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Facilitations between the introduced nitrogen-fixing tree, *Robinia pseudoacacia*, and nonnative plant species in the glacial outwash upland ecosystem of Cape Cod, MA

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Abstract. *Robinia pseudoacacia*, a nitrogen-fixing, clonal tree species native to the central Appalachian and Ozark Mountains, is considered to be one of the top 100 worldwide woody plant invaders. We initiated this project to determine the impact of black locust (*Robinia pseudoacacia*) on an upland coastal ecosystem and to estimate the spread of this species within Cape Cod National Seashore (CCNS). We censused 20 × 20 m plots for vegetation cover and environmental characteristics in the center of twenty randomly-selected *Robinia pseudoacacia* stands. Additionally, paired plots were surveyed under native overstory stands, comprised largely of pitch pine (*Pinus rigida*) and mixed pitch pine–oak (*Quercus velutina* and *Quercus alba*) communities. These native stands were located 20 m from the edge of the sampled locust stand and had similar land use histories. To determine the historical distribution of black locust in CCNS, we digitized and georeferenced historical and current aerial photographs of randomly-selected stands. Ordination analyses revealed striking community-level differences between locust and pine–oak stands in their immediate vicinity. Understory nonnative species richness and abundance values were significantly higher under *Robinia* stands than under the paired native stands. Additionally, animal-dispersed plant species tended to occur in closer stands, suggesting their spread between locust stands. *Robinia* stand area significantly decreased from the 1970's to 2002, prompting us to recommend no management action of black locust and a monitoring program and possible removal of associated animal-dispersed species. The introduction of a novel functional type (nitrogen-fixing tree) into this xeric, nutrient-poor, upland forested ecosystem resulted in 'islands of invasion' within this resistant system.

Introduction

Nonnative species that alter ecosystem functions are considered to have major impacts on native biodiversity (Vitousek 1990; Mack and D' Antonio 1998; Parker et al. 1999). Black locust (*Robinia pseudoacacia*), a nitrogen-fixing, clonal tree species, is considered to be one of the top 100 worldwide woody plant invaders (Cronk and Fuller 1995). This species, native to the central Appalachian and Ozark Mountains, has been planted and naturalized in Europe, the Middle East, Australia, New Zealand and all but one of the lower, contiguous 48 United States (Cronk and Fuller 1995; Mehrhoff et al. 2003). The biological characteristics of nitrogen fixation and vegetative reproduction are considered indicators of plant invasiveness (Daehler 1998). Prior to the invasion of *Robinia pseudoacacia*, there were no nitrogen-fixing, leguminous tree species native to Cape Cod (Sorrie and Somers 1999). Habitat invasibility has been found to drastically increase following the alteration of ecosystem properties by a nonnative species (Mack and D' Antonio 1998). Examples include nonnative species that have altered fire regimes (D' Antonio and Vitousek 1992), nutrient cycling (Vitousek and Walker 1989; Vitousek 1990), and the osmotic environment (Vivrette and Muller 1977; Kloot 1983) from historical levels which have resulted in permanently altered ecosystems that native species may not tolerate or cannot compete with the nonnative vegetation adapted to these altered environments.

Black locust, *Robinia pseudoacacia*, is a nitrogen-fixer in the legume family (Leguminoseae). Nitrogen fixation in locust species occurs by *Rhizobium* – a symbiotic bacteria – that forms within root nodules along the roots of the tree (Chapman 1935; Bormann et al. 1993; Deacon 1997). This activity leads to increased nitrogen availability and increased organic matter accumulation in the soil (Chapman 1935; Boring and Swank 1984; Bormann et al. 1993). In many temperate soils, particularly sandy soils such as those found on Cape Cod, nitrogen is a limiting nutrient (Dzwonko and Loster 1997). Soils under *Robinia pseudoacacia* stands have been found to have significantly greater total nitrogen, organic matter, and NO_3 than uneven-aged mixed oak (primarily *Quercus prinus*) forests in the southern Appalachians (Boring and Swank 1984). While black locust is a symbiotic nitrogen fixer with *Rhizobium*, pitch pine (*Pinus rigida*) is an associative nitrogen fixer with rhizosphere soil microbes. This difference in nitrogen fixation mechanism allows black locust to more efficiently accumulate nitrogen in the soil than pitch pine (94 kg/ha/years vs. 54 kg ha/years, Bormann et al. 1993). Chapman (1935) reported that with increased distance from black locust plantations in Ohio and Indiana, there was decreased total soil nitrogen as well as decreased height and diameter in other hardwood trees including *Fraxinus americana, Liriodendron tulipifera, Quercus prinus, Quercus velutina*, and *Catalpa speciosa*. He found higher densities of the nonnative orchard grass (*Dactylis glomerata*) within locust stands, which decreased in cover with distance from locust stands into the adjacent *Catalpa* (*C. speciosa*) plantations. He attributed this increased cover to higher nitrogen content in the soil, rather than greater light availability under the locust canopy, as grass development was only slightly better beneath large openings in the *Catalpa* canopy than elsewhere beneath this species.

