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Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England

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ABSTRACT

The factors that influence the invasion of natural habitats by nonnative plants remain poorly understood. We investigated abiotic, biotic, and human influences on the distribution and abundance of nonnative species in coastal upland habitats of southern New England and adjacent New York, US. We censused vegetation and sampled soils in 776, 20 × 20 m plots in natural areas and constructed a spatially referenced GIS database of the region that included land-use history, distance from roads, and surficial geology. Our results indicate that the modern distribution of nonnative plants is influenced by multiple, interdependent current and historical factors. Glaciolacustrine landforms had greater nonnative species richness and cover than beach-dune, moraine, and glacial outwash sand plain landforms. Extant open-canopied areas (i.e., grasslands, dunes, heather barrens, and old fields) harbored significantly greater nonnative species richness and cover than closed-canopy forests, heathlands, and shrublands. Additionally, soil calcium levels and native species richness were positively associated with nonnative species richness. Sites that were cultivated historically or experienced other soil disturbance had higher nonnative species richness than areas without soil disturbance. Overall, abiotic, biotic and historical land use affected levels of nonnative species richness whereas nonnative cover was largely associated with abiotic conditions, particularly soil characteristics. Because many rare coastal sandplain plants reach their greatest abundance on extant open-canopied habitats, efforts to restore native plants will involve tradeoffs between the benefits of expanded habitat for these species and increased risk of invasion by nonnative species.

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1. Introduction

The coastal sandplains of southern New England and adjacent New York support a range of forests, shrublands, heathlands, grasslands and barrens on xeric, nutrient poor soils, with many uncommon plant and animal species that are high priorities for conservation (Dunwiddie et al., 1996; Motzkin and Foster, 2002). Although the upland plant communities

in the region are thought to support generally lower levels of invasive plant species than inland areas with mesic, richer soils (personal observation, B.V.H. and G.M.), nonnative plant species are widely distributed and occasionally abundant in the coastal region, raising questions as to: (1) the factors that control patterns of nonnative distribution and abundance; and (2) the degree to which nonnative species in the region are likely to threaten uncommon native species. Globally,

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nonnative plants have invaded nature reserves on every continent, with the exception of Antarctica (Usher et al., 1988), and nonnative species have altered ecosystem processes (Ehrenfeld, 2003) and contributed in various degrees to the decline of rare native species in a variety of ecosystems (Clavero and Garcia-Berthou, 2005; Simberloff, 2005). However, the factors that govern susceptibility of natural habitats to biological invasion remain unresolved. The intrinsic susceptibility of habitats to invasion apparently results from interactions among the abiotic conditions of the recipient ecosystem, propagule pressure, resident native species, and levels of disturbance (Lodge, 1993; Lonsdale, 1999; Moyle and Light, 1996; Von Holle et al., 2003). A detailed understanding of the relative influence of these factors on the establishment and spread of nonnatives into natural habitats is critical for efforts to control nonnative plants.

In this study, we investigate the factors that are related to nonnative species distributions in the coastal region of southern New England and adjacent New York. The region is unified by similar geological and climatic conditions, and broadly similar histories of human and natural disturbance (Eberhardt et al., 2003; Foster and Motzkin, 2003; Motzkin et al., 2002). The region was largely forested prior to European arrival in the 17th century; extensive agriculture, wood-cutting, and other land uses subsequently resulted in a dramatic reduction in woodland cover and an expansion of openland habitats (Dunwiddie, 1990; Foster and Motzkin, 2003; Motzkin et al., 2002). For example, forest cover on Cape Cod was reduced to c. 41% by the mid-19th century, and the composition and structure of remaining woodlands were altered through repeated grazing, burning, and harvesting (Foster and Motzkin, 2003; Hall et al., 2002; Motzkin et al., 2002). Overgrazing in some coastal areas resulted in a loss of vegetation cover, wind erosion and dune development (Dunwiddie and Adams, 1995; Thoreau, 1865; Torrey and Allen, 1962). As a result of this intensive human land use, much of the region was considered “barren” in the mid-nineteenth century (Thoreau, 1865). Agricultural lands were widely abandoned across the northeastern United States in the late 19th through early 20th centuries (Foster et al., 1998) and forest cover in the coastal region increased through natural succession and planting of both native and nonnative species (Stone, 1999).

Native plant species distributions in coastal New England are strongly linked to surficial geology, soil conditions, and disturbance history (Eberhardt et al., 2003; Motzkin et al., 2002). In particular, historical land use has had an important and enduring influence on modern forest communities on both inland and coastal sandplains (Compton et al., 1998; Donohue et al., 2000; Eberhardt et al., 2003; Foster and Motzkin, 1998; Motzkin et al., 1996, 1999). For instance, on Cape Cod, forests on previously plowed sites frequently contain an overstory dominated by pitch pine (*Pinus rigida*) and an understory of the grass *Deschampsia flexuosa* and the shade-intolerant shrub *Arctostaphylos uva-ursi*, while continuously wooded areas support pine-oak woodlands with dense ericaceous understories (Eberhardt et al., 2003). Plant invasion of forest communities of southeastern New York were significantly, positively related to soil mineralization and nitrification rates as well as levels of calcium, magnesium and phosphorous (Howard et al., 2004). Similarly, in outwash com-

munities of Martha’s Vineyard, soils in agricultural grasslands had higher pH, rates of net nitrification, and extractable calcium and magnesium as well as higher levels of plant invasion than in pine plantations, pine plantations on formerly tilled soil, scrub oak shrublands, tree oak woodlands, burned tree oak woodlands, and sandplain grasslands (Neill et al., 2006). Despite extensive evidence that past land use strongly influences current native vegetation patterns (Foster et al., 1998), there have been few attempts to investigate how these historical factors influence nonnative species abundance and distribution (Lundgren et al., 2004; Pauchard et al., 2004).

