Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species[1]

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McDonald, R. I. (Graduate School of Design, Harvard University, Cambridge, MA 02138), G. Motzkin and D. R. Foster (Harvard Forest, Harvard University, Petersham, MA 01366). Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. J. Torrey Bot. Soc. 135: 260–271. 2008.—Despite concern over potential detrimental effects of non-native invasive species on human and natural systems, the factors controlling regional distributions of invasive species remain unresolved. Few studies have evaluated the influence of both environmental factors and disturbance history on invasive species distributions, or assessed synthetically the importance of landscape-level disturbances like historical land-use, forest harvesting, and contemporary forest fragmentation. We analyzed vegetation, soils, and recent and historical land-use and landscape context for forests across central and western Massachusetts to identify controls on invasive species distributions. Almost half (49.3%) of 148 randomly selected sites had at least one non-native invasive plant present, and invasive species occurred more frequently on former agricultural sites than in continuous woodlands. We used logistic regression to model the probability of finding the four most common species: Japanese barberry (*Berberis thunbergii* DC), glossy buckthorn (*Rhamnus frangula* L.), multiflora rose (*Rosa multiflora* Thunb. ex Murr.), and oriental bittersweet (*Celastrus orbiculata* Thunb.). Soil richness was the most important predictor of invasive presence, with rich soils (i.e., lower C:N) being more likely to have these species. The structure of the current forested landscape (i.e., the amount of forest within a 10 km buffer around a site) is also important, with sites that are surrounded by more forest being less likely to have invasives. After accounting for variation in C:N ratios and the structure of the current forested landscape, historical land-use was not a significant predictor of non-native species occurrence; however, C:N ratios may be influenced by historical land-use and by current vegetation, thus complicating interpretations of this edaphic variable. Recent forest harvesting increased the likelihood of invasive occurrence for some but not all species. Overall, our results suggest that regional patterns of invasive plant distributions result from a complex function of edaphic conditions, and present and historical land-uses.

Key words: *Berberis thunbergii*, *Celastrus orbiculata*, disturbance, edge effects, forest management, glossy buckthorn, invasive plant species, Japanese barberry, land-use legacies, Massachusetts, multiflora rose, oriental bittersweet, *Rhamnus frangula*, *Rosa multiflora*.

Non-native invasive plants may exert significant negative impacts on human and natural systems, making it critical to understand the factors that control the distribution of these species (Sakai et al. 2001, With 2002, Levine et al. 2004). Previous studies have identified the importance of environmental factors (e.g., light, soil nutrients, etc.) and disturbance, including relatively recent land-use changes (e.g., Verheyen et al. 2003), in controlling the establishment and spread of invasive plants (Hobbs and Huenneke 1992, Lonsdale 1999, Lugo and Helmer 2004). A substantial body of evidence suggests that historical land-use practices, sometimes centuries past, strongly affect the modern distributions of many native plant species (Foster and Aber 2004). However, few studies have evaluated historical land-use influences on invasive species distributions. In this paper, we present an analysis of the common non-native invasive plant species of central and western Massachusetts forests (USA) to determine the relative importance of historical land-use, modern land-use, and edaphic conditions in controlling the distribution of invasives. Few studies of invasives have been conducted at

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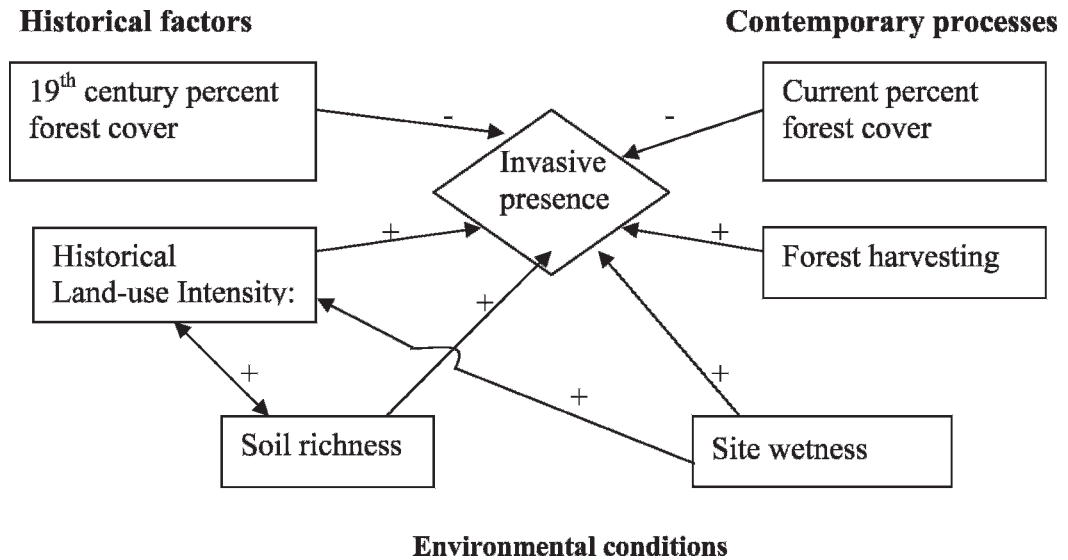
Fig. 1. Hypothesized relationship of environmental conditions, historical factors, and contemporary processes to invasive plant species presence in western Massachusetts. See text for an explanation of each factor, and the sign of its relationship to invasive presence. Note that soil richness and site wetness may directly affect invasives, and may also affect invasives through differences in historical land-use intensity among sites with different soils.

