early 20th century are less acidic and closer to potential seed sources (i.e., buildings, roads, and land-use boundaries) than 19th century agricultural sites (DeGasperis 2006). While current disparities in soil acidity between 19th- and 20th-century agricultural sites are minimal (pH = 4.73 ± 0.03 vs. 4.77 ± 0.03, respectively [mean ± SE]) and therefore unlikely to account for the apparent contrast in *B. thunbergii* establishment and

PLATE 1. Legacies of an agricultural past: a woodland stone wall delineating a dense thicket of *Berberis thunbergii* on the Prescott Peninsula (Quabbin Reservation, central Massachusetts, USA). Photo credit: B. G. DeGasperis.

spread, differences in proximity to putative seed sources (e.g., mean distance to roads [±SE] = 146.25 ± 11.23 m vs. 108.44 ± 7.64 m, respectively) are potentially more important. In order to assess the importance of potential seed source distance relative to agricultural disturbance, we compared *B. thunbergii* occurrence in 19th- and 20th-century agricultural sites at comparable distances from buildings, roads, and land-use boundaries. Even when we account for distance to potential seed sources, *B. thunbergii* occurs more frequently in sites that were cleared for agriculture in the early 20th century than in 19th-century agricultural sites (87% vs. 62% occurrence, respectively; DeGasperis 2006). Therefore, the apparent contrast in invasibility between 19th- and 20th-century agricultural sites is not adequately explained by modern edaphic variation alone and cannot be fully attributed to the proximity of putative seed sources. Our results suggest that the strong relationship between 20th-century land use and modern *B. thunbergii* distribution and abundance partly reflects spread from initial plantings, which was facilitated by their proximity to abandoned agricultural fields.

### Relative influence of contemporary forest harvesting

Forest harvesting is thought to promote the invasion of many species through direct dispersal of propagules on machinery, soil scarification, removal of litter, and increased light availability (Silveri et al. 2001). We therefore anticipated increases in frequency and abundance of *B. thunbergii* following harvesting (Scherer et

al. 2000, Silveri et al. 2001, Brown and Gurevitch 2004). However, our results suggest that the low- to moderate-intensity selective harvesting occurring in the study region does not alter patterns of *B. thunbergii* distribution and abundance across the landscape.

### Predictors of Berberis thunbergii invasion

Differences between best models of *B. thunbergii* occurrence and abundance suggest that these two measures of invasion are influenced by different sets of factors. Although historical land use and soil fertility were not independent, multiple regressions showed that occurrence was best described by edaphic characteristics. The frequency of occurrence was higher in sites with more nutrient-rich, less acidic, and siltier soils. These results are consistent with previous studies suggesting that invasive plants are more common on nutrient-rich sites (Huenneke et al. 1990, Pysek and Pysek 1995, Wiser et al. 1998, Stohlgren et al. 1999). Unfortunately, we were unable to determine whether modern edaphic conditions reflect natural variation or anthropogenic modification (Glitzenstein et al. 1990, Foster 1992, Bratton and Miller 1994). While soil fertility also had an affect on *B. thunbergii* abundance, distance to potential seed sources and post-introduction land use were significantly better predictors of this invasion metric. Since *B. thunbergii* was most abundant in areas both cleared for agriculture in the early 20th century and close to putative primary and secondary seed sources, we conclude that current population density may be a

function of population age, historical site disturbance, and soil fertility (Hobbs and Huenneke 1992, Deferrari and Naiman 1994, Wiser et al. 1998, Williamson and Harrison 2002, Foxcroft et al. 2004).

### Invasion ecology of Berberis thunbergii

The densest populations of *B. thunbergii* appear to have resulted from a combination of: (1) open site conditions in the early 20th century, (2) propagule availability, and (3) site fertility. Under these conditions, *B. thunbergii* appears to behave as a "persistent pioneer." It readily colonizes and flourishes in open, disturbed habitats but is also able to persist and expand locally through subsequent forest canopy development. Thus, our results suggest that patterns of invasion result in part from differences in invasibility between old fields and forests.

To a lesser extent, the current distribution of *B. thunbergii* reflects its ability to invade established forests. The extent to which *B. thunbergii* establishes and spreads into forests is largely influenced by soil fertility and proximity to putative seed sources. While invasions in post-agricultural forests are more frequent and denser than invasions in continuous woodlands, *B. thunbergii* occurs today in nearly 36% of sites that were wooded in the early 20th century. Since these occurrences cannot be attributed to historical plantings or agricultural disturbance, this is a minimum estimate of *B. thunbergii*'s invasion into forested sites over the past century. Therefore, even in the absence of agricultural disturbances, *B. thunbergii* is slowly dispersing across the forested landscape (Ehrenfeld 1997).

### Conclusions

Our data indicate that *B. thunbergii* invasion patterns are a product of complex interactions between modern edaphic conditions and historical land-use changes. While modern edaphic characteristics explained a significant portion of the variation associated with *B. thunbergii* distribution, knowledge of land-use history considerably improved our interpretation of population densities and potential invasion mechanisms. Our data support the hypothesis that historical land use influences plant invasions, in part by creating a "window of opportunity" in which a locally present invasive species can establish. In addition, these data indicate that historical land use may exert persistent influence on the distribution and abundance of many plant species through distinctive edaphic and biotic legacies. This suggests that habitat invasibility is not a static attribute, but a condition that varies over time. Davis et al. (2000) suggested that communities are more susceptible to invasion following increases in resource availability. The period of historical agricultural abandonment in New England represents a major pulse in resource availability, which resulted in dramatic and persistent changes in the distribution and abundance of locally present native and nonnative species. Many exotic species present during this period likely utilized this opportunity to naturalize in novel environments. Several studies have shown that invasibility varies with time since disturbance (Deferrari and Naiman 1994, Fike and Niering 1999, Meiners et al. 2002, Aragon and Morales 2003). However, our results suggest that the absolute time since disturbance is not as important as disturbance timing relative to propagule availability. Disturbance-generated gaps at times of limited propagule availability are less likely to result in invasive establishment and spread (Johnstone 1986). In this study, the influences of historical land use on plant invasions have persisted for nearly a century, despite subsequent natural and anthropogenic disturbances. In fact, as population infilling continues to amplify initial patterns of establishment and spread, the influences of historical land use may be more pronounced today than in the past (see Plate 1). Similar patterns presumably exist in many regions and for numerous native and nonnative species, although such patterns are frequently difficult to detect in areas with complex histories of introduction and disturbance. Therefore, given continued movement and planting of invasives, and the availability of nonnative propagules on the landscape today, it is likely that current land use will affect the course of biological invasions for years to come.

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## APPENDIX A

Study design, indicating the number of polygons sampled in each combination of pre- and post-introduction land use and modern harvest activity (*Ecological Archives* E088-193-A1).

## APPENDIX B

Non-edaphic environmental variables: means for historical and modern land-use categories (*Ecological Archives* E088-193-A2).

## APPENDIX C

Edaphic variables: means for historical and modern land-use categories (*Ecological Archives* E088-193-A3).

## APPENDIX D

Principal component analysis of non-edaphic environmental variables: factor loading matrix (*Ecological Archives* E088-193-A4).

## APPENDIX E

Principal component analysis of edaphic variables: factor loading matrix (*Ecological Archives* E088-193-A5).

## APPENDIX F

Multiple regression of disturbance variables and environmental principal components vs. *Berberis thunbergii* occurrence (*Ecological Archives* E088-193-A6).

## APPENDIX G

Multiple regression of disturbance variables and environmental principal components vs. *Berberis thunbergii* log-abundance (*Ecological Archives* E088-193-A7).