We document nonnative species distributions in the upland sandplain plant communities of coastal New England and New York in order to address the following specific hypotheses:

- Nonnative species are most frequent and abundant in habitats that currently have open (nonforested) canopies (Baker, 1986), low native species richness (Elton, 1958), and younger stands (Von Holle et al., 2003).
- Current nonnative species distributions result from spatial variation in recent (Hansen and Clewenger, 2005; Pino et al., 2005) and historical anthropogenic disturbances (distance from roads, patterns of historical agriculture).
- Nonnative species distribution and abundance are strongly correlated with edaphic conditions (Davis et al., 2000); in a region with generally xeric, nutrient poor soils, nonnative species are most frequent and abundant on sites with fine-textured, richer soils.

2. Materials and methods

2.1. Study region

To document the distribution of nonnative species in relation to modern vegetation and environmental conditions, we sampled vegetation and soils in 776, 20 × 20 m plots within upland habitats in six regions in coastal southern New England and adjacent New York state: Cape Cod, Long Island, and the coastal islands Block Island, Martha’s Vineyard, Nantucket, and Tuckernuck Island (Fig. 1).

2.2. GIS databases

We constructed a spatially referenced GIS database that allowed us to determine the distribution of nonnative species in relation to land-use history, distance from roads, and surficial geology. Derivative overlays included: major roads, surficial geology, political boundaries, historical land cover (including a series of overlays from the 1840s to the present), historical land use (1845–1861), and sample plot locations. We grouped the common surficial geologic types of Long Island, New York (Cadwell, 1999) with those of coastal Massachusetts (Oldale and Barlow, 1986): outwash, moraine, beach-dune, and glaciolacustrine deposits. Landforms unique to Long Island were ‘till’; and ‘artificial fill’, of anthropogenic origin. Small areas mapped as ‘mixed’ surficial geology for Block Island, Rhode Island (RIGIS, 1989) were excluded from all analyses. Two sources were used to determine land-cover in

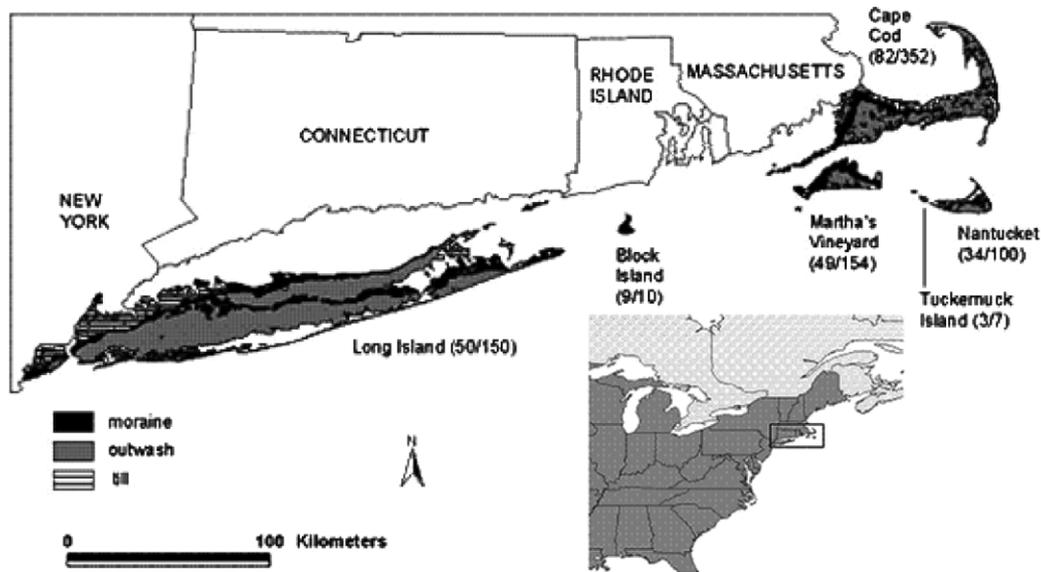


Fig. 1 – Map of study region. Numbers in parentheses indicate frequency (number of plots with at least one nonnative species/total number of sample plots) for each portion of the region. Two contrasting formations vary in relief and soil characteristics and influence native vegetation, fire and human land use: outwash areas are predominantly level or low relief and are dominated by coarse textured and xeric soils, whereas morainal and till areas are characterized by gentle to rolling topography supporting finer textured soils (Fletcher and Roffinoli, 1986; Foster and Motzkin, 2003).

the mid-nineteenth century: detailed (1:10,000 scale) US Coast and Geodetic Survey (USCGS) maps from 1845 to 1861, indicating woodlands, wetlands, roads, fencelines and buildings (Shalowitz and Reed, 1962); and for the inner portion of Cape Cod where USCGS maps were unavailable, land-cover was determined from a series of 1830 town maps (c. 1:20,000 scale); (Archives, 1830; Hall et al., 2002). Because few distinctions were made between forest types on the 1830 maps, we grouped vegetation cover into ‘wooded’ or ‘open’ (Hall et al., 2002).