Black locust is an early successional, shade intolerant tree species that is associated with cleared areas, old pastures, disturbed road sides, old burns and other locations where it was historically planted (Chapman 1935; Ogden 1961; Boring and Swank 1984; Bormann et al. 1993). The tree reproduces sexually from seed as well as vegetatively through stump and root sprouts, exhibiting rapid early growth in open areas that slows after 10–20 years and with a relative short life span (Boring and Swank 1984). Historically, black locust was planted as timber for fence posts, firewood, insulator pins for telephone and transmission lines, in addition to its soil amendment properties (Cuno 1919; Ogden 1961; Boring and Swank 1984). It was a highly valued species for the strong, rot-resistant wood (Clark 1986; Cuno 1919). Today, black locust stands are typically found at the sites of abandoned homesteads within the matrix of native pitch pine and oak forests and in close proximity to existing houses across Cape Cod.

The largely forested landscape of Cape Cod was drastically altered with the agricultural, wood-cutting and settlement activities of European settlers, commencing in the early 17th century (Motzkin et al. 2002; Foster and Motzkin 2003). Cape Cod forest cover was reduced to ca. 41% by the mid-19th century, with small patches of forest cover occurring in the outer Cape and the largest forests blocks occurring closer to the mainland (Hall et al. 2002; Motzkin et al. 2002). The composition and structure of the remaining woodlands was altered through repeated grazing, burning, harvesting and other activities (Motzkin et al. 2002; Foster and Motzkin 2003). Widespread agricultural abandonment in the late 19th and early 20th centuries resulted in an increase of forest cover of Cape Cod to 61% by 1951 through natural reforestation and planting efforts of both native and nonnative species (Stone 1999). Forest cover decreased again to 43% by 1990 following residential and commercial development (Stone 1999). However, forest spatial cover from the mid-19th century to modern times differs geographically. During the agricultural period, the forests patches were larger and more contiguous than the highly fragmented forest cover that exists today across Cape Cod. The current forest cover of the outer Cape, especially that contained within Cape Cod National Seashore, is the most contiguous of the Cape Cod region (Motzkin et al. 2002).

Native plant community composition in the glacial outwash upland habitats of Cape Cod is strongly influenced by land use history (Motzkin et al. 2002; Eberhardt et al. 2003). Eberhardt et al. (2003) identified three woodland types (pine–bearberry, pine–hairgrass, and pine–oak–sedge) within Cape Cod National Seashore associated with historical plowing disturbance. These community types had a characteristic overstory of *Pinus rigida* and the 'Pine–oak–sedge' community also included *Quercus velutina* in the overstory. *Deschampsia flexuosa, Schizachyrium scoparium, Chimaphila maculata, Trientalis borealis, Prunus serotina* and *Arctostaphylos uva-ursi* occur significantly more frequently in woodlands that were plowed historically. The ericaceous shrubs *Gualtheria procumbens*, *Vaccinium pallidum*, *Epigaea repens*, and *Gaylussacia baccata* occurred more frequently in areas that had not experienced any kind of soil disturbance, yet were logged historically to various degrees (Eberhardt et al. 2003).

Robinia pseudoacacia is thought to pose a threat to native species because of its ability to form dense, monospecific stands which may crowd out native vegetation via root suckers (Mehrhoff et al. 2003). Additionally, the soil enrichment properties of this species, especially in sandy areas, is thought to facilitate invasion of other nonnative species into these stands (Mehrhoff et al. 2003). The dispersal mechanisms of the nonnative species found within these stands may influence their spatial distributions; which could, in turn, influence the spread of these nonindigenous species and the community structure of the stands that they invade (Shigesada and Kawasaki 1997; Higgins and Richardson 1999; Levin et al. 2003). *Robinia pseudoacacia* was ranked tenth (out of 211 nonindigneous species) in significance of impact on native communities in Cape Cod National Seashore (Martin 2001). In 1991, there were 129 stands totaling 305 acres within the 43,604 acres of Cape Cod National Seashore (unpublished data, Cape Cod National Seashore). We initiated this project to quantify the impact of black locust on this coastal, upland ecosystem and to estimate the spread of this species within the National Seashore. We hypothesized that *Robinia pseudoacacia* would facilitate invasion by other nonnative plant species into these stands as a result of the nitrogen-fixing capability of this species. Secondly, we hypothesized that animal-dispersed nonnative species would have different spatial distributions than nonnative species with other dispersal mechanisms (wind, water, ballistic). Last, we hypothesized that black locust stands rapidly increased in landscape cover following agricultural abandonment and decreased following reforestation, given its adaptation to open areas. We tested these hypotheses by comparing the vegetation within the understories of randomly-selected black locust and paired native stands with similar land use histories. To understand the influence of dispersal mechanisms on the spatial distributions of nonnative species within locust stands, the community similarities of animal- and wind-dispersed species were calculated between black locust stands and were tested for association with distance between stands. Last, we used historical and modern aerial photographs in addition to dendrochronology to understand stand expansion trends over time.

