Windows of Opportunity: Historical and Ecological Perspectives on Plant Invasions

A thesis presented by

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Abstract

Attempts to determine the characteristics of habitats that render them invasible to non-native species have met with limited success. One possible explanation for this shortcoming may be that by focusing on modern biotic and abiotic conditions, most studies fail to 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. Despite the recognized importance of historical factors in controlling many native species distributions, few studies have incorporated historical landscape changes into models of invasive species distribution and abundance. I explore the possibility that the current distribution of invasive species may reflect legacies of historical land use despite nearly a century of forest succession and subsequent disturbances. I surveyed 159 currently forested sites for the occurrence and abundance of *Berberis thunbergii* (Japanese barberry), a problematic non-native shrub in Northeastern forests, relative to two distinct periods of historical land use, modern forest harvesting activity, and environmental and edaphic characteristics. *Berberis thunbergii* occurred more frequently and was more abundant in sites historically cleared for agriculture than in historically wooded sites. This relationship was strongest for areas in agriculture in the early 20th century when *B. thunbergii* was already established in the region. While land-use history is confounded with soil fertility and distance to putative seed sources, I suggest that the strong relationship between modern distribution and prior land use reflects historical colonization of abandoned agricultural lands and persistence through subsequent reforestation. Contrary to my expectations, recent forest harvesting did not influence the occurrence or abundance of *B. thunbergii* at the landscape scale. Multiple regressions indicate that historical land use and distance to putative seed sources are the strongest predictors of *B. thunbergii* abundance, while occurrence patterns are best described by edaphic characteristics. My results indicate that habitat invasibility must be considered in the context of changing landscape conditions. In particular, 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 and edaphic conditions. A thorough understanding of the factors that influence species distributions may become increasingly important as future environmental and landscape changes permit both native and non-native species to enter new habitats more frequently.

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Introduction

In a world undergoing dramatic human-induced environmental change, an understanding of the factors constraining the distribution of plant species is increasingly important. Whereas species migrations into new regions and ecosystems as a result of climate change have been well-documented in the paleoecological record, little is known about the factors controlling distributional patterns at local and landscape scales once species have migrated (Jacobson 1979, Delcourt and Delcourt 1988, Davis et al. 1998, Davis and Shaw 2001). Species are entering novel habitats at an unprecedented rate as a direct result of human activity. The spread of non-native species in their introduced ranges presents a unique opportunity to understand controls on species establishment and spread in novel environments.

Invasion by exotic species is widely recognized as one of the most serious threats to biodiversity (Clout 1995, Vitousek et al. 1997a, Mooney and Hobbs 2000, Sala et al. 2000). Globally, few ecosystems remain unthreatened by non-native biota (Vitousek et al. 1997b). However, at the landscape scale, non-native species are rarely ubiquitous, in part because habitats vary substantially in their susceptibility to invasion (Elton 1958, Crawley 1987, Ramakrishnan and Vitousek 1989, Levine and D'Antonio 1999, Lonsdale 1999, Davis et al. 2000). A range of factors are thought to influence the invasion process including: vegetation composition and structure, resource availability, disturbance regime, intrinsic properties of the invading species, and the number of individuals introduced to the novel environment (Elton 1958, Fox and Fox 1986, Swincer 1986, Ramakrishnan and Vitousek 1989, Hobbs and Huenneke 1992, Deferrari and Naiman

1994, Prieur-Richard et al. 2000, Von Holle and Simberloff 2005). However, studies investigating the factors that render habitats susceptible to invasion have yielded conflicting results (Davis et al. 2000, Smith et al. 2004). I suggest that an understanding of habitat invasibility must assess changing landscape and disturbance conditions over time scales that are relevant to the history and process of invasion for individual species. Although the process of invasion may span decades or centuries from the time of initial introduction, most studies investigate invasive species and invasibility in the context of the modern landscape. Few studies evaluate processes such as: timing of species introduction, past disturbance, or changing landscape setting (Aragon and Morales 2003, Lugo and Helmer 2004, Lundgren et al. 2004), despite the recognized importance of historical factors in controlling modern community composition and the distribution of many native plant species (Peterken and Game 1984, Matlack 1994a, Motzkin et al. 1996, Motzkin et al. 1999a, Donohue et al. 2000, Bellemare et al. 2002, Verheyen et al. 2003). I explore the possibility that past land use may be an important determinant of modern patterns of invasive species distribution and abundance.

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 through the middle of the 20th century (Hall et al. 2002). Similar intensities and scales of anthropogenic disturbance have been noted elsewhere in the world (Birks et al. 1988, Gomez-Pompa and Kaus 1992, Foster et al. 1999, Grove and Rackham 2001, Turner et al. 2003). Despite over a century of successional change, forest maturation, and recent harvesting, the legacies of this agricultural past continue to influence the modern forested landscape. In the Northeastern U.S., currently forested areas that were previously cleared for agriculture remain compositionally and biogeochemically distinct from adjacent areas that were continuously forested (Motzkin et al. 1996, 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, edaphic or biotic characteristics that favor non-native species.

The first hypothesis suggests that current patterns of invasion are influenced by ephemeral biotic and abiotic conditions at or anytime after an exotic species becomes locally established. Historical disturbances can influence native plant community composition by creating opportunities for the establishment of new species or reducing populations of established species (Motzkin et al. 1999b). Species with low colonization capabilities may be absent from a site for decades or centuries following disturbance simply because they have not had sufficient time or local propagules to recolonize (Donohue et al. 2000, Verheyen et al. 2003). Thus, current species distribution patterns may be a result of dispersal or establishment limitations after disturbance rather than historically or currently inhospitable site conditions. Conversely, species capable of dispersing to, germinating on and growing rapidly in disturbed, open habitats are typically well represented in newly redeveloping forests (Peterken and Game 1984, Matlack 1994b, Bossuyt et al. 1999, Vellend 2003, Verheyen and Hermy 2004). As the majority of invasive plant species thrive in disturbed habitats (Elton 1958, Baker 1986, Orians 1986, Crawley 1989), those present during the period of agricultural abandonment would have likely capitalized on the opportunity to establish on relatively open sites. Since most invasive plants in southern New England were initially introduced for horticulture (Rehder and Tucker 1936, Reichard and Hamilton 1997, Mack and Lonsdale 2001, Reichard and White 2001), their cultivation in yards and residential areas would have likely facilitated subsequent spread to adjoining agricultural fields. Thus, the influences of historical land use may depend upon the interaction of two factors: the timing of regional introduction and landscape conditions thereafter (**Figure 1**). If the historical process of agricultural abandonment and reforestation are important, I 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 influenced by current site conditions. Current patterns of environmental variation may reflect intrinsic differences in initial site characteristics or historical site modifications (Glitzenstein et al. 1990, Foster 1992, Bratton and Miller 1994). 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, often influence habitat invasibility (Hobbs 1989, Huenneke et al. 1990, Pysek and Pysek 1995, Cassidy et al. 2004), suggesting that non-native species may preferentially invade enriched former agricultural sites.

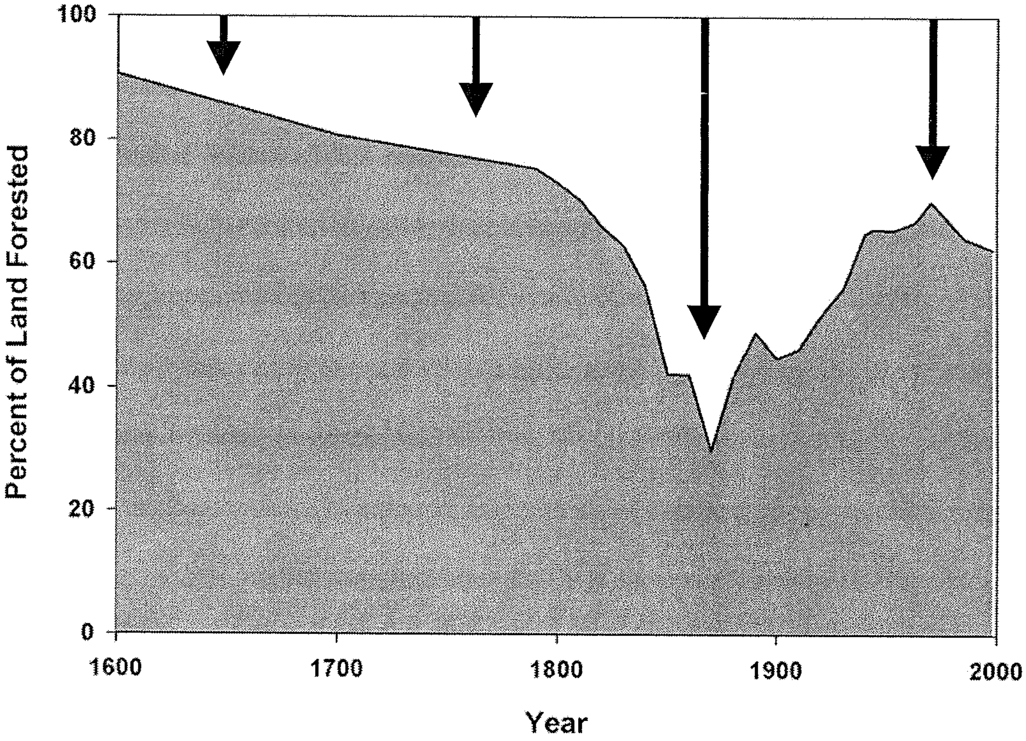


Figure 1. Forest change in Massachusetts from 1600 to 1998 with arrows indicating hypothetical non-native species introductions. Landscape conditions at or anytime after initial exotic species introduction may potentially influence establishment and subsequent spread. Modified from Foster (1995).

It should be noted that 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 enhanced site quality (Wiser et al. 1998, Aragon and Morales 2003, Barton et al. 2004, Foxcroft et al. 2004). In addition, the factors influencing initial invasive species establishment and spread may differ from those influencing secondary dispersal and spread (Wiser et al. 1998). Therefore, historical disturbances have the potential to influence habitat invasibility at various stages of invasion via different mechanisms.

In order to address these hypotheses and elucidate their underlying mechanisms, I evaluated the modern distribution and abundance of Japanese barberry (*Berberis thunbergii* DC), a woody invasive shrub, relative to landscape conditions pre- and post-species introduction, and environmental and edaphic variation. By relating modern distribution patterns to pre- and post- introduction landscape conditions and modern resource gradients, I assessed the extent to which *B. thunbergii* utilized the window of agricultural abandonment for establishment. I then compared the influences of historical land use with those of modern forest harvesting, a widespread, moderate-intensity disturbance prevalent on the landscape today. This not only allowed for a comparison of different disturbance types, intensities and times, but also enabled me to determine whether the influences of historical land use persist through subsequent disturbances. Finally, *B. thunbergii* distribution and abundance was modeled as a function of disturbance, environmental and edaphic variables to determine the set of factors best describing current patterns of invasion.

Specific questions addressed in this study include: (1) Do patterns of historical land use influence modern *B. thunbergii* distribution and abundance? (2) What is the influence of disturbance type and timing relative to the timing of introduction on current *B. thunbergii* distribution and abundance? (3) Which disturbance, environmental and edaphic variables best predict modern *B. thunbergii* distribution and abundance?

Methods

Study area

This study was conducted on the Quabbin Reservation's Prescott Peninsula (~5000 ha) located in central Massachusetts (Lat. 42°23'N, Long. 72°21'W) approximately 100 km west of Boston (**Figure 2**). The topography is characterized by rolling hills, with slopes rarely exceeding 30%. Soils are largely acidic sandy loams derived from glacial till, with smaller areas of outwash sands and organic muck (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% maintained as 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.