2.3. Vegetation and soils

Plots were located randomly within protected lands or conservation areas and were stratified by following two variables: mid-nineteenth century land cover (open vs. wooded) and surficial landform (beach-dune, lacustrine deposits, moraine, outwash, and till). Sample plots were constrained to upland sites; wetlands, active agricultural lands, sparsely vegetated beaches, coastal bluffs, dunes dominated by *Ammophila breviligulata* and sites recently disturbed by human activity were excluded.

Prior to sampling, plots were ground-truthed to ensure lack of current anthropogenic disturbance. Percentage cover of all vascular plant species was estimated in eight cover-abundance classes using modified Braun–Blanquet cover classes (Mueller-Dombois and Ellenberg, 1974), as in Motzkin et al. (2002): >1%, 1–3%, 3–5%, 6–15%, 16–25%, 26–50%, 51–75%, >75%. Each team member systematically walked the plot area, visually surveying species composition. An overall synopsis of the visual estimate of the percent cover of each species was agreed upon by the field sampling team. For statistical analyses, these cover classes were converted to the midpoint of each class, except when indicated otherwise. We determined the minimum stand

age by taking increment cores from one to three of the oldest-appearing (using our professional judgement) sound trees (>5 cm dbh) per stand.

We grouped each plot into four physiognomic types, according to the dominant vegetation cover of the current habitat (1. forest, 2. shrub, 3. heath, and 4. open habitat such as grasslands, dunes, heather barrens, and old fields). Plots with greater than 25% tree cover were placed within the ‘forest’ category. Shrublands contained less than 25% tree canopy and had greater than 25% cover of shrub species (e.g., *Quercus ilicifolia*, *Myrica pennsylvanica*, *Rosa carolina*, *R. virginiana*, *Viburnum dentatum*). Heathlands had less than 25% forest canopy cover and greater than 25% cover of the following ericaceous shrubs: *A. uva-ursi*, *Gaylussacia baccata*, *Vaccinium angustifolium* or *V. pallidum*. Open-canopied plots had less than 25% forest, shrub, or heath cover.

Two samples each of 0–15 and 15–30 cm depth mineral soils were collected using a 5 × 15 cm cylindrical steel corer. Aggregated (0–30 cm) samples were air dried, sieved (<2 mm), and analyzed by Brookside Labs, Inc. (New Knoxville, OH, USA) for texture, extractable nutrients (calcium, magnesium, sodium, and phosphorus) concentrations, (Mehlich, 1984), percentage of organic matter (Storer, 1984) and pH (1:1 in water). Although it was not feasible to determine plant available nitrogen for the large number of sites included in this regional study, we evaluated textural and cation gradients that have been shown to be strongly related to vegetation patterns in similar systems throughout the Northeast (Eberhardt et al., 2003; Olsvig et al., 1979).

2.4. Land-use history and human disturbance

In addition to historical sources, we used field methods to determine the land-use history of each sample plot by

examining soil profiles from pits dug into the B horizon for the presence/absence and depth of a plowed surface horizon (Ap) and by noting artifacts of human activity, including cut stumps, barbed wire, plow mounds and fence lines (c.f. Motzkin et al., 2002). Each plot was classified within one of four historical land use categories. Formerly *Cultivated* plots had a clear Ap (plowed) horizon and were not forested in the mid-19th century according to USCGS/1830 maps. *Disturbed* plots had a range of noncultivation soil disturbance, including storm overwash, vehicular disturbance, open dunes, etc. *Non-forested* plots did not have evidence of physical soil disturbance, however historical maps indicated that these areas were not forested in the mid-19th century. These sites were most likely used as unimproved pasture for domestic livestock (Foster et al., 1998). Former *woodlots* exhibited no soil disturbance and historical maps indicated they were forested; most woodlots were cut historically (Motzkin et al., 2002). Of the 776 surveyed plots, 42% were classified as cultivated, 16% as disturbed, 11% as nonforested, and 28% as woodlots (see Table S1 in Supplementary material).

2.5. Nonnative status

Plant nomenclature followed Sorrie and Somers (1999). A species was considered nonnative if its pre-European settlement range did not include southern New England and adjacent New York, as determined by Gleason and Cronquist (1991).

2.6. Statistical analyses

We determined significant correlates of nonnative species presence and abundance with anthropogenic and natural disturbance histories, environmental factors, and biological factors. We selected the variables a priori that we considered most likely to influence nonnative distribution and abundance (Burnham and Anderson, 2002). We conducted collinearity diagnostics on all selected, continuous variables [basal area, soil texture (%sand), organic matter, magnesium, native species richness, stand age, slope, pH, phosphorous (ppm), calcium (ppm), and sodium (ppm), and distance from roads] and removed variables with significant Variance Inflation Factors and levels of multicollinearity [basal area, soil texture (%sand), organic matter, magnesium]. Regression analyses were used to understand the dependence of plot nonnative species richness and cover on biotic factors (native species richness, stand age, current habitat type), physiographic and soil characteristics [slope, pH, phosphorous (ppm), calcium (ppm), and sodium (ppm)], occurrence of anthropogenic disturbance [land-use history, distance from roads (as a proxy for distance from human disturbance)] and surficial geological landform. We performed (Poisson or multiple) regressions on all of these variables, analyzing only single variables and not 2-way or 3-way interactions, as there were not enough data to make these comparisons. We used Poisson regression to evaluate nonnative species richness dependence on these biotic, abiotic, and anthropogenic factors. Overdispersion was present, thus we used the Pearson chi-square statistic to scale the variance function of the Poisson distribution. If a categorical variable was found to be statistically significant in the full model, contrasts were