this landscape scale (Forman 1995), as opposed to site-specific (e.g., Battles et al. 2001) or continental analyses (e.g., Stohlgren et al. 1999), with some notable exceptions (e.g., Deutschewitz et al. 2003, Chytry et al. 2005). We present baseline data on the distribution of invasives in the region and model their distribution. Our overall hypothesis is that the pattern of historical land-use continues to affect invasive species distributions, modulated by environmental conditions and contemporary processes (Fig. 1).

HYPOTHESES OF ENVIRONMENTAL AND HISTORICAL CONTROLS ON THE DISTRIBUTION OF INVASIVE SPECIES. Environmental conditions, particularly edaphic factors such as soil nutrients and site moisture, control the distribution of many forest plant species in the region (Motzkin et al. 1999, Bellemare et al. 2005). In particular, calcareous or mafic bedrock often gives rise to relatively rich soils, with higher base saturation and lower C:N ratios (Brady and Weil 2002), that support a greater diversity of native plant species than do poorer soils (Searcy et al. 2003, Bellemare et al. 2005). Similarly, mesic sites frequently support a greater diversity of native plant species than more xeric sites, and anecdotal evidence suggests that some invasives in our region thrive on mesic sites (Mehrhoff

et al. 2003, Searcy et al. 2003). We hypothesize that mesic, nutrient-rich sites will be more likely to support invasive species than xeric, nutrient-poor sites (Hobbs and Huenneke 1992, Stohlgren et al. 2003, Von Holle and Motzkin 2007).

In addition, we hypothesize that patterns of historical land-use may influence current invasive species distributions. From the 17th to 19th centuries, much of the northeastern U.S. was cleared for agriculture, with a mixture of cropland and pasture (Whitney 1994). Fertile portions of the landscape were generally used more intensively, while less fertile areas and sites inhospitable to agriculture often remained as woodlots. After 1880, the majority of agricultural land was abandoned, and allowed to reforest naturally (Hall et al. 2002). The legacy of the agricultural period continues to influence modern forest composition and soil properties (e.g., Compton et al. 1998, Foster et al. 1998, Motzkin et al. 1999, Compton and Boone 2000, Foster et al. 2003), suggesting that historical factors may similarly affect invasive species distributions (cf., Wu et al. 2004, Bertin et al. 2006). We hypothesize two main types of factors from the agricultural period that may influence the distribution of invasive species: 1) the pattern of regional exotic seed sources and 2) the effect of local land-use.

THE PATTERN OF REGIONAL EXOTIC SEED SOURCES. Agricultural regions were areas of introduction for many invasive species, as farmers often planted exotics in hedgerows and around houses (Mehrhoff et al. 2003, Stinson et al. 2007). Thus, while the landscape has changed dramatically over the last century, we predict that the distribution of invasives remains strongly correlated with patterns of historical agricultural use.

THE EFFECT OF LOCAL LAND-USE. Even in regions of widespread historical agricultural use, the majority of the landscape was not cropland but instead was maintained in less intensive uses like pasture or woodlots. The legacies of these land-use types vary substantially. The conditions in abandoned plowed fields were greatly altered from those of a closed-canopy forest: high light levels (e.g., Oosting 1942, Gill and Marks 1991); exposed mineral soil (e.g., Keever 1950, Inouye et al. 1987); and altered soil nutrient and texture characteristics (Richter et al. 2000). Abandoned pasture had relatively high light levels but generally less soil disturbance, while woodlot sites retained a roughly closed-canopy structure (Foster and Aber 2004). We hypothesize that former pastures and woodlots will have lower levels of invasives today than formerly plowed sites.

The forests of the northeastern U.S. continue to be modified by a range of human activities that may affect invasive species distribution (cf., McDonald and Urban 2006). Two main processes appear to be most important in modern forests: forest fragmentation and forest harvesting.

FOREST FRAGMENTATION. Residential and commercial development during the past several decades has resulted in forest loss, degradation, and isolation (cf., Riitters et al. 2002, Massachusetts Audubon 2003), which may have led to an increase in open weedy habitats and potential seed sources for some invasives (cf., Hobbs 2001, McDonald and Urban 2006). We hypothesize that sites that are currently surrounded by large open areas are more likely to have invasive species present than heavily wooded areas.