Methods

Field methods

To determine the impact of *Robinia pseudoacacia* on native and nonnative species distribution and abundance, we censused 20 × 20 m plots in the center of twenty randomly-selected *Robinia pseudoacacia* stands within Cape Cod National Seashore for vegetation cover and environmental characteristics. We visually approximated the center of the locust stands and surveyed plots with greater than 25% living canopy cover of *Robinia pseudoacacia*. Total canopy cover of each canopy strata was estimated visually. Percent cover of all herb, shrub and tree species were estimated in eight cover-abundance classes: (< 1%, 1–3%, 3–5%, 6–15%, 16–25%, 26–50%, 51–75%, > 75%). For statistical analyses, these cover classes were converted to the median of the range of each cover class for each species, except when indicated otherwise. Nomenclature follows Gleason and Cronquist (1991) and Sorrie and Somers (1999). We determined stand age by taking increment cores from the most central tree per stand and four additional trees along a 20 m transect which was oriented randomly from the central tree. We sampled single-stemmed individuals that did not appear to be stump resprouts (USDA 2004), the use of which could confuse stand age determination. We surveyed understory regeneration of *Robinia pseudoacacia* in the area surrounding the stand by counting the number of *R. pseudoacacia* seedlings, saplings, and root sprouts (< 1 m) from 20 m transects oriented randomly away from each corner of the plot. We characterized the soil properties by systematically taking four soil cores along a randomized diagonal axis through the stand. The top 10 cm of soil was sampled and pooled into one sample per plot. Samples were air dried, sieved (< 2 mm), and analyzed for texture using a Lamont soil texture unit (Forestry Suppliers). Extractable nutrients (calcium, magnesium, nitrogen, phosphorus and potassium concentrations) (Mehlich 1984), percentage of organic matter (Storer 1984), and pH (1:1 in water) were analyzed by Brookside Labs, Inc. (New Knoxville, OH, USA). We conducted paired *t*-tests of each individual soil characteristic and an unpaired *t*-test of plot scores generated by principle components analysis of edaphic composition by stand type.

Table 1. Average soil characteristic ± s.d. Soil characteristics were compared between paired native and *Robinia pseudoacacia* plots.

	Paired Native	*Robinia pseudoacacia*	*t*-statistic	*p*-value
pH	4.47 ± 0.4	4.34 ± 0.3	0.98	0.34
Organic matter (%)	3.70 ± 2.2	5.15 ± 1.9	2.24	0.03
Sulfur	27.5 ± 8.7	29.3 ± 3.6	0.71	0.49
P (ppm)	23.5 ± 14.9	89 ± 119.3	2.3	0.03
Ca (ppm)	182 ± 78.9	443 ± 338	3.17	0.005
Mg (ppm)	51.7 ± 21.4	71.1 ± 15.7	2.92	0.007
K (ppm)	28.7 ± 14.8	40.9 ± 9.5	2.8	0.009
Na (ppm)	31.5 ± 6.4	28.7 ± 4.4	1.39	0.18
Fe (ppm)	179.5 ± 50.4	190.3 ± 39.8	0.67	0.51
Mn (ppm)	8.3 ± 4.9	13.8 ± 11.8	1.76	0.09
Cu (ppm)	0.52 ± 0.1	0.61 ± 0.1	0.18	0.86
Zn (ppm)	1.9 ± 2.2	2.5 ± 2.3	0.75	0.46
Al (ppm)	450.8 ± 293.2	535.4 ± 178.8	1.67	0.11
N (%)	0.14 ± 0.1	0.27 ± 0.1	1.20	0.25
Sand (%)	73.3 ± .06	68.2 ± .07	0.86	0.40
Silt (%)	12.9 ± .04	19.7 ± .07	0.29	0.78
Clay (%)	13.7 ± .08	12.1 ± .08	1.18	0.25

After comparing the *p*-values to sequential Bonferroni-adjusted alphas, none of the comparisons are statistically significant. However, edaphic conditions were significantly different between stands, according to an unpaired *t*-test of plot scores generated by principle components analysis of (t = 3.8, p = .0007).