performed between levels of the covariate to determine differences between categories (Stokes et al., 2000). Additionally, we conducted multiple regression analyses with general linear models to understand the dependence of the total abundance, or cover, of nonnative species per plot on the biotic, abiotic, and anthropogenic factors listed above. General linear models were used to allow the use of categorical and continuous independent variables in the model (Zar, 1999). If a categorical variable was found to be statistically significant in the model, Tukey–Kramer tests were conducted among categories. If a plot did not have a value for a given variable, this data point was removed from analysis, rather than using a zero value. For example, open-canopy areas, heathland, and shrubland plots that did not have trees (>5 cm dbh) were not used for stand age analysis. Each variable was checked to meet assumptions of normality and dependent variables were checked with influence diagnostics (Zar, 1999). All variables in percentage format were arcsine-square root transformed to meet assumptions of normality (Zar, 1999). One outlier (46.5% cover of nonnative species), a plot with a canopy of the nonnative nitrogen-fixer, *Robinia pseudoacacia*, was reduced to the next-highest cover of nonnative species (39%) found, because of a significantly high influence on the model outcome (Sokal and Rohlf, 1995).

We investigated whether historical cultivation influenced individual nonnative species distributions by conducting Chi-square G-tests of independence (Zar, 1999) for each species that occurred in eight or more study plots of each current habitat type, using sequential Bonferonni adjustments (Rice, 1989). These tests were restricted to forests and shrublands because nearly all heathland and open-canopied plots had been plowed.

3. Results

3.1. Nonnative species distributions across the coastal landscape

Nonnative species were widespread but not abundant, occurring in 29.6% of the plots ($n = 230$). In plots with nonnative species, the mean number of nonnative species per plot was 2.8 (± 0.18 s.e.) with an average total cover of 6.3% (± 0.42 s.e.). There were 95 nonnative species (23% of all recorded species) and 314 native species documented in sample plots. The percentage of sample plots with at least one nonnative species differed by geographic region, with Cape Cod having the lowest percentage (23%) and Block Island the highest (90%) (see Table S2 in Supplementary material).

Abiotic, biotic and anthropogenic factors all influenced the richness and cover of nonnative plant species. Glaciolacustrine deposits (mean \pm s.e.: 2.44 ± 0.11) had significantly higher nonnative species richness than beach-dune (0.92 ± 0.02), moraine (0.76 ± 0.008), and sand plain (1.64 ± 0.004) geological deposits (Table 1). However, the average number of nonnative species in the glaciolacustrine deposits were not significantly different from that of till (4.0 ± 0.72) geological deposits. Poisson regression indicated that current open-canopied areas, historically *disturbed* (noncultivation soil disturbance) and *cultivated* sites, and plots with high soil calcium levels and native species richness were significantly positively correlated with

Table 1 – The association of nonnative species richness with biotic, abiotic, and anthropogenic factors, as indicated by Poisson regression (Model df = 424, Pearson Chi-Square = 542.98)

	Response variable	df	Param. estimate	p-value
Current habitat	Forest	1	0.14	0.61
	Heath	1	−0.62	0.19
	Open	1	1.40	<0.0001
	Shrub	0	–	–
Native richness		1	0.04	0.001
Stand age		1	−0.01	0.04
Historical land use	Disturbed	1	1.53	<0.0001
	Open	1	0.65	0.11
	Cultivated	1	1.64	<0.0001
	Woodlot	0	–	–
Slope		1	−0.02	0.35
pH		1	0.25	0.26
Phosphorous		1	0.001	0.42
Calcium		1	0.002	<0.0001
Sodium		1	0.02	0.12
Distance from roads		1	0.0001	0.82
Surficial geology	Beach-dune	1	0.11	0.76
	Lacustrine	1	1.72	<0.0001
	Moraine	1	0.30	0.13
	Sand Plain	0	–	–

Parameter estimates are provided for the association of the number of nonnative species per plot with the listed response variable. Negative parameter values indicate a decrease in nonnative species richness with increasing levels of the independent variable. The referent group for each categorical variable is marked with a ‘–’.

Table 2 – The association of nonnative cover with biotic, abiotic, and anthropogenic factors, as indicated by multiple regression, using general linear models (model $r^2 = 0.30$, $F = 10.2$, $p < 0.0001$)

Response variable	df	F value	Percent of model variance (%)
Historical land use	3	7.48***	11.6
Surficial geology	5	9.83***	25.4
Habitat	3	12.80***	19.9
Native richness	1	0.12	0.06
Stand age	1	2.14	1.1
Slope	1	6.28*	3.2
pH	1	11.25***	5.8
Phosphorous	1	28.02***	14.5
Calcium	1	33.43***	17.3
Sodium	1	2.05	1.1
Distance from roads	1	0.20	0.1

The dependent variable was the summed medians of nonnative cover per plot. Nonsignificant (unmarked), $P > 0.05$; *, $0.05 \geq P > 0.01$; **, $0.01 \geq P > 0.001$; ***, $0.001 \geq P > 0.0001$; and ****, $P < 0.0001$ for tests of significant differences between parameter and the chi-square values. Type I Sum of Squares was used, in the order listed below (Historical land use was first variable entered into model) to determine the percent variance each variable contributed to the model variance.

nonnative species richness while only minimum stand age was significantly negatively correlated with nonnative species richness. Similarly, multiple regression indicated that surficial

geology, current habitat type, levels of soil calcium and phosphorous, historical land use, soil pH, and slope were significantly correlated with the total cover of nonnative species, listed in order of importance (Table 2). Variables associated with soil characteristics (surficial geology, pH, P, Ca, Na) accounted for 64% of the model variation explaining nonnative cover (Table 2).