Ecology of Berberis thunbergii

Berberis thunbergii is a dense, spiny, perennial shrub native to central and southern Japan (Ohwi 1965). It can grow up to 2.4 m high and typically consists of numerous slender stems originating from the root collar, in addition to shoots arising from stolons and rhizomes within one to several decimeters of the root collar. Bee-pollinated flowers are produced from mid-April to May in the northeastern U.S., and numerous fleshy fruits, typically containing 1 to 2 seeds, mature during late summer and fall. Fruits typically persist on the shrub through the winter, presumably reflecting their low nutritional

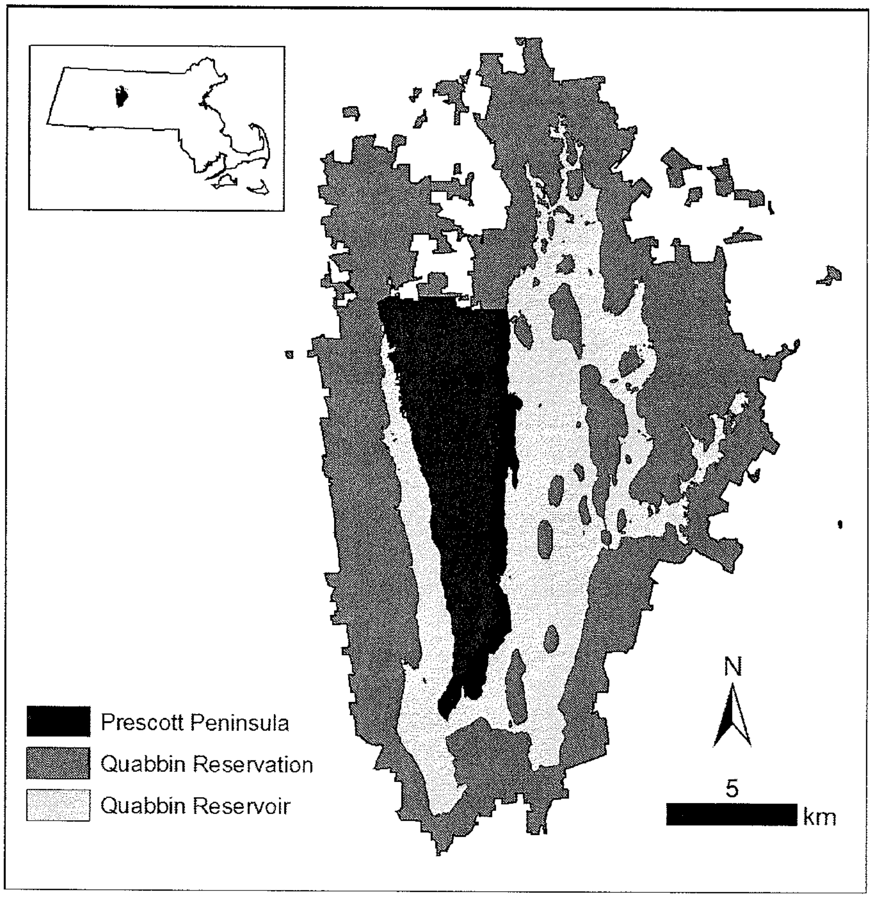


Figure 2. Location of the study area on the Prescott Peninsula within the Quabbin Reservation in north-central Massachusetts (see inset map).

content. Birds, deer, rabbits and rodents are known to feed on the fruits, although they typically do so only when other forage is scarce (Martin et al. 1951, Stiles 1980). While recruitment predominately occurs from seed (Ehrenfeld 1999), *B. thunbergii* also reproduces and spreads vegetatively via rhizomes and layering.

Established *B. thunbergii* shrubs may persist under dense canopies (< 1 – 2% full sun) and tolerate a wide range of soil moistures (< 10 to > 40% of bulk weight). Lack of adult plants in the driest and shadiest extremes probably reflects limitations on seedling establishment (Silander and Klepeis 1999). Once a plant is established and has at least three stems, it is subject to little or no mortality (Ehrenfeld 1999). 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). Seed dispersal is highly leptokurtic with 92% of seedlings occurring underneath or within 1 m of the canopy of a *B. thunbergii* shrub (Silander and Klepeis 1999). The ability of *B. thunbergii* to form dense thickets may partly be explained by positive density-dependent stem recruitment and a lack of density-dependent stem mortality (Ehrenfeld 1999). Cassidy et al. (2004) suggest that the distribution and abundance of *B. thunbergii* may be linked to nitrogen availability, with sites with higher rates of nitrification being more susceptible to *B. thunbergii* invasion.

History of Berberis thunbergii in the Northeastern U.S.

Silander and Klepeis (1999) compiled much of the historical background on *B. thunbergii* in the Northeastern U.S. *Berberis thunbergii* was first introduced as seed from

St. Petersburg, Russia to Boston's Arnold Arboretum in 1875 (Steffey 1985). Specimens were planted at the Arboretum a couple of years later and at the New York Botanic Garden in 1896 (Small 1935). By the late 1800's, *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 becoming naturalized in the region prior to 1910 (Silander and Klepeis 1999). By the 1920's, the United States Department of Agriculture (USDA) was promoting *B. thunbergii* in the major grain-growing areas of the Upper Midwest as an attractive substitute for common barberry (*Berberis vulgaris*), a widely planted European shrub found to be an alternate host of black stem wheat rust (*Puccinia graminis*) (Peterson 2003). *Berberis thunbergii* was likely planted around homesteads in Central Massachusetts by the 1920's. Since then, it has become a prominent understory species in many forests and natural areas across the region. It has only recently been recognized as seriously invasive and remains one of the most widely known and planted exotic shrubs in the United States (Steffey 1985, Weatherbee et al. 1998). Consequently, beginning in 2006, Massachusetts will follow New Hampshire in phasing out the importation and propagation of *B. thunbergii* over a 3-year period (http://www.mass.gov/agr/farmproducts/proposed_prohibited_plant_list.htm).

History and current management of the Prescott Peninsula

The Quabbin Reservoir Reservation (21450 ha) was created in 1939 to provide a drinking water supply for metropolitan Boston by damming and flooding the Swift River Valley and disincorporating the towns of Dana, Enfield, Greenwich and Prescott. All inhabitants within the Reservation were forced to relocate and their homes were either moved or bulldozed to the foundations. While the lowest elevations of these former towns were inundated with water, large portions of Prescott and Enfield remained above the waterline, isolated from the rest of the Reservation on a 17 km long peninsula. The history of the Quabbin region prior to the creation of the reservoir is typical of Massachusetts and much of the eastern U.S. By 1830, approximately 68% of the Peninsula was cleared for agriculture (**Figure 3a**) to support a population of 700-800 residents. Widespread abandonment of agricultural land in the second half of the 19th century left only 300 residents in Prescott by 1900 (Tougias 2002). By 1927, 60% of the Prescott Peninsula was covered by sproutland (young, regenerating forests) with only 21% remaining in agriculture (**Figure 3b**). While much of the surrounding landscape subsequently experienced substantial increases in residential and commercial development, the Prescott Peninsula has remained protected from development and closed to general public access since 1939. The Prescott Peninsula was originally set aside as a research area and is currently managed by the Massachusetts Department of Conservation and Recreation (DCR). Early forest management involved the reforestation of cropland and pastures with *Pinus resinosa*, *P. strobus* and *Picea abies* plantations and salvage logging in the aftermath of a major hurricane in 1938. In recent decades, management emphasis has shifted toward uneven-aged, mixed species silviculture. Patch, irregular shelterwood, and selection cuts are currently performed on a 20 to 30 year cycle to encourage structurally diverse forest development (Barten et al. 1998). 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 (**Figure 3c**).

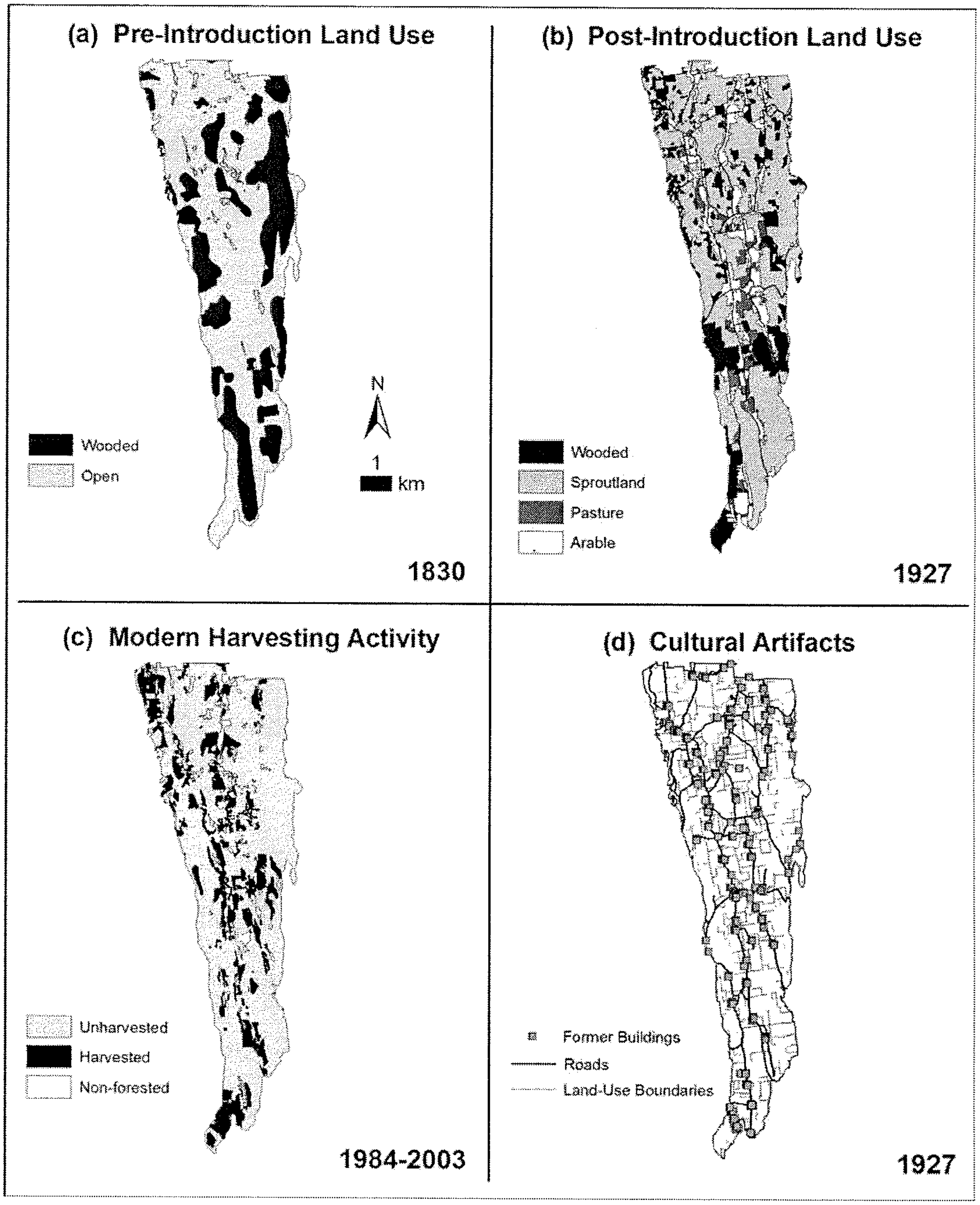


Figure 3. Maps of the Prescott Peninsula depicting land use prior to the introduction of *Berberis thunbergii* (1830) (a); post-introduction (1927) land use (b); modern land cover and harvesting activity (1984-2003) (c); and the distribution of buildings, roads, and land-use boundaries on the Prescott Peninsula in 1927 (d).