FOREST HARVESTING. Logging has been a common disturbance for centuries, with almost all of the region having been harvested historically and approximately 20% of forests subjected to moderate intensity harvest since 1984 (Kittredge et al. 2003, McDonald et al. 2006). Due to increased light (Scheller and Mladenoff 2002), soil scarification (Fredericksen and Pariona 2002), and the potential for dispersal of invasive propagules on logging equipment (e.g., moving seeds around, Battles et al. 2001), we hypothesize that areas harvested more intensively in the past two decades will be more likely to support invasive species.

To summarize, our goal is to quantify the importance of edaphic conditions, regional and local patterns of historical land use, recent harvesting, and forest fragmentation in controlling invasive species distributions in the forests of central and western Massachusetts. Our specific objectives are to determine whether: 1) modern invasive species distributions are related to patterns of historical land-use, 2) recent harvesting is associated with increased presence or abundance of invasive species, 3) landscape context affects the likelihood of invasive plant occurrence, and 4) regional patterns of invasive species distribution are related to edaphic gradients.

Materials and Methods. STUDY AREA. Our samples came from central and western Massachusetts, defined for this study as the portion of the state west of the Eastern Plateau (sensu Motts and O'Brien 1981, see Fig. 2). Parent material in the study region is predominantly glacial till in the hilly upland regions, with alluvium and glaciolacustrine and glaciofluvial deposits in the lowland valleys of the Connecticut and Housatonic rivers (Motts and O'Brien 1981). Soils are typically Inceptisols, with valley floodplains dominated by Entisols, and the Western Upland characterized by a mix of Inceptisols and Spodosols (Brady and Weil 2002). Climate varies with elevation: the number of growing degree days ($^{\circ}C$, with $0^{\circ}C$ baseline) varies from more than 3800 in the Connecticut River Valley to less than 2700 in high elevation sites in the Western Uplands. Precipitation is greatest in the Western Upland region (147 cm yr^{-1}) and is lower in the Connecticut River Valley (97 cm yr^{-1}), with snowfall being more prevalent at higher elevations (USDA-NRCS).

We analyzed in detail the four most common invasive species in the region. Taxonomy in this study follows Gleason and

1830 Forest Cover
Percent forest within 10km
■ 0%

0% - 4%   17% - 22%
4% - 11%   22% - 28%
11% - 17%   > 28%

1999 Forest Cover
Percent forest within 10km
■ < 23%

23% - 37%   57% - 69%
37% - 46%   69% - 80%
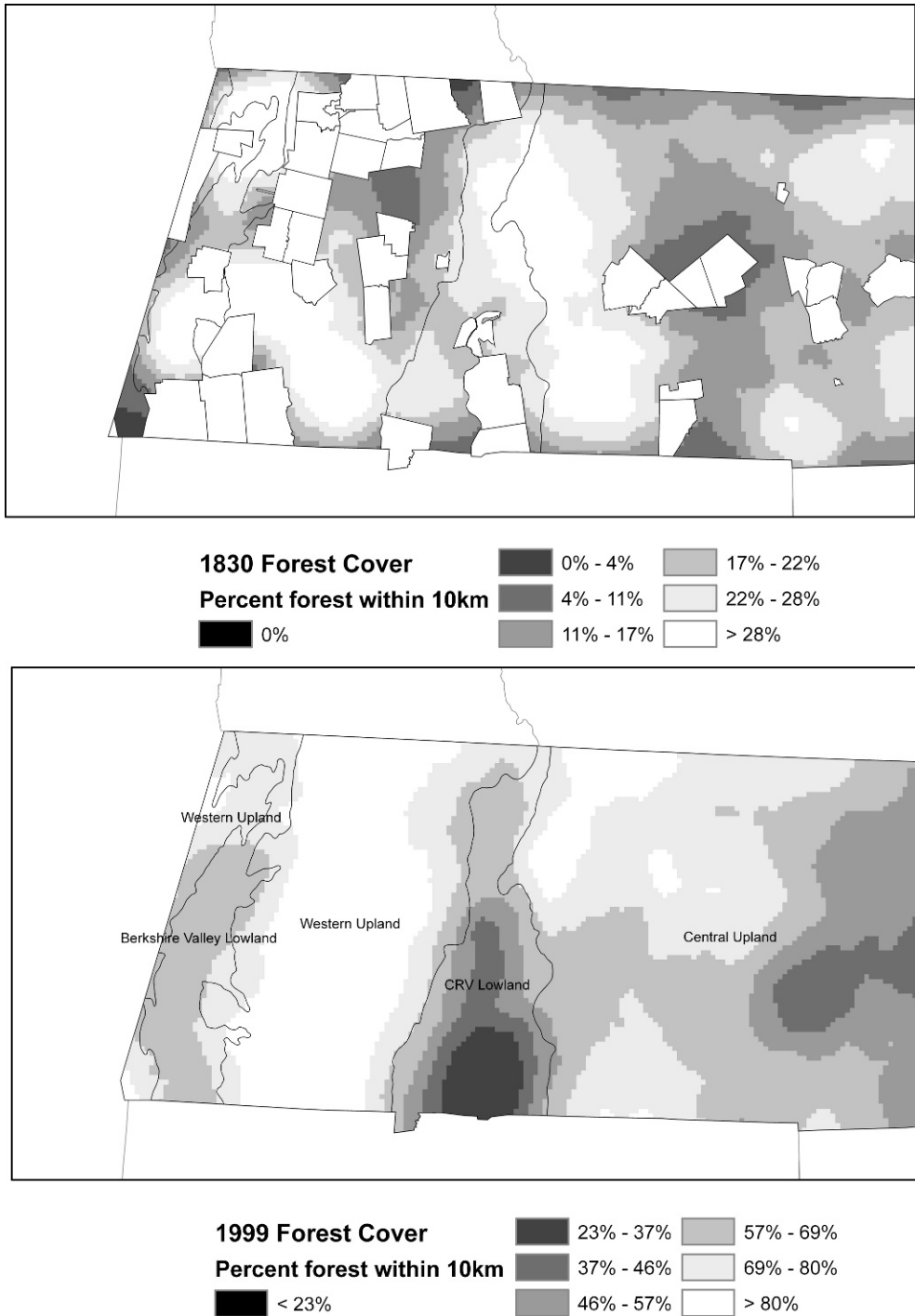46% - 57%   > 80%