3.1.1. Current habitat type

Native vegetation cover varied by site and region (see Table S3 in Supplementary material). Of the 446 forested plots, 81 were dominated by conifers (*Juniperus virginiana*, *P. rigida*), 190 by mixed canopy oak species (*Quercus alba*, *Q. velutina*, *Q. coccinea*), 146 by mixed pine-oak cover (*P. rigida* or *Pinus strobus* and canopy oak spp.), 21 by *P. rigida* and *Q. ilicifolia*; and eight plots had other deciduous species as the dominant forest cover. Of the shrubland plots, 70 were dominated by *Q. ilicifolia*, 7 by *M. pensylvanica*, and 98 by a mixture of shrub species such as *Q. ilicifolia*, *M. pensylvanica*, *R. carolina*, *R. virginiana*, and *V. dentatum*, which also commonly included *G. baccata* and *V. angustifolium*. The 56 heathland plots were dominated by various combinations of *A. uva-ursi*, *G. baccata*, *V. angustifolium*, and *V. pallidum*, and also commonly included lesser amounts of *Q. ilicifolia*, *P. rigida*, *Carex pensylvanica*, *Schizachyrium scoparium*, *M. pensylvanica*, and *D. flexuosa*. Open-canopied areas (97) included young dunes, which had sparse vegetation cover, heather barrens dominated by *Hudsonia ericoides* and/or *H. tomentosa*, and oldfields and grasslands dominated by various combinations of graminoids, forbs, and dwarf shrubs.

The occurrence of nonnative species was strongly related to the physiognomy of the extant vegetation. Open-canopied habitats (93.1%) had significantly greater frequency of nonnative species than shrub (61.8%) and forest (25.4%) cover types while there were no significant differences between heath (41.5%), shrub and forest habitats. The species and functional groups that invaded forested plots differed from those invading shrub, heath and open-canopied habitat types (Table 3). Nonnatives that occurred most frequently in forested plots included a tree species, *R. pseudoacacia* (5.4% of all forested plots); a shrub, *Lonicera morrowii* (3.4%); and a woody vine, *Lonicera japonica* (2.2%) (Table 3). *Achillea millefolium*, a perennial forb, was the most frequent nonnative invader of shrublands (18.3% of all shrub plots), followed by the perennial forb, *Rumex acetosella* (11.4%), and the perennial grass, *Festuca ovina* (8.0%). *R. acetosella* was the most frequent invader of heathlands (10.7%) and open-canopied areas (44.3%), followed by *A. millefolium* (8.9% in heath and 37.1% in open-canopy) and *F. ovina* (3.6% in heath and 27.8% in open-canopied areas).

3.1.2. Historical land use

Land-use history strongly determined the distribution and abundance of nonnative species (Tables 1 and 2). Previously cultivated sites (mean/plot \pm se: 1.42 ± 0.15) and those exhibiting other soil disturbance (1.02 ± 0.16) had the highest levels of nonnative species richness, whereas continuously wooded habitats (0.07 ± 0.03) and plots that were nonforested in the 19th century but did not experience soil disturbance (0.26 ± 0.09) supported the fewest nonnative species.

Table 3 – Count, frequency (%) and average percent cover of occupied plots of nonnative species in different habitat types