Site Selection

Currently forested areas were selected following a stratified random sampling design, with field sites stratified by pre-introduction (1830) land use, post-introduction (1927) land use, and recent harvesting activity (harvested versus unharvested since 1984). Pre-introduction land-cover data (open vs. wooded) were digitized from surveyed municipal maps from the 1830's (Hall et al. 2002). The 'open' category includes areas that were tilled, pastured, hayed or residential. Detailed 1927 real estate maps from the Quabbin Reservoir watershed were digitized to provide post-introduction land-cover data. In addition to classifying land use into arable, pasture, sproutland and woodland categories, these maps also indicate the location and type of buildings, roads and land-use boundaries (fences and walls). Forest harvests occurring within the study area from 1984 to 2003 were digitized based on information collected under the Massachusetts Forest Cutting Practices Act which requires submission of a Forest Cutting Plan (FCP) for any harvest greater than 87 m^3 (Kittredge et al. 2003, McDonald et al. 2006). This spatially explicit database contains information on the size of harvested areas and the species and volume of timber removed. I randomly sampled at least 9 polygons ≥ 0.5 ha in each of the 16 resulting strata (**Table 1**). Polygons dominated by hemlock (*Tsuga canadensis*) and *P. abies* 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 and edaphic characteristics. To characterize *B. thunbergii* distribution and

Table 1. Number of polygons sampled in each combination of pre- and post-introduction land use and modern harvest activity.

Pre-Introduction Land Use	Post-Introduction Land Use	Modern Harvesting Status	n
Wooded	Wooded	Unharvested	10
Wooded	Wooded	Harvested	9
Wooded	Sproutland	Unharvested	10
Wooded	Sproutland	Harvested	10
Wooded	Pasture	Unharvested	9
Wooded	Pasture	Harvested	10
Wooded	Arable	Unharvested	10
Wooded	Arable	Harvested	10
Open	Wooded	Unharvested	10
Open	Wooded	Harvested	10
Open	Sproutland	Unharvested	10
Open	Sproutland	Harvested	10
Open	Pasture	Unharvested	10
Open	Pasture	Harvested	11
Open	Arable	Unharvested	10
Open	Arable	Harvested	10

abundance within each polygon, 2 x 2 m plots, separated from each other and the polygon boundary by at least 20 m, were sampled along transect lines oriented based on polygon shape. The number of plots per polygon was proportional to polygon size (10 plots/ha). 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 total number of *B. thunbergii* stems was recorded. As percent frequency, percent cover and stem density (stems/m^2) were all highly correlated; they were combined into a synthetic measure of *B. thunbergii* abundance as follows:

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

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 transect plots, its presence was noted.

To characterize overstory vegetation and light conditions, I measured tree basal area and percent canopy cover in each polygon. Basal area was determined using an angle gauge (10 factor) and canopy cover was measured using a convex spherical densiometer in the southwest corner of transect plots.

I measured organic soil (O-horizon) depth and collected separate composite samples of organic and 0-15 cm mineral soil from five locations within each polygon. Mineral soils were sampled with a 5 cm x 15 cm cylindrical steel corer. In the laboratory, samples were air dried and sieved to < 2.0 mm. Both organic and mineral samples were analyzed for pH, percent organic matter, exchangeable Ca, Mg, K, Na, total exchange capacity, and Mehlich III extractable P, Mn, Zn, B, Cu, Fe and Al, at Brookside Laboratories in New Knoxville, OH. Mineral soils were also analyzed for sand, silt and clay content using a hydrometer (ASTM D422). Subsamples were ground to < 250 μm, oven dried at 80°C for 24 hours and sent to the University of Georgia's Analytical Chemistry Laboratory in Athens, GA for total C and N analysis. Since organic and mineral soil characteristics were significantly correlated, results are presented for mineral soils only (see **Appendices 1 & 2** for organic soil data).

Additional GIS Data

Mean distances to buildings, roads and land-use boundaries were calculated for each polygon using the 1927 land-use datalayer described above. A datalayer ranking soil drainage from 1 (excessively drained) to 5 (poor to very poorly drained), based on U.S. Soil Conservation classifications, was obtained from DCR. An area-weighted average was used to calculate mean soil drainage in each polygon. I calculated mean distance to streams using a MassGIS wetland datalayer (http://www.mass.gov/mgis/). A digital elevation model (DEM) with a 30 m horizontal resolution from the National Elevation Dataset (http://ned.usgs.gov/) was used to calculate slope and aspect using ArcView GIS 3.2 (Environmental Systems Research Institute 1999). Transformed radiative aspect (Roberts and Cooper 1989) was then calculated using the following formula:

$$TRASAP = \frac{\left(1-\cos\left(\frac{\pi}{180}\right)\right)*(aspect-30)}{2}$$

This formula transforms the circular aspect variable into a biologically relevant radiation index ranging from 0 to 1. N-NE oriented sites receiving lower incident radiation are assigned a value of zero while S-SW aspects exposed to higher incident radiation receive a value of one.

Data Analyses

Analyses were performed separately for: (1) *B. thunbergii* presence/absence in each polygon; and (2) the log-transformed abundance of *B. thunbergii* for those polygons where it was present in sample plots. Note that the log-abundance data contains fewer observations than the presence data, as it excludes those sites where *B. thunbergii* was absent or in very low abundance in the polygons and not recorded in my plots. By separately modeling the probability of presence and abundance when present, I am able to explore the possibility that different factors influence these two measures of invasion.

Effects of disturbance on Berberis thunbergii invasion

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 harvesting activity) was the single best predictor of *B. thunbergii* presence/absence and abundance. Prior to stepwise selection, I first fit a full model in order to test for significant interactions terms. G-tests of independence were used to test whether frequency of occurrence of *B. thunbergii* varied with the three main effects. Fixed effect one-way analysis of variance (ANOVA) tests were used to test for differences in mean abundance as a function of historical land use and harvesting. A posteriori comparisons of log-abundance data for post-introduction land use 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, I used logistic and linear regressions, respectively.

Relationships between disturbance, environmental and edaphic variables

The following environmental and edaphic variables had skewed distributions and were transformed to their natural logarithms: percent canopy cover; slope; distance to streams, buildings, roads, and land-use boundaries; percent organic matter (OM); total soil carbon (C) and nitrogen (N); C:N ratio; and concentrations of phosphorus (P), calcium (Ca), magnesium (Mg), potassium (K), percent base saturation (BSAT), boron (B), iron (Fe), manganese (Mn), copper (Cu), and zinc (Zn). Soluble sulfur (S) concentration was square-root transformed prior to analysis. Environmental and edaphic 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 environmental variables were separately ordinated using principal component analysis (PCA) (cf., Gotelli and Ellison 2004). I selected the first three edaphic principal axes and the first three environmental principal axes for use in multiple regression analyses. To ensure that assumptions of multicollinearity were met, I calculated correlations between environmental and edaphic principal axes prior to their inclusion in multiple regression analyses. Differences in principal axes among pre- and post-invasion land-use categories were tested using post-hoc Tukey-Kramer HSD tests. Prior these post-hoc comparisons, post-introduction arable and pasture land cover and sproutland and woodland land 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 investigate the key factors controlling *B. thunbergii* distribution and abundance, I modeled the occurrence and log-abundance of *B. thunbergii* as a function of anthropogenic disturbance, and environmental and edaphic variables. 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 (3 edaphic and 3 environmental). 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) which takes into account residual deviations and explicitly penalizes any superfluous parameters in a model (cf., Gotelli and Ellison 2004). All statistical analyses were performed using JMP 5.0.1.2 (SAS Institute 2003).

Inferential caveats

Several warnings are warranted. I have attempted to identify correlations between patterns of invasion and disturbance history or environmental and edaphic variation. However, significant correlations do not necessarily indicate causation or account for all possible mechanisms underlying these correlations. I model distribution and abundance of *B. thunbergii* as a function of numerous potentially important variables. This does not preclude the possibility that these variables may be surrogates for other unquantified factors. In addition, the large number of significance tests performed during my analyses increases the likelihood of reporting a few significant results simply due to chance. I have 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.

The Prescott Peninsula offers numerous advantages over other possible study areas but also has some anomalous features. The study area presents a unique opportunity to tease apart the relative influences of historical versus modern anthropogenic disturbances on patterns of *B. thunbergii* invasion because of its brief and finite history of *B. thunbergii* planting in the early 20th century, detailed pre- and post- introduction land-use maps, and lack of modern residential development. However, prohibition of hunting on the Prescott Peninsula from 1940 to 1991 led to dramatic increases in the deer population with densities reaching as high as 15 to 23 deer per km^2 in the late 1980's. Beginning in 1991, public hunting was reinstated in order to control the deer population. Deer are thought to contribute to the establishment and spread of *B. thunbergii* by dispersing seeds and selectively browsing native species. While deer may have contributed to the overall abundance of *B. thunbergii* on the Peninsula, it is unlikely that they would have influenced patterns of invasion relative to my sampling design. Despite the history of high deer densities and lack of modern development, this study provides insights that are relevant for many forest preserves and management areas in the eastern U.S.

Results

Influence of historical and modern disturbances

Of the three main effects tested, post-introduction land use was the single strongest predictor of *B. thunbergii* occurrence ($R^2 = 0.15$; $P < 0.001$). Sites used for agriculture (i.e. arable and pastureland) after *B. thunbergii* introduction are more likely to have *B. thunbergii* today than sites that were historically woodlands or sproutlands. *Berberis thunbergii* was found at 88% of early 20th century arable sites versus 36% of the historically wooded sites (**Figure 4b**). 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 cleared for agriculture in the early 19th century versus 58% of the wooded sites, but the difference was only marginally significant (**Figure 4a**). Recent harvesting did not influence *B. thunbergii* distribution with *B. thunbergii* occurring in 60% of harvested versus 70% of unharvested sites (**Figure 4c**). Similarly, harvest intensity (m^3/ha) and time since harvest were unimportant ($P = 0.72$ and $P = 0.25$, respectively).