FIG. 2.   Comparison of 1830 forest pattern (top panel) and 1999 forest pattern (bottom panel) for central and western Massachusetts. 1830 data were not available for towns that are left blank. The thin black lines are the boundaries of the physiographic regions used in this study, which are labeled in the bottom panel. Note the different grayscales used in the top and bottom panels.

Cronquist (1991). All four are woody and have animal-dispersed seeds. Japanese barberry (*Berberis thunbergii* DC), a deciduous shrub, was widely planted around human settlements (Garden and Forest Journal 1889) and along hedgerows (Ehrenfeld 1997) and apparently became naturalized in the study area in the 1910s (Silander and Klepis 1999). Glossy buckthorn (*Rhamnus frangula* L.), a deciduous, short tree, is most commonly reported east of the Connecticut River Valley (Mehrhoff et al. 2003). Multiflora rose (*Rosa multiflora* Thunb. ex Murr.) is a perennial thorny shrub that was widely planted to control erosion from the 1930s to the 1960s (Mehrhoff et al. 2003). Oriental bittersweet (*Celastrus orbiculata* Thunb.) is a perennial, deciduous woody vine (Silveri et al. 2001) that was planted as an ornamental after 1860 in coastal towns (APWG 2005), but apparently did not naturalize and spread in our area until after 1950 (Mehrhoff et al. 2003).

The field data used in this study originated as part of a broader project to document the effect of forest harvesting on vascular plant communities. Below, we describe the relevant methods in four sections: site selection from a larger database on harvesting, field methodology, creation of ancillary geospatial information, and statistical analyses.

SITE SELECTION. Harvesting information was derived from a spatially-explicit database of all (~13,000) harvest operations in Massachusetts from 1984–2003 (Kittredge et al. 2003). Under Massachusetts law, all harvests greater than 87 m³ that are not permanent land-cover changes (i.e., development) must be reported (Kittredge 1996, McDonald et al. 2006). Each forest cutting plan (FCP) includes the spatial boundary of a cut (the ''polygon''), as drawn by the landowner's agent on topographic maps, and an estimate of the volume of timber to be removed, in aggregate and by species. For this study, we evaluated harvest intensity, the average volume of wood removed per hectare (m³ ha⁻¹). Our field observations suggested that this metric adequately represents the intensity of harvest and is correlated with light availability on the forest floor. In logged polygons, harvesting was selective, removing specific individual and clumps of trees but leaving others standing.

We selected 148 polygons for field sampling in the summers of 2004 and 2005. One-hundred-eight of these polygons had FCPs, and were randomly selected from the larger FCP database with the constraint that polygons must have only had one harvesting event between 1984 and 2003. This distributed sampling across the study region in proportion to the density of harvesting events. For more details on the spatial pattern of cutting in Massachusetts, see McDonald et al. (2006). Forty polygons were ''control'' polygons, randomly placed in forest that was not harvested between 1984 and 2003. Control polygons were circular and were the same size as the average FCP within that physiographic region (Motts and O'Brien 1981): Connecticut River Valley (10.7 ha), Central Upland (11.3 ha), Berkshire Valley (12.6 ha), and Western Upland (15.9 ha).