The extent of the influence of *Robinia pseudoacacia* on species distribution was assessed by surveying paired plots under adjacent native-canopy stands with greater than 25% native and less than 5% black locust canopy cover. These native stands were located 20 m from the edge of the sampled locust stand, and had similar land use histories and proximity to roads. Paired native stands were not sampled if the sampled black locust stands did not have adjacent native stands with these characteristics. All locust and 'paired native' plots were located within land classified as 'open' in the mid-19th century (Hall et al. 2002). This land use category is comprised of historically plowed or pastured land (Eberhardt et al. 2003). All locust and 'paired native' plots had two or more of the six species associated with plowing disturbance occurred in the plot (Eberhardt et al. 2003). These proxy associations of historical land-use were used because direct methods of determining land use history were not permitted in the stands, owing to regulations prohibiting soil disturbance on US federal lands (US Congress 1999). We used Student *t*-tests to test for differences in total vegetation cover and richness between stand types. We used Kruskall–Wallis tests to determine if there were differences between the number and cover of native and nonnative species within locust and paired native stands. To determine if the stand types had different community compositions, we conducted a nonmetric multidimensional scaling (NMDS) analysis with 6 axes, 40 runs of real data and 50 runs of randomized data, with an instability criterion of 0.00001 with PC-ORD, version 4 (McCune and Mefford 1999). Last, we conducted *G*-tests of independence (Zar 1999), or the likelihood ratio of χ^2 analysis, for each species that occurred in $>20\%$ of all study plots to determine association of individual species with stand type.

Nonnative species distribution by dispersal type

We examined the relationship between the community similarity of nonnative species of differing dispersal types within black locust stands and the distance between locust stands to understand whether nonnative species that had animal or some other dispersal vector were experiencing different expansion trends across locust stands. Nonnative species occurring within locust stands were separated into two categories, (1) those species that are known to be bird or deer dispersed (*animal dispersal type*) and (2) those species that have other mechanisms of dispersal such as wind, water, or ballistic (*other dispersal type*) (Table 2, Uva et al. 1997; Royer and Dickinson 1999; Royal Botanical Gardens 2002; Mehrhoff et al. 2003; Miller 2003; Myers et al. 2004). If a species is dispersed both by animals and some other mechanism, it was classified as 'animal dispersed'. We determined pairwise distances between each of the 19 (out of 20) locust study stands with the measure tool of Arcview GIS 3.2 (one stand was mistakenly not referenced with a global positioning system). We expressed community similarity

Table 2. Nonnative species listed by dispersal type and occurrence (%) within *Robinia pseudoacacia* study plots.

Animal (bird, deer)		Other (wind, water, ballistic)	
Species	Occurrence (%)	Species	Occurrence (%)
Lonicera morrowi	84	*Holcus lanatus*	68
Lonicera japonica	79	*Convolvulus arvensis*	47
Poa pratensis	53	*Alliaria petiolata*	37
Rosa multiflora	47	*Anthoxanthum odoratum*	37
Ligustrum vulgare	37	*Saponaria officinalis*	32
Celastrus orbiculatus	32	*Humulus lupulus*	16
Berberis vulgaris	21	*Rumex acetosella*	16
Malus pumila	21	*Syringa vulgaris*	16
Solanum dulcamara	16	*Achillea millefolium*	11
Hedera helix	11	*Cichorium intybus*	11
Poa compressa	11	*Leonurus cardiaca*	11
Quercus robur	11	*Ailanthus altissima*	5
Vitis vulpina	11	*Allium vineale*	5
Berberis thunbergii	5	*Brassica juncea*	5
Eleagnus umbellata	5	*Calystegia sepium ssp. sepium*	5
Hieracium caespitosum	5	*Clematis ternifolia*	5
Lonicera tartarica	5	*Hypochaeris radicata*	5
Polygonatum biflorum	5	*Populus alba*	5
Potentilla recta	5	*Rumex crispus*	5
Stellaria media	5	*Scrophularia nodosa*	5
Taraxicum officinale	5	*Sedum telephium*	5
		Verbascum thapsus	5
		Vicia sativa ssp. nigra	5

of dispersal types between two locust stands as the percentage of species (*animal* or *other* dispersal type) shared by these stands (Findley and Findley 2001). For example, if a stand had 6 animal-dispersed species in common with the 10 animal-dispersed species contained in another stand, the animal-dispersed community similarity between these two stands was 60%. The community similarity of a stand with each of the other 18 stands was regressed against the distances between the stand with the other stands using simple regression analyses (Table 3). To correct for multiple testing, we took the p-values from the analyses, ranked them, and used the sequential Bonferroni technique of dividing a critical value of 0.05 by the rank of the p-values (Rice 1989).

Locust distribution

We monitored black locust stands for expansion by delineating historical and recent aerial photographs of 53 randomly chosen stands (Figure 1). The entire park was aerially photographed in 2002 allowing for complete coverage of all

Table 3. Relationships between the nonnative community similarity of dispersal types within black locust stands with the distance between locust stands.