Cover type (Number of invaded plots/total plot #)	Species	Count	% Freq	Average cover (%)	Functional group
Forest (76/446)	<i>Robinia pseudoacacia</i>	24	5.4	2.2	T
	<i>Lonicera morrowii</i>	15	3.4	1.5	S
	<i>Lonicera japonica</i>	10	2.2	0.8	WV
	<i>Achillea millefolium</i>	8	1.8	0.5	PF
	<i>Rumex acetosella</i>	8	1.8	0.5	PF
	<i>Anthoxanthum odoratum</i>	6	1.3	1.0	PG
	<i>Celastrus orbiculatus</i>	6	1.3	2.2	WV
	<i>Quercus robur</i>	5	1.1	1.1	T
Shrubland (74/175)	<i>Achillea millefolium</i>	32	18.3	0.6	PF
	<i>Rumex acetosella</i>	20	11.4	0.8	PF
	<i>Festuca ovina</i>	14	8.0	0.9	PG
	<i>Celastrus orbiculatus</i>	13	7.4	1.4	WV
	<i>Lonicera japonica</i>	12	6.9	2.2	WV
	<i>Lonicera morrowii</i>	11	6.3	3.3	S
	<i>Polygonum convolvulus</i>	9	5.1	0.5	AVF
	<i>Chrysanthemum leucanthemum</i>	8	4.6	1.1	PF
	<i>Hypochaeris radicata</i>	6	3.4	0.8	PF
	<i>Rosa rugosa</i>	6	3.4	4.7	S
	<i>Rosa multiflora</i>	4	2.3	1.8	S
	<i>Anthoxanthum odoratum</i>	3	1.7	0.5	PG
	<i>Dactylis glomerata</i>	3	1.7	2.0	PG
	<i>Phleum pratense</i>	3	1.7	2.2	PG
	<i>Poa pratensis</i>	3	1.7	0.5	PG
	<i>Aira praecox</i>	2	1.1	0.5	AG
	<i>Bromus tectorum</i>	2	1.1	0.5	AG
	<i>Cerastium vulgatum</i>	2	1.1	0.5	PF
	<i>Cirsium vulgare</i>	2	1.1	0.5	BF
	<i>Malus spp.</i>	2	1.1	1.3	T
<i>Plantago lanceolata</i>	2	1.1	0.5	PBAF	
<i>Polygonum cespitosum</i>	2	1.1	0.5	AF	
Heath (18 /56)	<i>Rumex acetosella</i>	6	10.7	0.5	PF
	<i>Achillea millefolium</i>	5	8.9	0.5	PF
	<i>Festuca ovina</i>	2	3.6	0.5	PG
	<i>Hypochaeris radicata</i>	2	3.6	0.5	PF
	<i>Lonicera japonica</i>	2	3.6	0.5	WV
Open (75/97)	<i>Rumex acetosella</i>	43	44.3	0.6	PF
	<i>Achillea millefolium</i>	36	37.1	0.6	PF
	<i>Festuca ovina</i>	27	27.8	3.3	PG
	<i>Anthoxanthum odoratum</i>	21	21.6	1.1	PG
	<i>Celastrus orbiculatus</i>	15	15.5	0.6	WV
	<i>Lonicera japonica</i>	12	12.4	1.5	WV
	<i>Hypochaeris radicata</i>	11	11.3	0.5	PF
	<i>Lonicera morrowii</i>	11	11.3	1.1	S
	<i>Plantago lanceolata</i>	11	11.3	0.5	PBAF
	<i>Rosa multiflora</i>	6	6.2	2.8	S
	<i>Aira praecox</i>	5	5.2	0.5	AG
	<i>Chrysanthemum leucanthemum</i>	5	5.2	1.2	PF
	<i>Dactylis glomerata</i>	5	5.2	3.1	PG
	<i>Linaria vulgaris</i>	5	5.2	1.1	PF
	<i>Poa pratensis</i>	5	5.2	1.5	PG
	<i>Cirsium vulgare</i>	4	4.1	0.5	BF
	<i>Eleagnus umbellata</i>	4	4.1	1.3	ST
	<i>Potentilla recta</i>	4	4.1	0.9	PF
	<i>Robinia pseudoacacia</i>	4	4.1	4.3	T
	<i>Rudbeckia hirta</i>	4	4.1	0.5	BPF
	<i>Vicia cracca</i>	4	4.1	4.1	PF
	<i>Berberis thunbergii</i>	3	3.1	0.5	S
	<i>Daucus carota</i>	3	3.1	0.5	BF
	<i>Malus spp.</i>	3	3.1	1.0	T
	<i>Verbascum thapsus</i>	3	3.1	0.5	BF

Table 3 – continued

Cover type (Number of invaded plots/total plot #)	Species	Count	% Freq	Average cover (%)	Functional group
	<i>Bromus tectorum</i>	2	2.1	1.3	AG
	<i>Hieracium pilosella</i>	2	2.1	0.5	PF
	<i>Pinus sylvestris</i>	2	2.1	2.3	T
	<i>Polygonum convolvulus</i>	2	2.1	0.5	AVF
	<i>Rosa rugosa</i>	2	2.1	0.5	S
	<i>Silene vulgaris</i>	2	2.1	0.5	PF
	<i>Vicia spp.</i>	2	2.1	0.5	PF

Functional group abbreviations indicate the following: A = annual, B = biennial, P = perennial, F = herbaceous (other than G or V), G = grasslike (Poaceae, Juncaceae, Cyperaceae), S = shrub, T = tree, W = woody, V = vine (Gould et al., 1998).

Historical plowing exerted a strong influence on the distribution of the most common nonnative species of forests and shrublands. Three of the five most common nonnative invaders of forests (*R. acetosella*, *L. japonica*, and *R. pseudoacacia*) were significantly associated with historically plowed plots (Fig. 2A). Additionally, two of the three most common nonnative invaders of shrublands (*Dactylis glomerata*, *Rosa rugosa*) were significantly associated with historically plowed plots (Fig. 2B).

4. Discussion and conclusion

4.1. Nonnative species distributions across the coastal landscape

The flora of the northeastern United States has the highest proportion of nonnative species in the continental United States (Withers et al., 1998), which may result from the length of time since European settlement and high levels of nonna-