FIELD PROTOCOL. At each polygon, sampling proceeded at two spatial scales: polygon-level and stand-level. First, we conducted a complete search of the entire polygon for any non-native invasive plant species. The number of person-minutes spent searching each polygon for invasive species was recorded, to see if there were effects of search intensity on invasive species detection. As no trend was apparent we feel confident that there were no search biases across polygons. Data from this polygon-level scale were used to determine controls on the presence/absence of an invasive.

Although polygons were relatively homogeneous in plant composition and harvest intensity, there were occasional small patches of other types (e.g., small cleared areas used to store logs during cutting). We restricted our sampling to the dominant stand within the polygon. Within this stand we randomly located ten sampling points, at least 50 m from one another. At each point, a 400 m² circular plot (11.3 m radius) was searched, and abundance estimated for each invasive species using a 4-point scale: absent, rare (a single individual), uncommon (2–10 individuals), common (> 10 individuals). These stand-level data were used to calculate invasive species frequency and average abundance for the dominant stand in each polygon. Due to logistical limitations this stand-level sampling did not occur for 20 of our polygons.

In the center of the largest stand, we dug a soil pit to a depth of at least 50 cm, to search for a plow (Ap) horizon and other evidence of

anthropogenic disturbances. A composite soil sample of the top 15 cm of mineral soil from four locations was used to characterize soil texture and nutrients (Brookside Laboratories). For six of the 128 polygons with stand-level data, soil samples could not be analyzed due to insufficient sample weight. Variables used in our analysis are the percent sand, percent base saturation, P and S concentrations (ppm), and C:N ratio of the mineral soil.

The presence or absence of an Ap horizon, as well as other in situ evidence of land-use such as the presence of stone walls (evidence of likely clearing for pasture or cultivation) or barbed wire (evidence of likely use for pasture after the late 19th century introduction of barbed wire), was used to classify the polygon into one of three categories of historical land-use: woodlot, if the site apparently remained continuously forested (no Ap horizon, no nearby stone walls or barbed wire, and no old-field white pine); pasture, if the site was historically used as rough, unimproved pasture (nearby stone walls or barbed wire, no Ap horizon); and plowed, if there was clear evidence the soil had been cultivated in the past (an Ap horizon). This classification was checked by comparing land-use data from the 1830s (Hall et al. 2002) and detailed land-use maps by the Works Progress Administration for the 1930s, where available. A review of these polygons and the historical data sources indicates that the land-use history inferred for the area around the soil pit is representative of the vast majority of the area of each polygon.

ANCILLARY GEOSPATIAL DATA. Geospatial data sources were used to measure the historical landscape context, the current landscape context, and soil wetness. All three measurements were then incorporated into a model of the probability of finding an invasive (see below).

Forest and openlands for the agricultural period were digitized from maps of 1830 land-use (Hall et al. 2002), except for several towns where data are not available. Data were reclassified to a simple two-class system: forested or open (i.e., cultivated or pasture land). For each polygon we calculated the percent forest in 1830 within a 10 km² buffer around it, as a measure of the historical landscape context.

Contemporary land-cover data were taken from MassGIS (http://www.mass.gov/mgis/), and derive from the Resource Mapping Project at the University of Massachusetts. Land-cover data were manually classified from 1:25000 color aerial photographs from 1999. The classification system has 37 categories, and is similar to an Anderson classification system (Anderson et al. 1976). To increase temporal consistency in the classification scheme, we reclassified land-use data to seven classes: forest, highly developed (e.g., urban centers), lightly developed (e.g., suburban homes), agricultural, water, wetland, and non-agricultural open (e.g., lawns, power-line right of ways). For each polygon we calculated the percent forest in 1999 within a 10 km² buffer around it, as a measure of the current landscape context.

A digital elevation model from MassGIS (5 m resolution) was resampled to 30 m resolution to ease the computational burden. As a measure of topographically-derived wetness, the Topographic Convergence Index (TCI) was calculated for all cells (Beven and Kirkby 1979). TCI is a log-transformed ratio of uphill contributing area and slope, with high values associated with floodplains and values near 0 associated with dry ridges.

STATISTICAL ANALYSIS. Summary statistics for each invasive species encountered were tabulated: the percent of polygons in which an invasive species was present; how frequent the invasive was within invaded polygons (i.e., the proportion of the ten sample points having the invasive); and how abundant invasives were where they occur (i.e., the abundance values for sample points having the invasive).