Dispersal type	Sign	Parameter estimate	r^2	p-value
Animal (bird, deer)	–	0.00003	0.32	0.01
	–	0.00002	0.25	0.03
	–	0.00002	0.34	0.01
	–	0.000003	0.03	0.48
	–	0.00003	0.36	0.01
	–	0.00002	0.33	0.01
	+	0.0000002	0.00	0.98
	+	0.00001	0.03	0.48
Other (Wind, ballistic)	–	0.00002	0.11	0.18
	+	0.000004	0.01	0.70
	+	0.000006	0.02	0.57
	+	0.00001	0.06	0.32
	–	0.000009	0.07	0.29
	–	0.00002	0.15	0.12
	–	0.00002	0.13	0.14
	–	0.000009	0.08	0.25
	+	0.00002	0.07	0.30
	–	0.00001	0.10	0.21
	–	0.000001	0.003	0.85
	–	0.00001	0.11	0.19

Each row indicates a simple regression of a stand with the community similarity and distance between this stand and the other 18 black locust study stands. Only plots with greater than 2 wind-dispersed species and 4 animal-dispersed species were analyzed. All data are transformed using the arcsine transformation (Zar 1999). Cell numbers are parameter estimates of the simple regressions. No tests were statistically significant after comparison to Bonferonni-adjusted alpha values.

chosen stands. A historical photograph, older than 20 years, was matched to each identified stand. Because of the limited availability of historical, aerial photographs, we required the use of historical photographs from two different years (1970, 1978). If there was more than one historical match for the identified 2002 photographed stand, we chose the clearest historical photo. If both sets were equally interpretable, then the oldest photo was chosen. The stands from each current and historical photograph were delineated, scanned, and georeferenced in the geocorrection module of Erdas Imagine 8.5. Using the calculation tool in ESRI ArcGIS, area was computed for each stand for each year. Stand delineation was performed by hand, using a 0.5 mm pen and photographs of varying scale (1:40,000 for 1970, 1:24,000 for 1978, and 1:12,000 for 2002). The expansion trend was tested using paired Student's t-tests of the differences in area (current – historical area). Additionally, stands were placed in one of two categories (<5 m from the road or >5 m) to investigate the proximity of the stand to a road as affecting stand expansion. The change in stand area by road distance category was tested with an unpaired t-test.

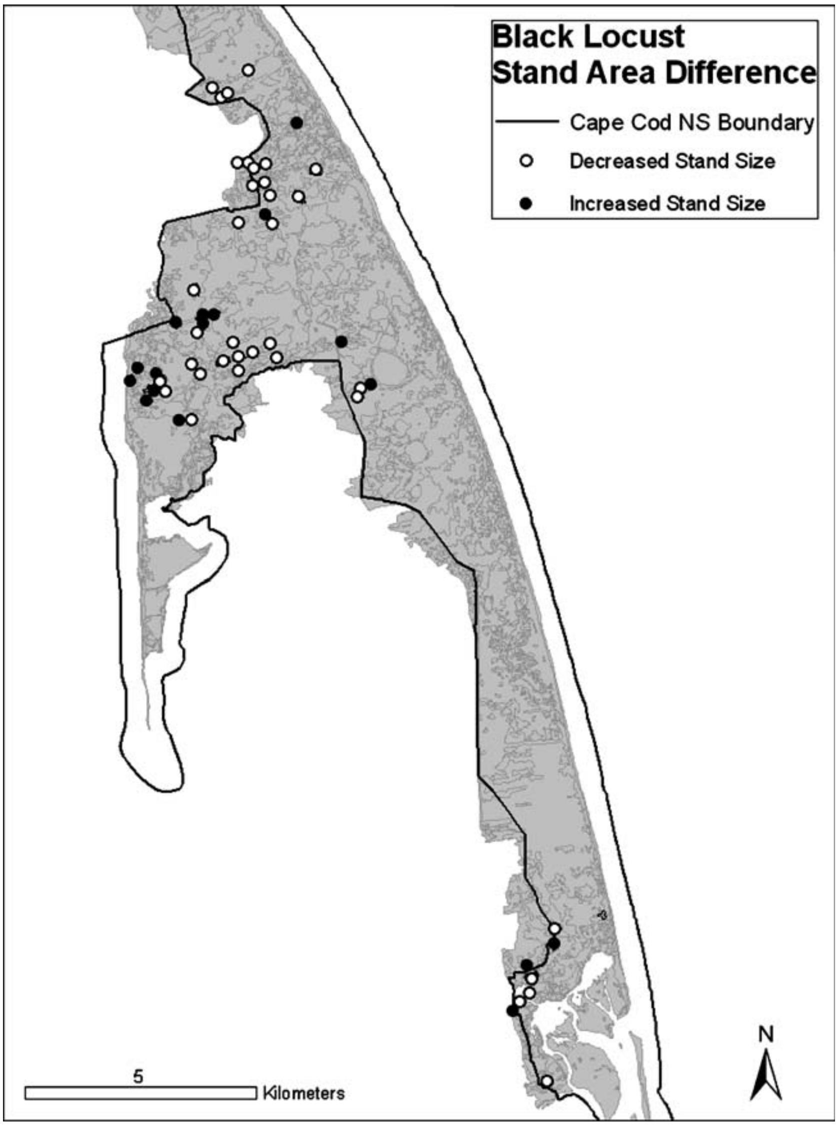


Figure 1. Black locust stands within Cape Cod National Seashore that increased in area (black) and those that decreased in area (white) from the 1970's to 2002.