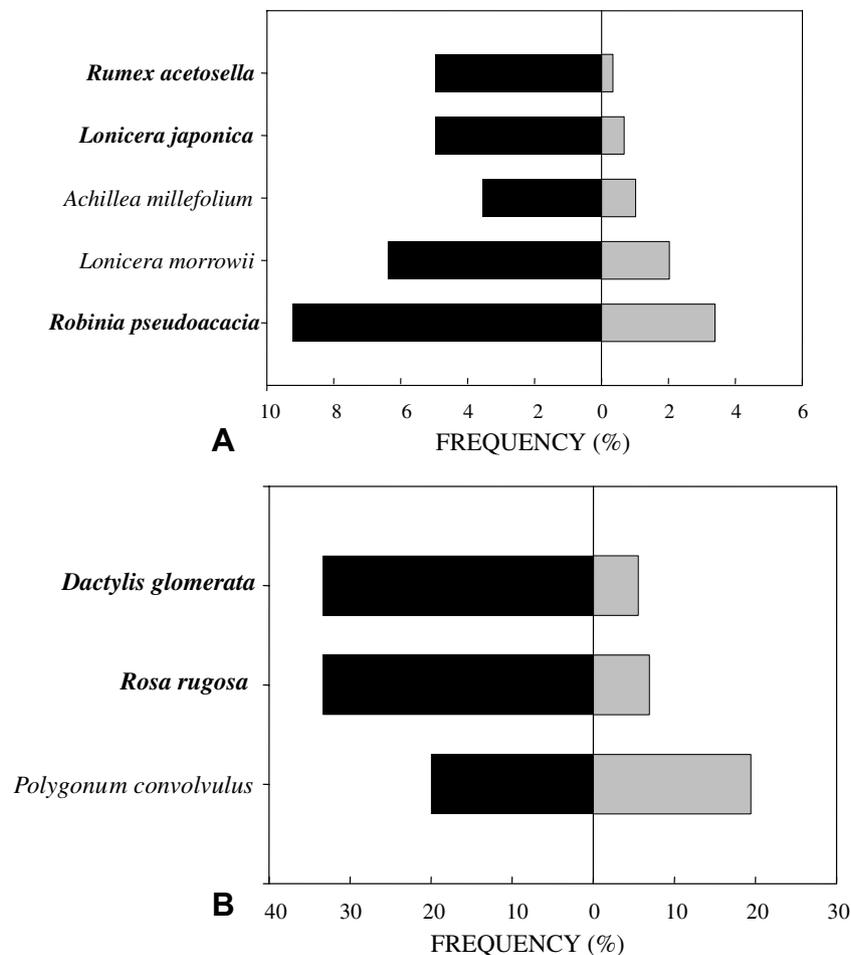


Fig. 2 – G-tests of historically plowed (black) vs. unplowed (gray) stands for each species that occurred in eight or more study plots of forest (A; n = 437) and shrub (B; n = 169) habitats. Those species significantly associated with historically plowed areas are in bold.

tive species introduction. However, only five of the nonnative species (*Celastrus orbiculatus*, *L. japonica*, *L. morrowii*, *R. pseudoacacia*, *Rosa multiflora*) that occurred most frequently within our Massachusetts sites (occurring in at least 7 out of the 613 MA plots) are listed among the top 32 most invasive nonnative species of upland habitats of this state (Mehrhoff, 2005). The average nonnative cover (6.3%) of invaded plots falls within the lower end of the range of nonnative plant cover in published United States floral surveys and in numerous studies (D'Antonio et al., 2000; Gilbert and Lechowicz, 2004; Trager et al., 2004). No single nonnative species in our survey was a clear dominant across all sites. Taken together, this suggests that the coastal areas we studied may be relatively resistant to invasion by many of the nonnative species common in upland habitats of the northeastern United States; this presumably results from the fact that few invasives can thrive in the stressful environmental conditions on the xeric, nutrient-poor soils in the coastal region, and competition from a suite of species adapted to these conditions.

Where they do occur in the coastal region, the distribution of nonnative plants was influenced by both environmental and historical land use factors. Although no one factor appears most responsible for modern nonnative distribution and abundance, our results indicate that the number and cover of nonnative species is strongly related to surficial geology, current vegetation structure, soil characteristics, historical land use, and native richness. In particular, there were strong differences in invasion of natural areas between landforms, extant habitat types, and historical land use types in the study region. However, the model of nonnative species abundance across the landscape explained only 30% of the variation. Thus, there are other factors which were not measured in this study that apparently influence the distribution of nonnative species across the landscape, such as the regeneration strategy of nonnative species in this landscape, the size of the intact natural areas the plots were surveyed in (Lindemayer and McCarthy, 2001), edge to interior ratio of natural areas (Cadenasso and Pickett, 2001), or levels of propagule pressure (Von Holle and Simberloff, 2005). It should be noted that species richness, and not cover, of nonnative plants was significantly associated with native species richness. This may be due to both native and nonnative species responding positively to increasing spatial heterogeneity in the environment (Davies et al., 2005), or to increased propagule pressure of nonnatives with increasing native richness (Lonsdale, 1999). The lack of correlation between cover of nonnatives and native richness in this system suggests that native species richness is unimportant in regulating the abundance of nonnatives in this system at the scale studied (20 × 20 m plots). The most likely influences on the abundance of nonnatives in this system are soil characteristics and native species composition (e.g. presence of woody canopy cover). This is consistent with other studies of invasion of natural areas, where the controls of nonnative species establishment differ from those of dominance (de Gruchy et al., 2005).

4.1.1. Soil fertility effects

Our results indicating that frequency and cover of nonnative species distribution in natural areas are positively correlated with soil nutrients are consistent with studies elsewhere in

the Northeast (Howard et al., 2004; Neill et al., 2006). The strong association of the total cover of nonnative species with soil nutrients may result from differences in the initial site conditions in combination with greater resource (calcium, phosphorus) availability on historically cultivated sites from agricultural amendments (e.g. liming and fertilization, Compton and Boone, 2000). Similarly, the increased occurrence of nonnatives on glacio-lacustrine deposits may result from inherent differences in soil characteristics of differing landforms (Oldale, 1992). Some nonnative species (e.g., *Alliaria petiolata*, *C. orbiculatus*, and *Poa pratensis*) prefer mesic sites (Meekins and McCarthy, 2001; USDA, 2005), presumably contributing to their high frequency and cover on finer-textured lacustrine soils. Additionally, there may be indirect associations of nonnative species with landform, where certain areas that were farmed or physically disturbed resulted in higher levels of invasive species. For instance, the glaciolacustrine deposits of Cape Cod were heavily used for agriculture and currently support high human population densities, and high levels of nonnative species. Last, nonnative species may alter soil fertility and chemistry (Ehrenfeld, 2003), biota (Callaway et al., 2004), and pH (Ehrenfeld et al., 2001), which can influence colonization trajectories of native and nonnative plants. However, there were no 'dominant' nonnative invaders found in this system, which may lessen the likelihood of significant changes in soil characteristics resulting from nonnative species.