Early 20th century land use was also the single strongest predictor of *B. thunbergii* abundance ($R^2 = 0.20$; $P < 0.001$). *Berberis thunbergii* was most abundant in early 20th century arable sites and least abundant in former sproutlands (**Figure 5b**). Although post-hoc comparisons indicated that arable and sproutland were the only significantly different land-use categories, the mean abundance of *B. thunbergii* was 3 times greater in arable sites than in sites that were wooded in the early 20th century. While pre-introduction land use had a marginal influence on *B. thunbergii* presence, the trend

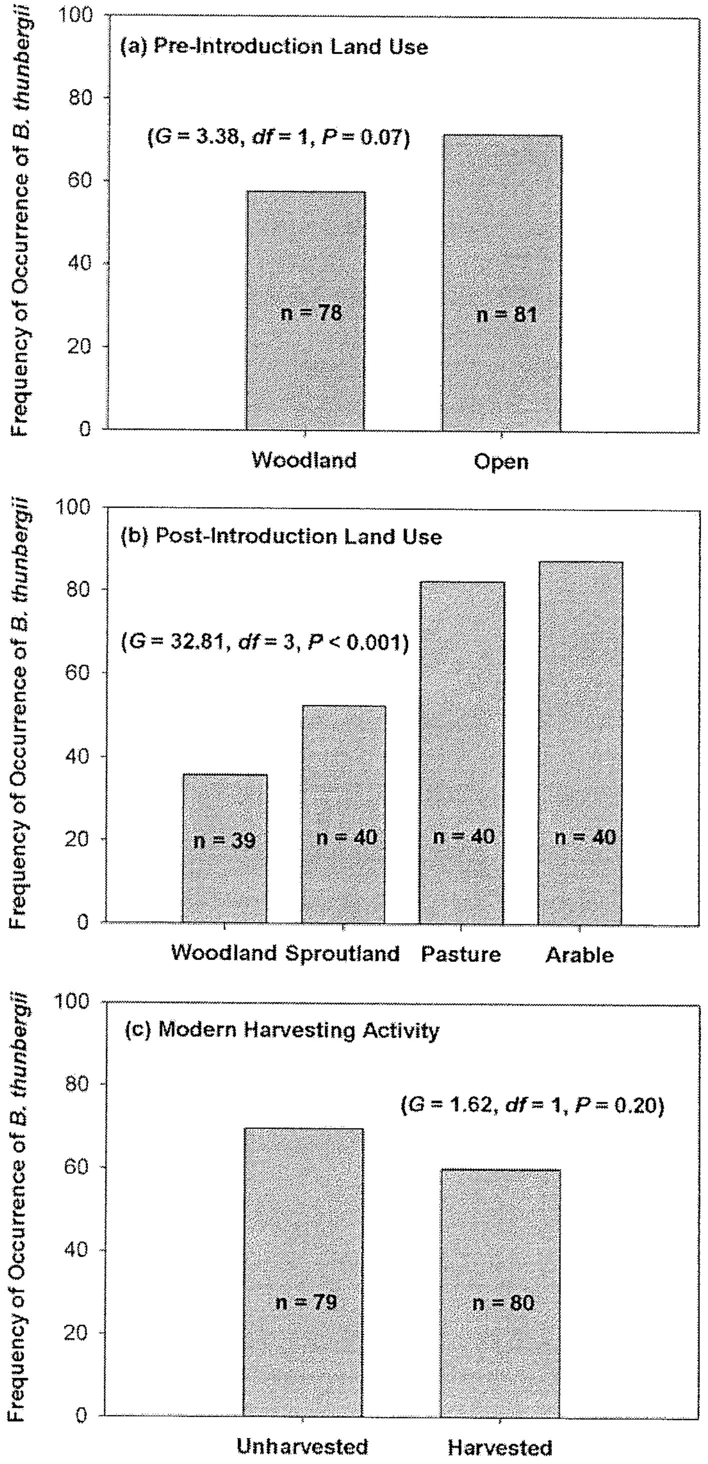


Figure 4. Frequency of occurrence of *Berberis thunbergii* relative to: (a) pre-introduction land use; (b) post-introduction land use; and (c) modern harvesting activity.

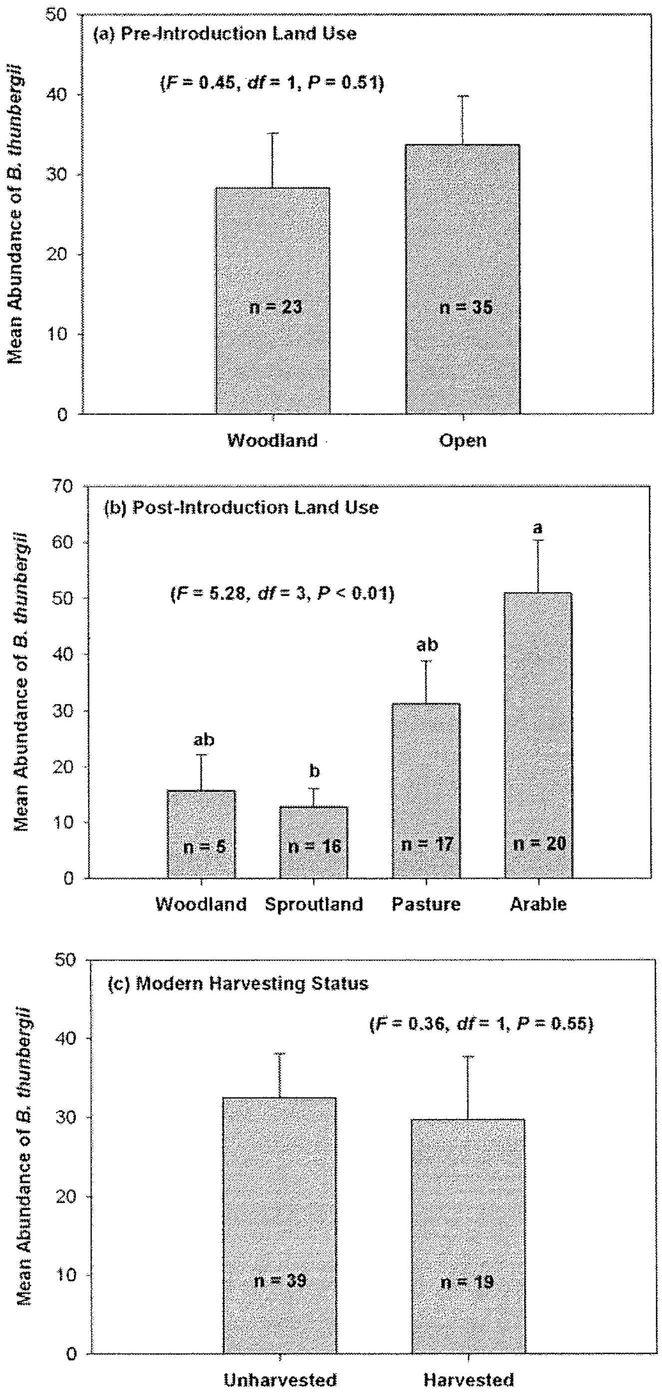


Figure 5. Mean *Berberis thunbergii* abundance relative to: (a) pre-introduction land use; (b) post-introduction land use; and (c) modern harvesting activity. Standard error bars are shown. Means with different letters are significantly different ($\alpha = 0.05$) according to Tukey-Kramer HSD pairwise comparisons.

towards higher abundance on sites that were open in the early 19th century was not significant (**Figure 5a**). Surprisingly, whether or not a site was harvested in the past 21 years did not influence *B. thunbergii* abundance (**Figure 5c**). Furthermore, harvest intensity and time since harvest had no discernable influence on *B. thunbergii* abundance ($P = 0.93$ and $P = 0.73$, respectively).

Interrelationships of disturbance, environmental and edaphic variables

Sites that were open in the early 19th century were generally flatter and were associated with lower incident radiation than wooded sites (**Table 2**). Pastures in the early 20th century had lower incident radiation and were closer to roads than woodlands. Early 20th century arable sites were closer to streams, buildings and roads than wooded sites. Harvested sites had less canopy cover and total basal area and were flatter and farther from streams than unharvested sites.

Overall, soils were remarkably similar among land-use categories. Soils on early 19th century agricultural sites were generally finer-textured and more moderately drained with higher pH, percent base saturation, percent nitrogen, and zinc concentrations than sites that were wooded (**Table 3**). Sites that were used for agriculture in the early 20th century had more poorly-drained and siltier soils with thinner organic layers, higher pH, percent base saturation and nitrogen, and lower percent 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 percent nitrogen, and lower pH,

Table 2. Environmental variables: means for historical and modern land-use categories. Abbreviations and units of measurement are as follows: % canopy cover, basal area (m^2/ha), slope (degrees), transformed radiative aspect (TRASAP), distance to streams, buildings, roads and land-use boundaries (LUB; [m]). Kruskal-Wallis statistics (*H*) followed by an * are significantly different at $P < 0.05$.

	Pre-Introduction Land Use			Post-Introduction Land Use					Modern Harvesting Activity		
	Wooded	Open	*H*	Wooded	Sproutland	Pasture	Arable	*H*	Unharvested	Harvested	*H*
Canopy	72.86	72.03	0.70	73.20	73.26	72.36	70.95	0.78	80.64	64.34	47.80*
Basal	27.87	28.20	0.00	28.20	29.53	26.91	27.51	1.35	33.60	22.55	54.89*
Slope	8.33	5.61	16.53*	7.96	7.09	6.55	6.20	7.04	7.83	6.08	5.73*
TRASAP	0.66	0.57	3.91*	0.72^{a}	0.66^{ab}	0.48^{b}	0.62^{ab}	11.70*	0.59	0.64	1.57
Streams	127.55	116.29	0.52	162.33^{a}	121.66^{ab}	109.53^{ab}	94.75^{b}	11.50*	108.4	135.05	6.73*
Buildings	319.67	316.55	0.48	405.00^{a}	373.33^{a}	313.69^{a}	182.48^{b}	37.93*	337.31	299.09	0.93
Roads	173.06	146.25	1.21	242.00^{a}	180.79^{ab}	120.98^{bc}	95.90^{c}	35.18*	163.59	155.27	0.21
LUB	85.09	67.32	2.15	88.30	90.31	63.79	62.04	5.69	71.85	80.16	0.20

Table 3. Edaphic variables: means for historical and modern land use categories. Abbreviations and units of measurement are as follows: organic depth (OD; [cm]), % organic matter (OM), total exchange capacity (TEC; [me/100g]), % base saturation (BSAT). Soil texture is measured in % sand, silt, clay. Soil drainage classes range from 1 (excessively drained) to 5 (poor to very poorly drained). Carbon and nitrogen are reported in percent of total soil. All other soil nutrients are in ppm. Kruskal-Wallis statistics (*H*) followed by an * are significantly different at $P < 0.05$. Means with different letters are significantly different ($\alpha = 0.05$) according to Tukey-Kramer pairwise comparisions.

	Pre-Introduction Land Use			Post-Introduction Land Use					Modern Harvesting Activity		
	Wooded	Open	*H*	Wooded	Sproutland	Pasture	Arable	*H*	Unharvested	Harvested	*H*
Sand	56.55	54.12	4.13*	57.86	55.00	53.84	54.61	4.05	55.71	54.92	1.80
Silt	34.69	40.70	29.56*	34.28^{b}	36.97^{ab}	40.89^{a}	38.79^{ab}	12.61*	37.38	38.13	1.20
Clay	8.75	5.18	27.43*	7.85^{a}	8.03^{a}	5.27^{b}	6.60^{ab}	10.83*	6.91	6.95	0.02
OD	3.41	3.51	0.68	3.94^{a}	3.71^{a}	3.36^{ab}	2.85^{b}	25.62*	3.38	3.54	0.44
Drainage	2.61	2.93	5.70*	2.24^{c}	2.62^{bc}	3.00^{ab}	3.20^{a}	29.48*	2.91	2.63	3.09
OM	32.17	31.46	2.62	33.86	35.33	30.22	27.89	6.34	31.04	32.57	2.79
TEC	6.69	7.21	0.00	6.47	7.14	6.82	7.37	2.79	6.96	6.95	0.00
pH	4.65	4.73	4.60*	4.59^{b}	4.66^{ab}	4.74^{ab}	4.79^{a}	16.69*	4.73	4.65	6.35*
BSAT	37.31	38.50	4.25*	34.65^{b}	37.67^{ab}	38.55^{a}	40.68^{a}	14.77*	38.79	37.05	8.00*
C:N	19.51	18.63	0.97	22.48^{a}	20.15^{b}	17.38^{c}	16.32^{c}	57.85*	18.31	19.80	4.41*
C	4.47	4.86	1.97	4.73^{ab}	5.09^{a}	4.81^{ab}	4.05^{b}	10.42*	4.85	4.49	2.16
N	0.24	0.27	5.04*	0.22^{b}	0.26^{ab}	0.28^{a}	0.25^{ab}	10.65*	0.27	0.24	5.34*
Ca	347.70	374.16	0.34	300.35	372.09	356.30	413.86	4.12	369.18	353.31	0.25
Mg	53.97	59.12	3.08	49.45	55.63	58.39	62.66	4.93	57.85	55.35	2.44
K	53.48	55.06	2.56	54.05	53.99	53.08	56.03	5.71	57.31	51.28	7.09*
Na	13.50	13.80	0.23	13.99	13.61	13.19	13.84	1.53	13.63	13.67	0.76
S	33.88	35.68	1.01	34.92	34.94	35.21	34.13	1.55	34.71	34.89	5.50*
P	29.41	31.01	0.24	26.73^{b}	26.36^{b}	33.36^{a}	34.33^{a}	23.35*	30.92	29.53	0.64
B	0.38	0.39	1.25	0.39^{b}	0.37^{ab}	0.38^{a}	0.40^{a}	8.61*	0.38	0.39	2.94
Fe	116.57	120.22	1.08	135.66^{a}	121.61^{ab}	109.49^{bc}	107.63^{c}	8.82*	114.60	122.25	2.04
Mn	23.55	23.52	0.63	20.77^{b}	22.21^{ab}	25.15^{ab}	25.93^{a}	11.03*	22.30	24.77	0.38
Al	954.77	990.62	1.66	958.95	969.46	1003.61	959.81	3.78	987.78	958.50	0.06
Cu	1.16	1.10	2.37	0.93^{b}	1.09^{b}	1.07^{b}	1.42^{a}	21.48*	1.21	1.05	2.02
Zn	3.46	3.69	6.76*	3.21	3.42	3.76	3.92	3.33	3.65	3.52	1.27