Based on this information, the four most commonly occurring invasive species (*Berberis thunbergii*, *Rhamnus frangula*, *Rosa multiflora*, and *Celastrus orbiculata*) were chosen for more detailed analysis. For each species, the binary response variable was the presence or absence at a polygon. This variable was seen as a function of a set of potentially explanatory variables: TCI; harvest intensity (m³ ha⁻¹); forest buffer (% forest within 10 km) in 1830; forest buffer in 1999; soil characteristics; historical land-use; and physiographic region (Motts and O'Brien 1981, see Fig. 2).

A logistic regression analysis with binomial error term was conducted using the GLM function in SPLUS (Venables and Ripley 1999), such that the log odds-ratio (logit) is a linear function of potentially explanatory

Table 1. Non-native invasive plant species occurring in more than 1% of the sampled polygons.

Species	Percent of polygons ($n = 148$)	Frequency within polygons with invasives	Cover class within invaded fixed-radius plots		
			Rare cover class	Un-common cover class	Common cover class
Berberis thunbergii	31.8%	23%	57%	21%	21%
Rosa multiflora	24.3%	14%	67%	17%	17%
Celastrus orbiculata	16.2%	20%	71%	13%	15%
Rhamnus frangula	10.8%	30%	73%	23%	2%
Rhamnus cathartica	8.1%	23%	46%	38%	17%
Lonicera morrowii	7.4%	23%	56%	24%	21%
Alliaria petiolata	6.8%	16%	21%	37%	42%
Euonymus alata	4.1%	10%	63%	38%	0%
Robinia psuedoacacia	2.7%	19%	45%	27%	27%
Berberis vulgaris	2.0%	15%	100%	0%	0%
Elaeagnus umbellata	2.0%	20%	50%	25%	25%
Ligustrum vulgare	2.0%	0%		none	
Acer plantanoides	1.4%	5%	100%		
Phragmites australis	1.4%	3%	100%		
Polygonum cuspidatum	1.4%	0%		none	
Any invasive species	49.3%	27%	61%	21%	18%

variables. The logit is just one kind of link function in a generalized linear model, which in this case transforms a probability (ranging from 0 to 1) into a linear function (ranging from $-\infty$ to $+\infty$). Other link functions (probit, complementary log-log) could be used instead of the logit (see Pindyck and Rubinfeld 1998), but preliminary testing showed that their use did not change our regression results significantly. We report the results of the logistic regression due to its ease of interpretation; for example, a coefficient equal to $\ln(2)$ (0.693) means that for every unit increase in an explanatory variable, the odds of finding an invasive species increase by a factor of 2 (e.g., from 2:1 to 4:1).

To deal with potential issues of multicolinearity in our set of potentially explanatory variables, we used forward stepwise regression. Variables were removed or added based on the AIC value of the model, using the AICstep function of the MASS library of SPLUS (Venables and Ripley 1999). Interaction terms between two continuous variables were allowed to be added to the model, as long as the main effects had already entered the model. Interaction terms involving categorical variables were excluded a priori from the scope of the stepwise selection, as the sample size was too low to allow for accurate estimation of the many coefficients involved. As changes during the stepwise selection are made to the model when the overall AIC is improved by the change, this method of selection does not guarantee that all variables in the final model (i.e., after selection) will have coefficients significantly different than zero.

Results. *Berberis thunbergii* was the most common invasive, occurring in 31.8% of the polygons we visited (Table 1), followed by *Rosa multiflora* (24.3%), *Celastrus orbiculata* (16.2%), and *Rhamnus frangula* (10.8%). Invasives occurred in nearly half (49.3%) of the polygons, but the average frequency of occurrence within an invaded polygon was low (27%). Furthermore, invasive species occurred predominantly (61%) with a cover class of rare. *Alliaria petiolata*, which was uncommon among the polygons (6.8%) and infrequent within invaded polygons (16%), stood out as being notably abundant where it occurs. A post hoc analysis indicated that *B. thunbergii*, *R. multiflora*, and *C. orbiculata* were all positively associated with one another ($\chi^2 > 10$, $P < 0.001$ in all three pair-wise analyses), but that *R. frangula* was only positively associated with *R. multiflora* ($\chi^2 = 9.9$, $P = 0.0038$).