Results

Soil characteristics

Soil nutrients (P, Ca, Mg, K, Mn, N) and percent organic matter were higher under *Robinia* than paired native stands, with almost a doubling of total nitrogen. However, none of the individual edaphic characteristics were significantly different between stands, after Bonferonni corrections (Table 1), suggesting that there is substantial variability within and among stands in these soil properties, or that the sample sizes were not large enough. However, when considered together, the edaphic characteristics were significantly different between stand types, according to an unpaired t-test of plot scores generated by principle components analysis (Table 1, t-test of PCA scores, $t = 3.8$, $p = 0.0007$).

Black locust and native stand composition

On average, the upper canopy cover of the locust and adjacent native stands were 44% and 36%, respectively, and were not statistically significantly different, according to unpaired Student t-tests. Paired native stands were dominated by the overstory species *Pinus rigida* (71%), with 29% stands containing mixed pitch pine–oak (*Quercus velutina or Quercus alba)* communities. Total plant species richness and cover were significantly higher within *Robinia* stands than within the native pine and mixed pine–oak stands, according to unpaired Student's t-tests (richness $t = 4.81$, $p < 0.0001$; cover $t = 3.29$, $p = 0.002$). These patterns were largely driven by an increase in nonnative species richness and cover within the black locust stands. The native and nonnative richness and percent cover values of the black locust and paired native stands were significantly different, according to Kruskal–Wallis tests (Figure 2a, richness; $\chi^2 = 49.7$, df $= 3$, $p < 0.0001$; Figure 2b, cover; $\chi^2 = 38.5$, df $= 3$, $p < 0.0001$). Understory nonnative species richness and percent cover values were statistically significantly higher under *Robinia* stands than under the paired native stands, according to Tukey–Kramer post-hoc tests. However, understory nonnative species richness in *Robinia* stands was significantly lower than native species richness within those stands and in paired native stands. Nonnative species in *Robinia* stands were significantly lower in percent cover than native species within paired native stands; however, nonnative species cover was not significantly different than native cover in *Robinia* stands. Native species richness and percent cover were no different between locust and native stands.

Native species richness in *Robinia* plots was significantly, positively predicted by the average age of the stand, according to simple regression analysis ($r^2 = 0.45$, $p = 0.0066$). In contrast, nonnative species richness and the total species richness of the plot were not related to the average age of the *Robinia* stand.

A nonmetric multidimensional analysis (NMDS) reveals disparate communities associated with black locust and native pitch pine and pitch pine–oak communities (Figure 3), which may be due to the different edaphic characteristics of the soils between the *Robinia* and native pine/oak communities. Decreases in axis one and increases in axis two of the NMDS were associated