percent base saturation, potassium and soluble sulfur concentrations than unharvested sites.

Interrelationships of principal components and disturbance variables

I selected the first three principal axes from the separate ordinations of environmental and edaphic variables for use in stepwise multiple regressions to determine the best predictors of *B. thunbergii* occurrence and abundance. Environmental axis 1, constructed mainly from distance to buildings, roads and land-use boundaries, was named 'seed sources' (**Table 4**). Environmental axis 2 ('overstory') was constructed mainly from canopy cover and total basal area, which were positively correlated ($r = 0.62$; $P < 0.001$). Environmental axis 3, primarily loaded by slope, aspect and distance to streams, was named 'topography'. Areas that were further from streams tended to have steeper slopes and received lower incident radiation. See **Appendix 3** for correlations among environmental variables.

Edaphic axis 1 ('soil nutrients') was constructed primarily from macronutrients including nitrogen, magnesium and potassium (**Table 5**). Edaphic axis 2 ('soil chemistry') 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 percent sand and silt, which were negatively correlated ($r = -0.87$; $P < 0.001$). See **Appendix 4** for correlations among edaphic variables.

Several of the environmental and edaphic principal components were moderately correlated. 'Seed sources' was negatively correlated with 'soil nutrients' ($r = -0.33$; $P < 0.001$) and positively correlated with 'soil chemistry' ($r = 0.32$; $P < 0.001$). 'Overstory'

Table 4. Principal component analysis of environmental variables: factor loading matrix. Primary loading factors are shown in bold.

Parameter	Axis 1 'Seed Sources'	Axis 2 'Overstory'	Axis 3 'Topography'
Canopy Cover	0.13	**0.64**	-0.04
Basal Area	0.13	**0.61**	-0.28
Slope	0.16	0.36	**0.40**
Aspect	0.28	-0.20	**-0.56**
Distance to Streams	0.24	-0.10	**0.64**
Distance to Buildings	**0.48**	0.04	0.02
Distance to Roads	**0.57**	-0.12	-0.14
Distance to Land-Use Boundaries	**0.50**	-0.18	0.09

Table 5. Principal component analysis of edaphic variables: factor loading matrix. Abbreviations are as follows: organic depth (OD), % organic matter (OM), total exchange capacity (TEC), and % base saturation (BSAT). Primary loading factors are shown in bold.

Parameter	Axis 1 'Soil Nutrients'	Axis 2 'Soil Chemistry'	Axis 3 'Soil Texture'
% Sand	-0.10	0.11	**0.45**
% Silt	0.13	-0.15	**-0.42**
% Clay	-0.08	0.11	0.05
OD	-0.16	0.26	-0.12
Soil Drainage	0.17	-0.28	-0.05
OM	0.28	0.24	-0.28
TEC	0.24	0.22	0.21
pH	0.02	**-0.40**	-0.05
BSAT	0.02	**-0.41**	-0.05
C:N	-0.25	0.29	0.02
C	0.25	0.27	-0.28
N	**0.35**	0.08	-0.26
Ca	0.27	0.11	0.23
Mg	**0.35**	0.01	0.20
K	**0.31**	0.02	0.02
Na	0.19	0.12	0.19
S	-0.16	0.10	-0.13
P	-0.02	-0.15	0.19
B	0.07	0.02	0.10
Fe	-0.01	0.34	0.08
Mn	0.25	-0.13	0.26
Al	0.06	0.10	-0.23
Cu	0.21	0.04	0.07
Zn	0.24	-0.10	0.10

was positively correlated with 'soil nutrients' ($r = 0.19$; $P < 0.05$) and negatively correlated with 'soil chemistry'($r = -0.19$; $P < 0.05$). Sites that were cleared for agriculture in the early 20th century were significantly closer to 'seed sources' and had less acidic 'soil chemistry' 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

Multiple regression analysis indicated that edaphic characteristics ('soil chemistry' and 'soil nutrients') were the best overall predictors of *B. thunbergii* occurrence ($R^2 = 0.42$; **Table 6**). 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 environmental axes in the model of *B. thunbergii* occurrence. The strongest predictors of *B. thunbergii* abundance were 'seed sources' and post-introduction land use ($R^2 = 0.40$; **Table 7**). Adding edaphic characteristics ('soil nutrients' and 'soil chemistry') modestly increased the accuracy of the model ($R^2 = 0.49$).

Table 6. Multiple regression of disturbance, and environmental and edaphic principal components vs. *Berberis thunbergii* occurrence.

	df	X^2	P	Coefficient
Occurrence ($R^2 = 0.43$)				
Model	3	84.98	< 0.001	
Intercept			< 0.001	-1.38
'Soil Chemistry'	1	27.37	< 0.001	1.02
'Soil Nutrients'	1	26.46	< 0.001	-0.85
'Soil Texture'	1	1.48	0.22	-0.19

Table 7. Multiple regression of disturbance, environmental and edaphic variables vs. *Berberis thunbergii* abundance.

	df	F	P	Coefficient
Abundance ($R^2 = 0.49$)				
Model	4	12.71	< 0.001	
Intercept			< 0.001	2.35
'Seed Sources'	1	11.44	< 0.01	-0.38
Post-Introduction Land Use	1	6.38	0.01	-0.35
'Soil Nutrients'	1	9.18	< 0.01	0.18
'Soil Chemistry'	1	1.62	0.21	-0.10

Discussion

Influences of historical land use

The historical clearing of more than 50% of the Massachusetts landscape for agriculture in the mid-19th century (Hall et al. 2002) represents a widespread and intense disturbance. Similarly, much of the eastern United States has been modified by over 300 years of human land-use activities that have dramatically altered the composition, structure and function of most ecosystems (Foster 1992). Such historical activities exert persistent influences on modern species distributions by directly altering environmental and edaphic characteristics (Compton et al. 1998, Compton and Boone 2000) and by affecting the likelihood that species will persist or become established on sites with differing histories (Myster and Pickett 1990, Donohue et al. 2000, Verheyen et al. 2003). Despite considerable concern about invasive species and substantial research emphasis on understanding habitat invasibility, the potential influence of historical factors in determining patterns of invasive species distribution and spread has not been well studied. In particular, no studies have explicitly examined the effects of changing landscape conditions throughout the invasion process on modern distribution and abundance patterns of exotic species. *Berberis thunbergii* occurred more frequently and at greater abundance in areas previously cleared for agriculture, indicating that legacies of historical land use persist for many decades following agricultural abandonment and natural forest redevelopment.

Importance of the timing of disturbance

While historical land use influences modern occurrence and abundance patterns of *B. thunbergii*, the strength of the relationship varies depending on the timing of the agricultural disturbance relative to invasive 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 of *B. thunbergii* largely reflect: (1) historical establishment in abandoned agricultural fields at or anytime after local introduction, and/or (2) modern environmental (e.g. distance to potential seed sources) and edaphic differences between pre- and post-introduction agricultural sites. In order to differentiate between these two factors, I assessed the potential importance of current environmental and edaphic variation between sites that were 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, Glitzenstein et al. 1990, Motzkin et al. 1996, Koerner et al. 1997, Compton and Boone 2000, Eberhardt et al. 2003), I documented two potentially important differences between pre- and post-introduction agricultural sites. Sites cleared for agriculture in the 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. While current disparities in soil alkalinity between 19th and 20th century agricultural sites are minimal (pH of 4.73 vs. 4.77, respectively) and therefore unlikely to account for the apparent contrast in *B. thunbergii* establishment and spread, differences in proximity to putative seed sources (e.g. roads; 146.25 m vs. 108.44 m, respectively) cannot be readily discounted. In order to assess the importance of potential seed source distance relative to agricultural disturbance, I compared *B. thunbergii* occurrence in 19th and 20th century agricultural sites at comparable distances from buildings, roads and land-use boundaries. Even when I 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; $P = 0.01$). Therefore, current patterns of invasion are not adequately explained by modern edaphic variation associated with historical modifications or initial site conditions and cannot be fully attributed to the proximity of putative seed sources.

I conclude that modern *B. thunbergii* distribution and abundance patterns largely reflect spread from initial plantings, which was facilitated by their proximity to abandoned agricultural fields. Since *B. thunbergii* vigor is enhanced under high light conditions (Silander and Klepeis 1999), it is likely that secondary establishment and growth would have been favored in the initial years following agricultural abandonment. Therefore, had *B. thunbergii* been planted more commonly adjacent to wooded areas, it is likely that secondary establishment and spread would have been reduced.

Relative influence of disturbance types

Statewide, selective harvesting is the most important ongoing anthropogenic disturbance to forests, with ~20% of forests having been harvested since 1984 (Kittredge et al. 2003, McDonald et al. 2006). While not as intense or extensive a disturbance as historical agriculture, harvesting is thought to promote the invasion of many species through direct dispersal of propagules on machinery, soil scarification, removal of litter cover and increasing light availability (Silveri et al. 2001). Both aboveground biomass and fruit production of *B. thunbergii* are positively correlated with light intensity (Silander and Klepeis 1999). I therefore anticipated increases in frequency and abundance of *B. thunbergii* following harvesting that would be evident in landscape-level distribution patterns. Several studies have documented such patterns relative to logging activity for other non-native species (Scherer et al. 2000, Silveri et al. 2001, Brown and Gurevitch 2004). It was therefore surprising that harvesting had no discernable impact on landscape-level *B. thunbergii* occurrence or abundance patterns. If fact, there were very weak trends for reduced frequency and abundance following harvesting. A study of black cherry (*Prunus serotina*) in Belgium, where it is an invasive tree, found that the species occurred at lower densities in logged areas, perhaps as a result of competition with densely regenerating native vegetation (Godefroid et al. 2005). After harvesting, dense populations of hay-scented fern (*Dennstaedtia punctilobula*) and raspberries (*Rubus spp.*) may interfere with *B. thunbergii*'s seedling recruitment. *Dennstaedtia punctilobula*, in particular, is considered a native invasive species within the study area and has been shown to inhibit tree seedling regeneration (de la Cretaz and Kelty 1999, de la Cretaz and Kelty 2002). Fecundity of established *B. thunbergii* populations might also be reduced as a result of accidental or intentional perturbation by harvesting machinery, although it is unclear to what extent this occurs within the study area. Despite dramatic effects on overstory composition and structure, forest harvesting does not appear to strongly influence *B. thunbergii* distribution and abundance patterns. These results suggest that selective harvesting, using logging practices that mitigate soil disturbance, may simply not result in sufficiently severe disturbance to alter patterns of *B. thunbergii* invasion across the landscape.