4.1.2. Cover type

Open-canopied areas currently harbor the greatest richness of nonnative species which are, for the most part, early successional weedy species, rather than invasive dominants. Nonnatives were found more frequently in open-canopied areas, however the relation between invasion and canopy closure does not appear to be incremental. Heathlands, shrublands, and forested areas that differ physiognomically, had similar levels of nonnative species, signifying that woody canopy cover is associated with lower frequencies of invasion in this system. The occurrence of nonnative species in forests appears to be limited to the few species that can withstand closed canopy, acidic soils with high litter cover, and the low levels of soil nutrients that occur in these coastal forests.

The timing of reforestation in the northeastern United States during the early 20th century influenced the current distribution and abundance of nonnative species. The four most frequently occurring nonnative species within each current habitat type (Table 3, e.g. *R. pseudoacacia*, *L. morrowii*, *L. japonica*, and *A. millefolium* for forests) were documented in New England herbaria before the turn of the 20th century (i.e., prior to agricultural abandonment) (Mehrhoff et al., 2003), suggesting that these nonnative species might have colonized the highly disturbed sites sometime after abandonment and are legacies of early-successional, weedy communities. In this case, early-successional nonnative species, such as *A. millefolium*, *Anthoxanthum odoratum*, *F. ovina*, and *R. acetosella* which colonized old-fields and disturbed areas following abandonment would be expected to slowly disappear from reforesting areas. Recently-abandoned agricultural fields that currently occur on Martha's Vineyard had significantly greater levels of nonnative species richness and cover than sandplain grassland habitat

with no evidence of recent agricultural disturbance (Neill et al., 2006). Thus, the fact that extant forests in this region that had historically been cultivated had greater levels of nonnative species than those without soil disturbance supports the hypothesis that nonnative species richness and cover in this system decline with time as habitats undergo succession. However, the extent to which nonnative establishment and spread occurred soon after agricultural abandonment versus more recently is largely unknown.

4.1.3. Historical land use

Our results indicate that historical soil disturbances exert a persistent influence on the distribution and abundance of the common nonnative species of this region, whereas proximity to current roads did not influence invasion. Similarly, Lundgren et al. (2004) studied environmental correlates of the ten most invasive terrestrial nonnative plant species in the Quinebaug Highlands of northern Connecticut and southern Massachusetts, and found that land use from the 1930s has stronger influence on modern invasive distributions than current land use (roads, trails). In our system, sites with evidence of historical soil disturbance that were unrelated to agriculture had levels of invasion comparable to formerly cultivated sites. In contrast, sites that did not experience intensive soil disturbance currently have low numbers and cover of nonnative species regardless of whether they were wooded or nonforested historically. Thus, historical soil disturbance may have permanently altered resource conditions or enabled establishment of species that, once established, are able to persist but that are unable to establish on undisturbed soils.

Vegetation on sites with different land use histories have been shown to be associated with different, character-based functional groups (Verheyen et al., 2003). Suites of 'disturbance specialists', many of which were nonnative species, likely invaded abandoned cultivated and disturbed lands in the coastal region, with slow recolonization and succession of later-successional species (mostly native), in the stressful coastal environment (Dunwiddie et al., 1996). Those areas without continued disturbance became reforested or shrub-dominated, with subsequent lower levels of nonnatives than open-canopied areas. The nonnative species capable of persisting in or invading forests are more tolerant of shade, deeper organic layers, etc. This suggests that functional characteristics of species influence their ability to invade and persist within specific vegetation types.

4.2. Concluding remarks

The mosaic landscape of the coastal northeastern United States contains many rare native communities and habitat types (Dunwiddie et al., 1996) and their distributions are influenced by a range of historical and natural processes (Clarke and Patterson, 2006). Likewise, we have demonstrated that nonnative species distributions in natural areas in this region are influenced by abiotic, biotic and anthropogenic factors. Recognition of the association of nonnative species with landforms with richer soils, open-canopy habitat types, and historically disturbed sites will aid land managers in prioritizing habitats in this region for management. Maps that combine underlying surficial geology, current vegetation

cover, as well as historically disturbed sites can serve as starting points for documenting nonnative species distributions and evaluating control priorities.

The most effective nonnative plant management in this landscape may simply be to encourage natural reforestation (Simberloff et al., 2002) or establishment of native plant cover without severe soil disturbance (Lezberg et al., 2006). Ecosystem recovery from the impacts of land use can be expedited through restoration activities (Hobbs and Mooney, 2005). However, restoration to woody cover may conflict with conservation of rare plant species, many of which are associated with open-canopy habitats and disturbed soils (Clarke and Patterson, 2006). If soil scarification or other soil disturbance is performed for restoration purposes, these sites should be closely monitored for nonnative species encroachment. Facilitating native plant recolonization with seed additions in the xeric, nutrient-poor soils of this region will serve two functions: the reestablishment of native diversity and the resistance of native vegetation to further spread of nonnative species.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.biocon.2006.10.044](https://doi.org/10.1016/j.biocon.2006.10.044).

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