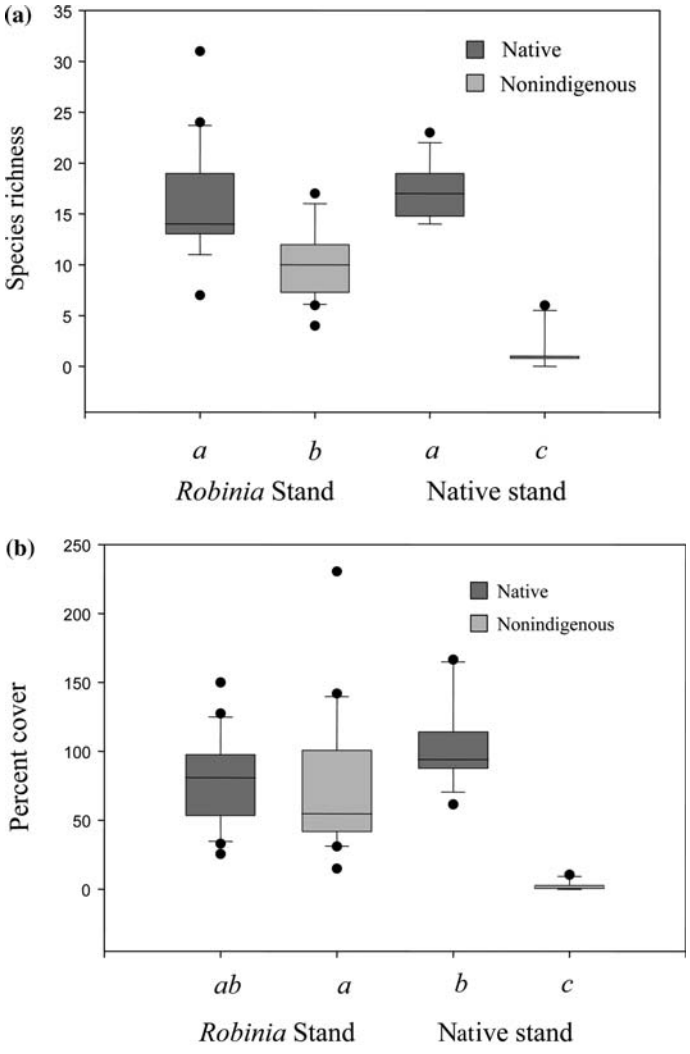


Figure 2. Nonnative species richness (a) is significantly higher under *Robinia* stands than paired, native stands (Kruskal–Wallis, $\chi^2 = 49.7$, df $= 3$, $p < 0.0001$). Additionally, nonnative percent cover (b) values were statistically significantly higher under *Robinia* stands than under the paired native stands (Kruskal–Wallis, $\chi^2 = 38.5$, df $= 3$, $p < 0.0001$). Data were categories of species cover class and associated environmental parameters. Different letters indicate Tukey–Kramer post-hoc p values < 0.05.

with increased potassium, nitrogen, sulfur, magnesium and calcium content. Moreover, the two native stands closest in multivariate space to the locust stands had greater soil organic composition and nutrient content than the other paired native stands. The native species *Solidago rugosa, Rubus allegheniensis, Rosa carolina*, and *Galium aparine* were significantly associated with

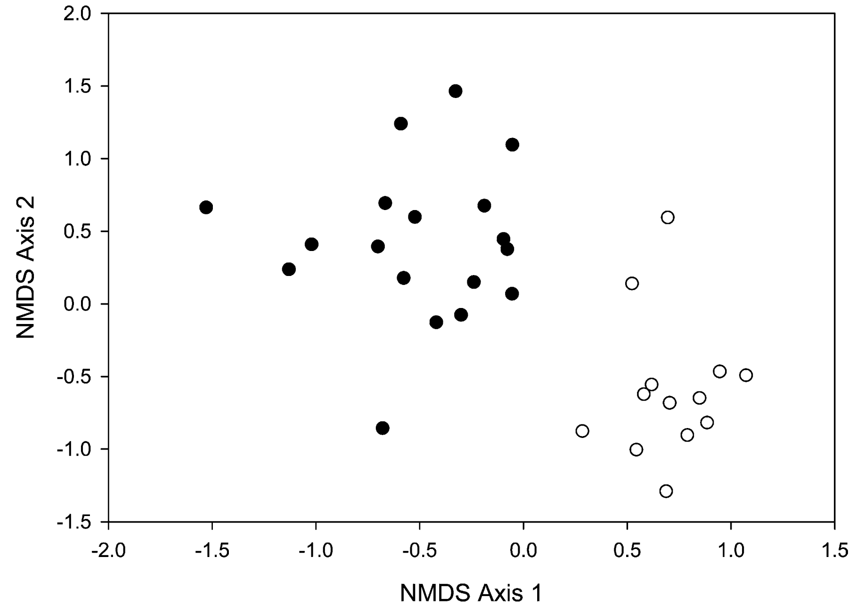


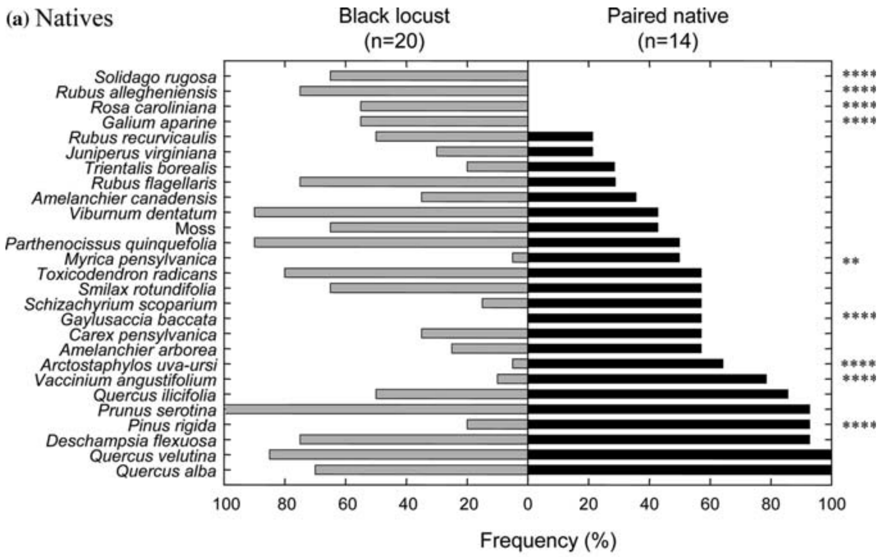
Figure 3. Nonmetric multidimensional scaling of black locust plots (black dots) and paired native (clear dots) stands. The two-dimensional solution had a final stress value of 11.07, and a final instability of 0.00011.

black locust stands and *Myrica pensylvanica*, *Gaylusaccia baccata*, *Arctostaphylos uva-ursi*, *Vaccinium angustifolium*, and *Pinus rigida* were significantly associated with native pitch pine and mixed pine–oak stands (Figure 4a), according to *G*-tests of independance. The nonnative species *Rosa multiflora*, *Poa pratensis*, *Convolvulus arvensis*, *Holcus lanatus*, *Lonicera morrowii*, and *Lonicera japonica*, were significantly associated with black locust stands (Figure 4b). There were no nonnative species that were significantly associated with native pine and pine–oak stands.