Predictors of Berberis thunbergii invasion

Separate models of *B. thunbergii* occurrence and abundance suggest that these two measures of invasion are influenced by different sets of factors. Even though historical land use and soil fertility were not independent, multiple regressions showed that, all else being equal, 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 in productive, nutrient-rich sites (Huenneke et al. 1990, Pysek and Pysek 1995, Wiser et al. 1998, Stohlgren et al. 1999). Although *B. thunbergii* occurrence was correlated with post-introduction land use, current distribution patterns were more strongly predicted by edaphic conditions. While soil fertility also influenced *B. thunbergii* abundance, it explained a relatively small amount of the observed variability. Distance to potential seed sources and post-introduction land use were significantly better predictors of abundance. *Berberis thunbergii* was most abundant in areas both cleared for agriculture in the early 20th century and close to putative primary and secondary seed sources. This suggests that population density may be a function of both age and historical site disturbance. Other studies have found a relationship between invasive species abundance and distance to primary seed sources (Wiser et al. 1998, Foxcroft et al. 2004) and disturbances (Hobbs and Huenneke 1992, Deferrari and Naiman 1994, Williamson and Harrison 2002).

Invasion ecology of Berberis thunbergii

While interpretation of historical land-use patterns does not allow me to predict where invasions will occur in the future, it allows me to differentiate between probable invasion mechanisms. The densest populations of *Berberis thunbergii* appear to have developed through a combination of open site conditions and seed availability. 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 through subsequent forest canopy development. Sexual reproduction is greatest under high light conditions but also occurs to a lesser extent under low light conditions (Silander and Klepeis 1999). My results suggest that patterns of invasion result in part from differences in invasibility between old-fields and forests. However, while invasions in historical woodlands are less frequent and sparser than invasions in former agricultural areas, *B. thunbergii* occurred in nearly 36% of the sites that were wooded in the early 20th century. Since these occurrences cannot be attributed to historical plantings or agricultural disturbance, they represent *B. thunbergii*'s invasion into wooded sites over the past century. Therefore, even in the absence of agricultural disturbances, *B. thunbergii* is slowly dispersing across the landscape (Ehrenfeld 1997).

Conclusions

My data support the hypothesis that historical land use influences some plant invasions, in part by creating a 'window of opportunity' in which a locally present invasive species can establish. Modern distribution and abundance patterns of *B. thunbergii* reflect historical establishment and spread in abandoned agricultural fields. Other studies have similarly recognized the importance of both disturbance and seed availability as key determinants of habitat invasibility (Deferrari and Naiman 1994, Wiser et al. 1998, Williamson and Harrison 2002, Aragon and Morales 2003, Foxcroft et al. 2004, Von Holle and Simberloff 2005). Disturbance-generated gaps in the absence of propagule availability do not ensure invasive establishment and subsequent spread (Johnstone 1986). My results suggest that habitat invasibility is not a permanent attribute, but a condition that can vary 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 pulse in resource availability for both locally present native and non-native species. 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, my results suggest that absolute time since disturbance is not as important as disturbance timing relative to propagule availability. Such a historical perspective on biological invasions may resolve some of the conflicting and ambiguous results of previous invasibility studies and provide insight into long-term invasion processes. An understanding of the factors constraining the distribution and spread of non-native invasive plant species is essential for efficiently predicting and managing biological invasions. Knowledge of both site and species histories proved important for identifying potentially invaded sites within my study area. If we neglect to acknowledge landscape history, we limit our ability to interpret modern invasion patterns. In this study, the influences of historical land use on modern plant invasions have persisted for nearly a century despite subsequent natural and anthropogenic disturbances. Similar patterns presumably exist across the region, although they are likely more difficult to interpret in increasingly more urban conditions. Therefore, given the availability of non-native propagules on the landscape today, it is likely that current land use will effect the course of biological invasions for years to come.

While exotic species are commonly singled-out from native flora and fauna, an understanding of the factors constraining their establishment and spread is increasingly relevant to interpreting all species distributions. Species frequently enter new landscapes following the removal of pre-existing barriers to their dispersal, establishment, growth or reproduction (Johnstone 1986). As modern environmental conditions change in response to natural processes and human activities, both native and exotic species will likely enter novel habitats more frequently. I conclude that current and future species distributions must be interpreted in the context of dynamic landscape conditions.

Literature Cited

Aragon, R., and J. M. Morales. 2003. Species composition and invasion in NW Argentinian secondary forests: effects of land use history, environment and landscape. Journal of Vegetation Science **14**:195-204.

Baker, H. G. 1986. Patterns of plant invasion in North America. Pages 44-57 *in* H. A. Mooney and J. A. Drake, editors. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Barten, P. K., T. Kyker-Snowman, P. J. Lyons, T. Mahlstedt, R. O'Connor, and B. A. Spencer. 1998. Massachusetts: managing a watershed protection forest. Journal of Forestry **96**:10-15.

Bellemare, J., G. Motzkin, and D. R. Foster. 2002. Legacies of the agricultural past in the forested present: an assessment of historical land-use effects on rich mesic forests. Journal of Biogeography **29**:1401-1420.

Birks, H. H., H. J. Birks, P. E. Kaland, and D. Moe, editors. 1988. The Cultural Landscape: Past, Present, and Future. Cambridge University Press, Cambridge.

Bossuyt, B., M. Hermy, and J. Deckers. 1999. Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. Journal of Ecology **87**:628-638.

Bratton, S. P., and S. G. Miller. 1994. Historic field systems and the structure of maritime oak forests, Cumberland Island National Seashore, Georgia. Bulletin of The Torrey Botanical Club **121**:1-12.

Brown, K. A., and J. Gurevitch. 2004. Long-term impacts of logging on forest diversity in Madagascar. Proceedings of the National Academy of Sciences of the United States of America **101**:6045-6049.

Cassidy, T. M., J. H. Fownes, and R. A. Harrington. 2004. Nitrogen limits an invasive perennial shrub in forest understory. Biological Invasions **6**:113-121.

Clout, M. 1995. Introduced species: the greatest threat to global biodiversity. Species **24**:34-36.

Compton, J. E., and R. D. Boone. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology **81**:2314-2330.

Compton, J. E., R. D. Boone, G. Motzkin, and D. R. Foster. 1998. Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: role of vegetation and land-use history. Oecologia **116**:536-542.

Crawley, M. 1987. What makes a community invasible? *in* A. Gray, M. Crawley, and P. Edwards, editors. Colonization, Succession, and Stability. Blackwell Scientific, London.

Crawley, M. J. 1989. Chance and timing in biological invasions. Pages 407-423 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions: A Global Perspective (Scope 37). John Wiley & Sons Ltd, New York.

Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. Journal of Ecology **88**:528-534.

Davis, M. B., R. R. Calcote, S. Sugita, and H. Takahara. 1998. Patchy invasion and the origin of a hemlock-hardwoods forest mosaic. Ecology **79**:2641-2659.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science **292**:673-679.

de la Cretaz, A. L., and M. J. Kelty. 1999. Establishment and control of hay-scented fern: a native invasive species. Biological Invasions **1**:223-236.

de la Cretaz, A. L., and M. J. Kelty. 2002. Development of tree regeneration in fern-dominated forest understories after reduction of deer browsing. Restoration Ecology **10**:416-426.

Deferrari, C. M., and R. J. Naiman. 1994. A multiscale assessment of the occurrence of exotic plants on the Olympic Peninsula, Washington. Journal of Vegetation Science **5**:247-258.

Delcourt, H. R., and P. A. Delcourt. 1988. Quaternary landscape ecology: relevant scales in space and time. Landscape Ecology **2**:23-44.

Donohue, K., D. R. Foster, and G. Motzkin. 2000. Effects of the past and the present on species distribution: land-use history and demography of wintergreen. Journal of Ecology **88**:303-316.

Eberhardt, R. W., D. R. Foster, G. Motzkin, and B. Hall. 2003. Conservation of changing landscapes: vegetation and land-use history of Cape Cod National Seashore. Ecological Applications **13**:68-84.

Ehrenfeld, J. G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC). Journal of the Torrey Botanical Society **124**:210-215.

Ehrenfeld, J. G. 1999. Structure and dynamics of populations of Japanese barberry (*Berberis thunbergii* DC.) in deciduous forests of New Jersey. Biological Invasions **1**:203-213.

Elton, C. S. 1958. The Ecology of Invasions by Animals and Plants. Methuen and Company Ltd., London.

Fike, J., and W. A. Niering. 1999. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. Journal of Vegetation Science **10**:483-492.

Foster, D. R. 1992. Land-use history (1730-1990) and vegetation dynamics in central New-England, USA. Journal of Ecology **80**:753-772.

Foster, D. R. 1995. Land-use history and four hundred years of vegetation change in New England. Pages 253-319 *in* B. L. Turner, editor. Principles, Patterns and Processes of Land Use Change: Some Legacies of the Columbian Encounter. SCOPE Publication. John Wiley & Sons Ltd, New York.

Foster, D. R., M. Fluet, and E. R. Boose. 1999. Human or natural disturbance: landscape-scale dynamics of the tropical forests of Puerto Rico. Ecological Applications **9**:555-572.

Fox, M. D., and B. J. Fox. 1986. The susceptibility of natural communities to invasion. Pages 57-66 *in* R. H. Groves and J. J. Burdon, editors. Ecology of Biological Invasions. Cambridge University Press, New York.

Foxcroft, L. C., M. Rouget, D. M. Richardson, and S. Mac Fadyen. 2004. Reconstructing 50 years of *Opuntia stricta* invasion in the Kruger National Park, South Africa: environmental determinants and propagule pressure. Diversity and Distributions **10**:427-437.

Glitzenstein, J. S., C. D. Canham, M. J. McDonnell, and D. R. Streng. 1990. Effects of environment and land-use history on upland forests of the Cary Arboretum, Hudson Valley, New York. Bulletin of The Torrey Botanical Club **117**:106-122.

Godefroid, S., S. S. Phartyal, G. Weyembergh, and N. Koedam. 2005. Ecological factors controlling the abundance of non-native invasive black cherry (*Prunus serotina*) in deciduous forest understory in Belgium. Forest Ecology and Management **210**:91-105.

Gomez-Pompa, A., and A. Kaus. 1992. Taming the wilderness myth. Bioscience **42**:271-279.

Gotelli, N. J., and A. M. Ellison. 2004. A Primer of Ecological Statistics. Sinauer Associates, Inc., Sunderland.

Grove, A. T., and O. Rackham. 2001. The Nature of Mediterranean Europe: An Ecological History. Yale University Press, New Haven.

Hall, B., G. Motzkin, D. R. Foster, M. Syfert, and J. Burk. 2002. Three hundred years of forest and land-use change in Massachusetts, USA. Journal of Biogeography **29**:1319-1335.