Forest cover was low throughout the study area in the 1830s, ranging from 0–40% forest cover in a 10 km buffer (Fig. 2, top panel). Lowest forest cover occurred in the southern Berkshire Valley and the middle Central Upland. Forest cover was much higher in 1999 (Fig. 2, bottom panel), 40–90%, and was lowest near the city of Springfield, in the southern portion of the Connecticut River Valley. There was no significant correlation between the 1830 and 1999 land cover variables ($P > 0.05$).
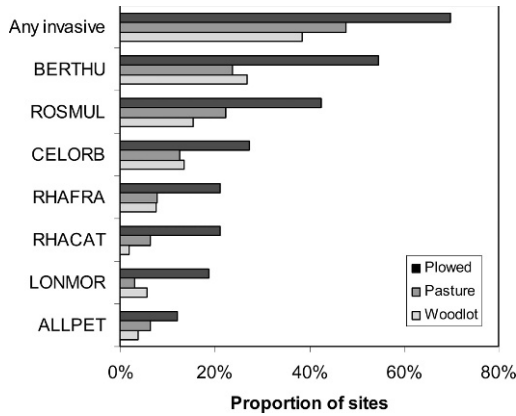
FIG. 3.   The proportion of polygons that have an invasive species for three historical land-uses: plowed, rough pasture, and continuously forested woodlots. Species are abbreviated by the first three letters of their genera and specific epithet: BERTHU (*Berberis thunbergii*), ROSMUL (*Rosa multiflora*), CELORB (*Celastrus orbiculata*), RHAFRA (*Rhamnus frangula*), RHACAT (*Rhamnus cathartica*), LONMOR (*Lonicera morrowii*), ALLPET (*Alliaria petiolata*).

Historical land-use was correlated with invasive presence, with formerly plowed polygons being more than twice as likely to have an invasive species as continuous woodlots (Fig. 3). Former pastures were generally intermediate between plowed and woodlot polygons, with variation among species. Plowed soils had greater sand content than woodlot polygons, and occurred on polygons with higher TCI, perhaps due to the association of plowing with level sites (cf., Hall et al. 2002). Base saturation was greater in former plowed areas than in continuous woodlots, although for our data, C:N ratios were not correlated with historical land-use. Similarly, P and S were not correlated with historical land-use.

The strongest predictor of *Berberis thunbergii* occurrence was the C:N ratio (Table 2). The odds of finding *B. thunbergii* (i.e., the odds-ratio) were 1.5 times higher for each unit decrease in the C:N ratio. There was a significant effect of P as well, with each 10 ppm increase in P decreasing the odds of finding *B. thunbergii* by a factor of 1.3. Harvest intensity and the forest buffer in 1999 were both marginally significant, with increased harvesting and decreased forest nearby both increasing the odds of finding *B. thunbergii*.

Landscape structure in 1999 was a marginally significant predictor of *Rhamnus frangula* occurrence, with polygons that have a greater proportion of forest cover being less likely to have *R. frangula* (Table 3). For example, the odds of finding *R. frangula* were 1.6 times higher at a polygon with 50% forest buffer than a polygon with 90% forest buffer. There was a trend toward polygons with lower C:N ratios and in the Connecticut River Valley being more likely to have *R. frangula*, but this was not statistically significantly.

The most important predictor of *Rosa multiflora* was base saturation (Table 4). The odds of finding *R. multiflora* were 2.7 times higher for each 10% increase in base saturation. Less soluble S and lower C:N also significantly increased the odds of finding *R. multiflora*. Finally, harvest intensity influenced the probability of finding *R. multiflora*; an increase in intensity from 0 m³/ha to 40 m³/ha increased the odds of finding *R. multiflora* by a factor of 2.2.

The major factor correlated with the presence of *Celastrus orbiculata* was C:N ratio (Table 5). The odds of finding *C. orbiculata* were 1.3 times higher for each unit decrease in the C:N ratio. Landscape structure in both 1830 and 1999 were also significant; polygons with a greater proportion of forest cover were less likely to have *C. orbiculata*. For example, the odds of finding *C. orbiculata* were 22.3 times higher at a polygon with 50% forest in 1999 than a polygon with 90% forest in 1999.

Discussion. Invasive vascular plant species are common in the forests of Massachusetts,

Table 2.   Parameters and statistics for the logistic regression of the probability of the presence of *Berberis thunbergii*. Null model: 159.2 deviance on 122 d.f. Final model: 114.3 deviance on 118 d.f., $P < 0.001$.

Variable	Deviance	P	Coefficient	SE
Intercept	Null		10.5	2.6
C:N ratio	31.8	< 0.001	-0.402	0.088
Harvest intensity	3.46	0.063	0.0112	0.0060
Forest buffer 1999	3.26	0.071	-5.58	2.3
Phosphorous	6.36	0.012	-0.0287	0.015

Table 3. Parameters and statistics for the logistic regression of the probability of the presence of *Rhamnus frangula*. Null model: 91.2 deviance on 122 d.f. Final model: 80.1 deviance on 117 d.f., $P = 0.050$.

Variable	Deviance	P	Coefficient	SE
Intercept	Null		0.454	2.9
C:N ratio	2.0	0.16	−0.110	0.081
Forest buffer 1999	3.0	0.085	−1.20	3.7
Physiographic region	6.1	0.11		
Berkshire Valley			0	Reference
Connecticut River Valley			0.824	0.65
Central Upland			0.116	0.27
Western Upland			−0.507	0.29

occurring in almost half of all forested polygons. The relatively broad scale of our sampling (sampling units > 10 ha) allowed us to detect infrequent populations of invasives that would have been missed with smaller units, explaining the relatively large proportion of polygons with exotics. Corresponding with the regional pattern of soil richness and current forest fragmentation, invasives are more common in the Connecticut River Valley and Berkshire Valley than in the Uplands. These two lowland regions also had more intensive historical land-use; historical land-use is a good univariate correlate of the modern presence of invasives.