Hobbs, R. J. 1989. The nature and effect of disturbance relative to invasions. Pages 389-405 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions: A Global Perspective (Scope 37). John Wiley & Sons Ltd, New York.

Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: implications for conservation. Conservation Biology **6**:324-337.

Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology **71**:478-491.

Jacobson, G. L. 1979. Paleoecology of white pine (*Pinus strobus*) in Minnesota. Journal of Ecology **67**:697-726.

Johnstone, I. M. 1986. Plant invasion windows: a time-based classification of invasion potential. Biological Reviews of the Cambridge Philosophical Society **61**:369-394.

Kittredge, D. B., A. O. Finley, and D. R. Foster. 2003. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. Forest Ecology and Management **180**:425-442.

Koerner, W., J. L. Dupouey, E. Dambrine, and M. Benoit. 1997. Influence of past land use on the vegetation and soils of present day forest in the Vosges mountains, France. Journal of Ecology **85**:351-358.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos **87**:15-26.

Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. Ecology **80**:1522-1536.

Lugo, A. E., and E. Helmer. 2004. Emerging forests on abandoned land: Puerto Rico's new forests. Forest Ecology and Management **190**:145-161.

Lundgren, M. R., C. J. Small, and G. D. Dreyer. 2004. Influence of land use and site characteristics on invasive plant abundance in the Quinebaug Highlands of southern New England. Northeastern Naturalist **11**:313-332.

Mack, R. N., and W. M. Lonsdale. 2001. Humans as global plant dispersers: getting more than we bargained for. Bioscience **51**:95-102.

Martin, A., H. S. Zim, and A. L. Nelson. 1951. A guide to wildlife food habits. Dover Publications, New York, NY.

Matlack, G. 1994a. Plant demography, land-use history, and the commercial use of forests. Conservation Biology **8**:298-299.

Matlack, G. R. 1994b. Plant species migration in a mixed-history forest landscape in eastern North America. Ecology **75**:1491-1502.

McDonald, R. I., G. Motzkin, M. S. Bank, D. B. Kittredge, J. Burk, and D. R. Foster. 2006. Forest harvesting and land-use conversion over two decades in Massachusetts. Forest Ecology and Management **227**:31-41.

Meiners, S. J., S. T. A. Pickett, and M. L. Cadenasso. 2002. Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography **25**:215-223.

Mooney, H. A., and R. J. Hobbs. 2000. Invasive Species in a Changing World. Island Press, Washington, D.C.

Motzkin, G., D. Foster, A. Allen, J. Harrod, and R. Boone. 1996. Controlling site to evaluate history: vegetation patterns of a New England sand plain. Ecological Monographs **66**:345-365.

Motzkin, G., W. A. Patterson, and D. R. Foster. 1999a. A historical perspective on pitch pine-scrub oak communities in the Connecticut Valley of Massachusetts. Ecosystems **2**:255-273.

Motzkin, G., P. Wilson, D. R. Foster, and A. Allen. 1999b. Vegetation patterns in heterogeneous landscapes: the importance of history and environment. Journal of Vegetation Science **10**:903-920.

Myster, R. W., and S. T. A. Pickett. 1990. Initial conditions, history and successional pathways in 10 contrasting old fields. American Midland Naturalist **124**:231-238.

Ohwi, J. 1965. Flora of Japan. Smithsonian Institution, Washington, DC.

Orians, G. H. 1986. Site characteristics favoring invasions. Pages 133-148 *in* H. A. Mooney and J. A. Drake, editors. Ecology of Biological Invasions of North America and Hawaii. Springer-Verlag, New York.

Peterken, G. F., and M. Game. 1984. Historical factors affecting the number and distribution of vascular plant species in the woodlands of central Lincolnshire. Journal of Ecology **72**:155-182.

Peterson, P. D. 2003. The common barberry: the past and present situation in Minnesota and the risk of wheat stem rust epidemics. PhD dissertation. North Carolina State University, Raleigh.

Prieur-Richard, A. H., S. Lavorel, K. Grigulis, and A. Dos Santos. 2000. Plant community diversity and invasibility by exotics: invasion of Mediterranean old fields by *Conyza bonariensis* and *Conyza canadensis*. Ecology Letters **3**:412-422.

Pysek, P., and A. Pysek. 1995. Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. Journal of Vegetation Science **6**:711-718.

Ramakrishnan, P. S., and P. M. Vitousek. 1989. Ecosystem-level processes and the consequences of biological invasions. Pages 369-388 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological Invasions: A Global Perspective (Scope 37). John Wiley & Sons Ltd, New York.

Rehder, A., and E. M. Tucker. 1936. On the history of the introduction of woody plants into North America. National Horticultural Magazine **October**:245-257.

Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. Conservation Biology **11**:193-203.

Reichard, S. H., and P. White. 2001. Horticulture as a pathway of invasive plant introductions in the United States. Bioscience **51**:103-113.

Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution **43**:223-225.

Roberts, D. W., and S. V. Cooper. 1989. Concepts and techniques of vegetation mapping. Pages 90-96 *in* Land Classifications Based on Vegetation: Applications for Resource Management. USDA Forest Service General Techinical Report INT-257, Ogden, UT.

Sala, O. E., F. S. Chapin, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff, M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global biodiversity scenarios for the year 2100. Science **287**:1770-1774.

Sargent, C. S. 1889. New or little known plants: *Berberis thunbergii*. Garden and Forest **2**:52.

Scherer, G., D. Zabowski, B. Java, and R. Everett. 2000. Timber harvesting residue treatment. Part II. Understory vegetation response. Forest Ecology and Management **126**:35-50.

Silander, J. A., and D. M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. Biological Invasions **1**:189-201.

Silveri, A., P. Dunwiddie, and H. Michaels. 2001. Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. Biological Invasions **3**:379-389.

Small, J. 1935. Asiatic immigrants in the botanical gardens-I. Journal of New York Botanical Gardens **36**:73-74.

Smith, M. D., J. C. Wilcox, T. Kelly, and A. K. Knapp. 2004. Dominance not richness determines invasibility of tallgrass prairie. Oikos **106**:253-262.

Steffey, J. 1985. Strange relatives: the barberry family. American Horticulturist **64**:4-9.

Stiles, E. W. 1980. Patterns of fruit presentation and seed dispersal in bird-disseminated woody plants in the eastern deciduous forest. American Naturalist **116**:670-688.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. Ecological Monographs **69**:25-46.

Swincer, D. E. 1986. Physical characteristics of sites in relation to invasions. Pages 67-76 *in* R. H. Groves and J. J. Burdon, editors. Ecology of Biological Invasions. Cambridge University Press, Cambridge.

Tougias, M. 2002. Quabbin: a history and explorers guide, 1st edition. On Cape Publications, Yarmouth, MA.

Turner, B. L., J. Geoghegan, and D. Foster, editors. 2003. Final Frontiers: Integrated Land Change Science and Tropical Deforestation in Southern Yucatan. Oxford University Press, Oxford.

Vellend, M. 2003. Habitat loss inhibits recovery of plant diversity as forests regrow. Ecology **84**:1158-1164.

Verheyen, K., and M. Hermy. 2004. Recruitment and growth of herb-layer species with different colonizing capacities in ancient and recent forests. Journal of Vegetation Science **15**:125-134.

Verheyen, K., O. Honnay, G. Motzkin, M. Hermy, and D. R. Foster. 2003. Response of forest plant species to land-use change: a life-history trait-based approach. Journal of Ecology **91**:563-577.

Vitousek, P. M., C. M. D'antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997a. Introduced species: a significant component of human-induced global change. New Zealand Journal of Ecology **21**:1-16.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997b. Human domination of earth's ecosystems. Science **277**:494-499.

Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. Ecology **86**:3212-3218.

Weatherbee, P. B., P. Somers, and T. Simmons. 1998. A guide to invasive plants in Massachusetts. Massachusetts Division of Fisheries and Wildlife.

Westveld, M., R. I. Ashman, H. I. Baldwin, R. P. Holdsworth, R. S. Johnson, J. H. Lambert, H. J. Lutz, L. Swain, and M. Standish. 1956. Natural forest vegetation zones of New England. Journal of Forestry **54**:332-338.

Williamson, J., and S. Harrison. 2002. Biotic and abiotic limits to the spread of exotic revegetation species. Ecological Applications **12**:40-51.

Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. Ecology **79**:2071-2081.

Appendix 1. Correlations among organic (rows) and mineral (columns) soil variables: $|r| > 0.15$ are significant at $P < 0.05$. Abbreviations are: % organic matter (OM), total exchange capacity (TEC), % base saturation (BSAT).

	lnN	lnC	lnC:N	lnOM	TEC	pH	lnBSAT	Sqrt S	lnP	lnCa	lnMg	lnK	Na	lnB	lnFe	lnMn	Al	lnCu	lnZn
N	0.12																		
C	-0.08	0.09																	
C:N	-0.32	-0.21	0.28																
OM	-0.06	0.18	0.41	0.17															
TEC	0.21	0.06	-0.30	0.13	0.16														
pH	0.27	0.06	-0.41	0.13	0.05	0.32													
lnBSAT	0.27	0.06	-0.41	0.13	0.06	0.31	0.30												
lnS	0.23	0.06	0.34	0.11	0.11	0.06	0.05	-0.23											
lnP	0.19	-0.01	-0.37	0.03	0.03	0.02	0.02	-0.13	0.39										
lnCa	0.31	0.07	-0.47	0.14	0.19	0.17	0.17	-0.27	0.05	0.28									
lnMg	0.37	0.11	-0.51	0.21	0.15	0.15	0.16	-0.23	-0.02	0.20	0.39								
lnK	0.11	0.05	-0.14	0.11	-0.02	0.11	0.12	-0.16	-0.01	-0.02	-0.01	0.17							
Na	0.09	0.05	-0.09	0.05	-0.04	0.09	0.09	-0.12	-0.05	-0.02	0.08	-0.12	0.07						
lnB	0.00	0.04	0.06	0.01	0.00	-0.02	-0.02	-0.08	0.02	-0.01	0.05	-0.05	0.03	-0.01					
lnFe	0.05	-0.06	-0.20	-0.03	0.05	0.03	0.03	-0.31	0.03	0.10	0.07	0.01	-0.02	-0.16	-0.28				
lnMn	0.02	-0.09	-0.19	-0.09	0.09	0.01	0.01	-0.01	0.17	0.11	0.07	-0.01	0.05	0.04	-0.09	0.53			
Al	0.19	0.01	-0.35	0.03	0.07	0.17	0.14	-0.37	0.11	0.17	0.15	0.14	0.07	-0.21	-0.49	0.30	0.06		
lnCu	0.32	0.20	-0.27	0.24	0.21	-0.03	-0.04	-0.34	-0.04	0.25	0.23	0.28	0.12	-0.11	-0.25	0.23	0.13	0.35	
lnZn	0.04	-0.05	-0.15	0.02	-0.02	0.23	0.23	0.01	0.04	0.03	-0.03	0.10	-0.13	-0.08	-0.20	0.11	0.13	0.11	0.32

Appendix 2. Organic soil variables: means for historical and modern land use categories. Abbreviations and units of measurement are as follows: % organic matter (OM), total exchange capacity (TEC; [me/100g]), % base saturation (BSAT). Carbon and nitrogen are reported in percent of total soil. All other soil nutrients are in ppm. Kruskal-Wallis statistics (*H*) followed by an * are significantly different at $P < 0.05$. Means with different letters are significantly different ($\alpha = 0.05$) according to Tukey-Kramer pairwise comparisions.

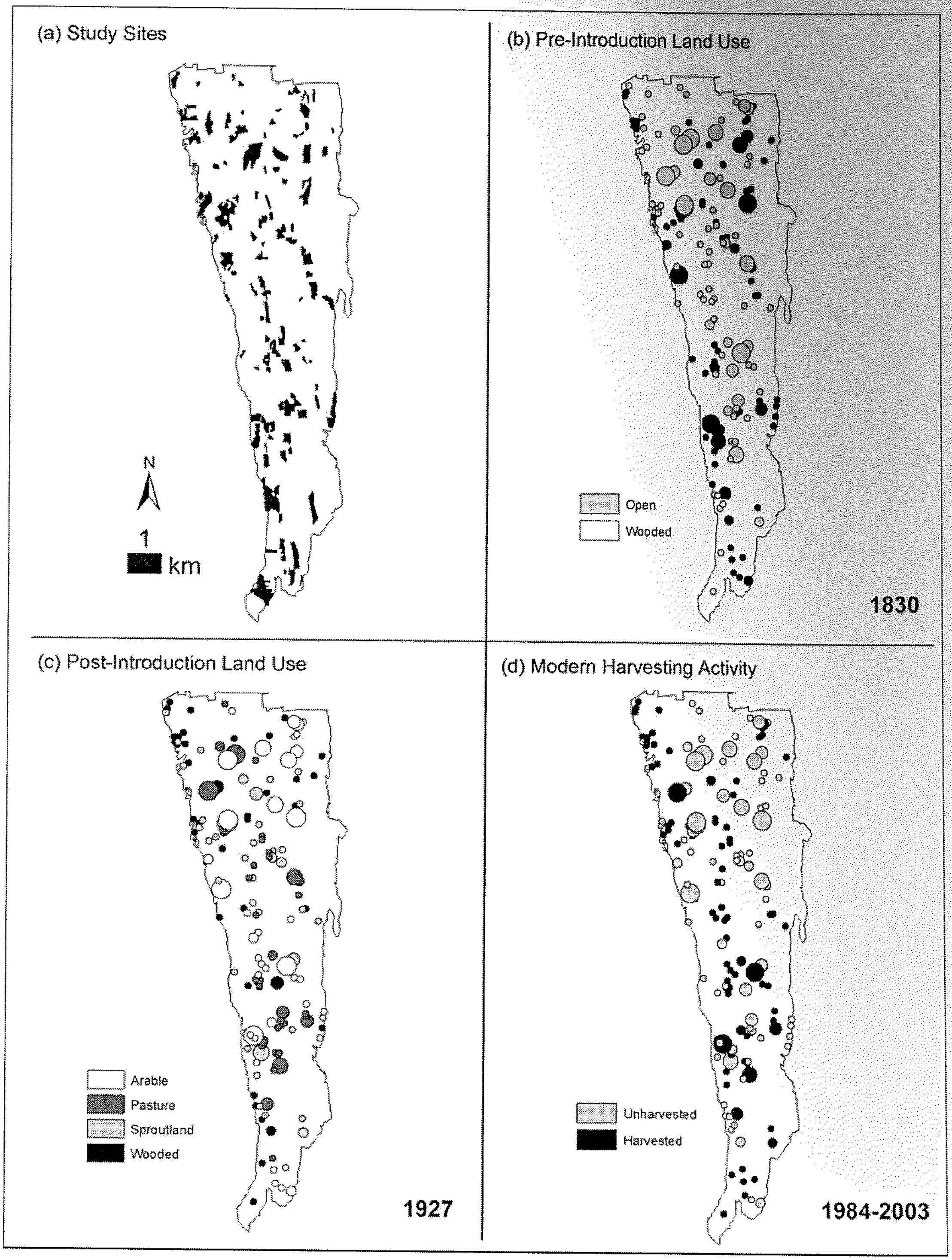
	Pre-Introduction Land Use			Post-Introduction Land Use					Modern Harvesting Activity		
	Wooded	Open	*H*	Wooded	Sproutland	Pasture	Arable	*H*	Unharvested	Harvested	*H*
OM	56.62	54.96	0.51	61^{a}	61.44^{a}	53.28^{ab}	47.68^{b}	17.23*	53.20	58.30	3.37
TEC	8.54	9.87	8.78*	8.37^{b}	8.73^{ab}	9.86^{a}	9.86^{a}	10.20*	8.79	9.63	4.17*
pH	4.33	4.30	0.44	4.18^{b}	4.33^{a}	4.34^{a}	4.42^{a}	20.19*	4.37	4.27	4.67*
BSAT	32.93	32.39	0.29	29.8^{b}	32.91^{a}	33.05^{a}	34.73^{a}	19.42*	33.69	31.65	4.42*
C:N	20.42	20.36	0.09	20.83	20.35	20.35	20.06	0.85	20.11	20.67	1.10
C	27.84	28.64	0.42	29.58	29.66	27.75	26.08	5.80	26.81	29.63	4.05*
N	1.37	1.42	0.80	1.42	1.48	1.37	1.31	4.86	1.33	1.45	3.34
Ca	388.45	447.19	4.13*	323.55^{c}	389.8^{bc}	467.8^{ab}	486.88^{a}	25.91*	401.86	434.11	1.25
Mg	73.31	80.65	4.66*	65.68^{b}	75.08^{ab}	81.45^{a}	85.33^{a}	18.89*	77.49	76.58	0.31
K	76.37	75.89	0.01	78.53	75.80	72.25	78.05	2.21	79.53	72.81	5.30*
Na	12.95	13.55	3.47	13.66	13.30	12.80	13.28	4.49	13.29	13.21	0.00
S	21.68	24.10	4.76*	22.63	22.80	23.30	22.88	1.37	23.90	21.94	5.38*
P	30.10	32.90	1.66	29.71	29.03	33.03	34.23	6.77	31.95	31.10	2.43
B	0.33	0.36	1.38	0.40	0.33	0.32	0.34	6.43	0.34	0.35	2.88
Fe	91.35	98.36	0.57	94.68	93.48	94.00	97.43	0.30	97.81	92.06	0.74
Mn	40.36	39.61	0.07	37.21	38.10	41.08	43.40	3.10	35.27	44.58	4.97*
Al	391.94	447.60	2.43	373.05	402.70	468.45	433.93	5.40	451.23	389.79	2.68
Cu	0.93	0.82	0.70	0.74	0.88	0.82	1.05	5.42	1.00	0.74	3.43
Zn	5.09	5.27	0.50	4.77	4.96	5.38	5.59	0.91	5.21	5.15	0.17

Appendix 3. Correlations among environmental variables: $|r| > 0.15$ are significant at $P < 0.05$. Abbreviations are as follows: transformed radiative aspect (TRASAP), distance to streams, buildings, roads and land-use boundaries (LUB).

	Canopy Cover	Basal Area	Slope	TRASAP	Streams	Buildings	Roads	LUB
Canopy Cover	1.00							
Basal Area	0.62	1.00						
Slope	0.28	0.17	1.00					
TRASAP	-0.10	0.01	-0.08	1.00				
Streams	0.01	-0.14	0.13	-0.08	1.00			
Buildings	0.09	0.12	0.17	0.17	0.14	1.00		
Roads	0.06	0.06	0.01	0.37	0.21	0.44	1.00	
LUB	-0.05	-0.04	0.07	0.16	0.21	0.36	0.56	1.00

Appendix 4. Correlations among edaphic variables. $|r| > 0.15$ are significant at $P < 0.05$. Abbreviations are as follows: organic depth (OD), % organic matter (OM), total exchange capacity (TEC), % base saturation (BSAT).

	Sand	Silt	Clay	OD	Drainage	lnOM	TEC	pH	lnBSAT	lnC:N	lnC	lnN	lnCa	lnMg	lnK	Na	lnS	lnP	lnB	lnFe	lnMn	Al	lnCu	lnZn
Sand	1.00																							
Silt	-0.87	1.00																						
Clay	-0.06	-0.44	1.00																					
OD	-0.03	-0.02	0.10	1.00																				
Drainage	-0.24	0.25	-0.06	-0.28	1.00																			
OM	-0.31	0.25	0.04	0.04	0.04	1.00																		
TEC	0.15	-0.12	-0.03	0.01	0.00	0.25	1.00																	
pH	-0.07	0.16	-0.18	-0.23	0.28	-0.18	-0.23	1.00																
lnBSAT	-0.08	0.17	-0.20	-0.24	0.29	-0.19	-0.24	0.99	1.00															
lnC:N	0.26	-0.28	0.11	0.45	-0.51	-0.08	-0.06	-0.21	-0.21	1.00														
lnC	-0.21	0.20	-0.03	0.09	-0.01	0.89	0.22	-0.16	-0.17	0.02	1.00													
lnN	-0.32	0.32	-0.08	-0.15	0.27	0.81	0.22	-0.02	-0.03	-0.51	0.85	1.00												
lnCa	0.16	-0.11	-0.07	-0.12	0.06	0.21	0.93	-0.02	-0.03	-0.16	0.19	0.24	1.00											
lnMg	0.05	0.03	-0.14	-0.30	0.28	0.34	0.47	0.05	0.05	-0.36	0.27	0.42	0.52	1.00										
lnK	-0.13	0.16	-0.09	-0.15	0.20	0.43	0.34	0.07	0.08	-0.23	0.39	0.45	0.37	0.55	1.00									
Na	0.16	-0.10	-0.09	-0.09	-0.02	0.18	0.39	-0.12	-0.13	-0.13	0.16	0.20	0.35	0.58	0.12	1.00								
lnS	-0.09	0.08	0.00	0.33	-0.18	-0.14	-0.07	-0.12	-0.10	0.21	-0.14	-0.22	-0.17	-0.30	-0.15	-0.10	1.00							
lnP	0.11	-0.05	-0.10	0.01	0.13	-0.29	-0.04	0.09	0.09	-0.20	-0.29	-0.13	-0.04	-0.03	0.05	-0.04	0.14	1.00						
lnB	0.05	-0.06	0.02	0.00	0.06	0.06	0.03	-0.02	-0.02	-0.07	0.04	0.07	0.03	0.22	0.10	-0.10	0.14	0.21	1.00					
lnFe	0.20	-0.17	-0.03	0.38	-0.29	0.23	0.12	-0.34	-0.34	0.49	0.29	-0.01	-0.01	0.11	0.13	0.08	0.11	-0.01	0.27	1.00				
lnMn	0.13	-0.08	-0.06	-0.46	0.19	0.05	0.24	0.06	0.05	-0.49	0.03	0.28	0.31	0.50	0.39	0.26	-0.31	0.25	0.13	-0.11	1.00			
Al	-0.13	0.15	-0.08	0.01	-0.12	0.29	0.27	-0.04	-0.05	-0.07	0.28	0.27	0.25	-0.11	-0.03	0.05	0.35	-0.20	-0.14	-0.29	-0.13	1.00		
lnCu	-0.14	0.13	-0.01	-0.03	0.11	0.18	0.23	-0.14	-0.14	-0.28	0.14	0.27	0.23	0.36	0.30	0.12	-0.03	0.22	0.25	0.13	0.20	-0.08	1.00	
lnZn	-0.14	0.21	-0.17	-0.23	0.21	0.16	0.22	0.10	0.09	-0.28	0.02	0.16	0.29	0.45	0.42	0.11	-0.28	0.04	0.23	-0.02	0.34	-0.08	0.40	1.00



Appendix 5. Maps of the Prescott Peninsula indicating the location of study sites (a), and the distribution and abundance of *B. thunbergii* relative to: pre-introduction (1830) land use (b); post-introduction (1927) land use (c); and modern harvesting activity (1984-2003) (d).