Our analysis of the four most common invasive species shows that environmental conditions, or at least soil characteristics, are the most important correlates of their distributions. All four species are more likely to occur in soils with a lower C:N ratio, which typically correspond with higher levels of plant-available nitrogen such as NH_4 (Brady and Weil 2002). However, while C:N ratios may generally represent an integrative variable of 'soil fertility', caution is warranted in interpretation of C:N ratios as a causative driver of invasive species distributions because C:N ratios: 1) are frequently altered in complex ways by land-use and other disturbances (Compton and Boone 2000), 2) reflect, in part, the vegetation that has occupied a site over time, and 3) may be altered by the

subsequent presence of invasive species. For instance, the presence of *Berberis thunbergii* on a site may decrease the C:N ratio (Silander and Klepis 1999). It is curious that we found no statistically significant variation in C:N among land-use types, unlike Compton and Boone (2000); this may be due to the relatively large edaphic gradient that we sampled, resulting in high variance in C:N ratios.

Contemporary processes also appear important in controlling invasive species distributions. The landscape context in 1999 is significant or marginally significant in predicting the presence of all four species, and in all cases polygons with more intact forest around them were less likely to have invasives (cf., Parks et al. 2005). This may be because open areas are often source populations for invasives, and being surrounded by such areas makes a polygon more likely to acquire an invasive propagule (Pauchard and Alaback 2004, McDonald and Urban 2006). Polygons with more intensive harvests were more likely to have *Berberis thunbergii* and *Rosa multiflora*, perhaps as a result of soil disturbance or increased light associated with harvesting. In contrast, *Celastrus orbiculata* presence is not correlated with harvest intensity, contrary to the results of Silveri et al. (2001).

The influence of historical factors from the 19th century on invasive species is unclear. As Fig. 3 demonstrates, there is a correlation between historical land-use and the presence

Table 4. Parameters and statistics for the logistic regression of the probability of the presence of *Rosa multiflora*. Null model: 136.6 deviance on 122 d.f. Final model: 95.5 deviance on 117 d.f., $P < 0.001$.

Variable	Deviance	P	Coefficient	SE
Intercept	Null		4.61	2.8
Base saturation	14.2	< 0.001	0.0992	0.037
Harvest intensity	6.7	0.0094	0.0193	0.0067
Soluble sulfur	7.5	0.0063	−0.0476	0.021
Forest buffer 1999	7.6	0.0057	−7.98	2.5
C:N ratio	5.1	0.024	−0.152	0.071

Table 5.   Parameters and statistics for the logistic regression of the probability of the presence of *Celastrus orbiculata*. Null model: 115.5 deviance on 122 d.f. Final model: 97.2 deviance on 119 d.f., *P* < 0.001.

Variable	Deviance	*P*	Coefficient	SE
Intercept	Null		8.43	2.6
C:N ratio	7.3	0.007	−0.233	0.074
Forest buffer 1830	5.8	0.016	−6.20	2.4
Forest buffer 1999	5.3	0.022	−7.78	3.5

of invasives; areas of more intense historical land-use like plowing are more likely to have invasives. However, historical land-use is not statistically related to the probability of finding an exotic after accounting for soil characteristics and contemporary processes. There are two possible ways to interpret this finding, depending on whether one views land-use as mostly affecting soils or being affected by soils (Fig. 1). Certainly, our data are consistent with the former interpretation, as are the findings of Compton and Boone (2000): it is possible that past land-use affects invasives indirectly by modifying the soil. The latter interpretation would be that intensive past land-use and invasives are both correlated with rich soils, and past land-use has no causal effect on invasive presence. However, we do not find for our dataset a correlation between C:N ratio (one measure of soil richness) and past land-use, perhaps making this latter interpretation less plausible. Thus, while the potential causal mechanisms are confounded, our results overall highlight a pattern that we suspect is broadly true: invasive plant species are most common in the uplands of central New England on sites with mesic, fertile soils that were used for historical agriculture. Finally, the results from our observational study emphasize the need for detailed spatio-temporal data on invasive species spread in combination with field experiments to resolve causal mechanisms that control invasive distributions.

In summary, our results indicate that regional patterns of invasive plant distributions develop as species-specific responses to edaphic characteristics, the current and historical landscape context, and forest harvesting regimes. Of these, the edaphic characteristics of a site and its current landscape context are the best predictors of whether a site supports invasive species.

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