Dispersal of nonnative species between black locust stands

Animal dispersal may play a role in the distribution of nonnative species within black locust stands. Six out of the eight tests of the degree of similarity of nonnative animal-dispersed species composition between black locust stands were negatively related to the distance between stands. While none of these tests were statistically significant, these relationships explained up to 36% of the variance of the distribution of animal-dispersed species (Table 3). Locust stand composition of nonnative species with other dispersal mechanisms (wind, ballistic, water) was unrelated to distance between stands (Table 3). The range of pairwise stand distances was 185 m to 2.3 km.

(a) Natives



(b) Nonnatives

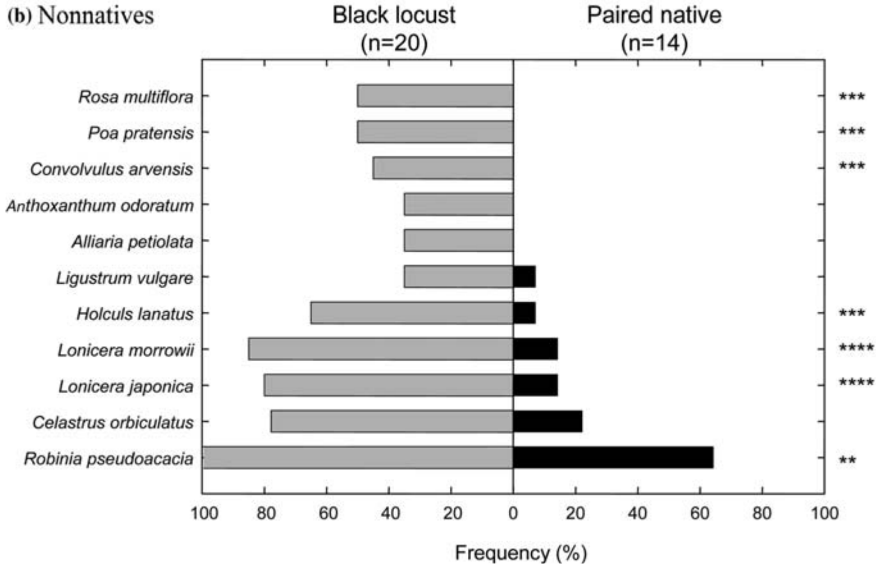


Figure 4. Frequency of occurrence (%) of common native (a) and nonnative (b) plant species within *Robinia pseudoacacia* and paired native study stands in Cape Cod National Seashore. Only species occurring on at least 7 plots (20% of total) are shown. Significance of the likelihood ratio of the χ^2 tests is indicated at the $p < 0.01$ (**), $p < 0.001$ (***), $p < 0.0001$ (****), levels after accounting for multiple comparisons.

Robinia pseudoacacia distribution

The majority of black locust stands (43 out of 53) decreased in area from its historical size, with an average decrease of 2,610 m^2 ± 2,551 s.d. (Figure 1). Stand area did not change significantly from 1970 to 1978, according to paired Student t-tests of the historical stand area subtracted from the current size. Thus, the 1970 and 1978 stands were lumped together as the 'historical' stands. *Robinia* stand area significantly decreased over time, according to paired t-tests of historical and current stand size ($t = -6.49$, $p < .0001$). Moreover, this decrease did not depend on whether the stand was close (< 5 m) or farther away (> 5m) from roads (unpaired t-test, $t = 1.42$, $p = 0.16$). Additionally, current understory regeneration of black locust was negligible. Twenty-five percent of plots had an average of 3 sprouts in the surveyed 20 m plot periphery. Understory locust regeneration is statistically significantly related to the proximity of the stand to the road and is not significantly related to the age of the stand, according to significance values of individual parameters of the logistic regression analysis [Pearson $\chi^2 = 2.2$, Locust regeneration likelihood = 0.62–0.004 (distance to road) –0.002 (average stand age)]. Nonnative species richness within *Robinia* stands was unrelated to the distance from roads, indicating that locust stands closer to roads are not experiencing greater invasion by nonnative species.

The range of tree ages in the sampled stands was 8–80 years, with an average age of 41.6 (± 18.2) years. Tree ages were variable within a stand, suggesting that natural expansion occurred from parent trees. The average age of these stands is much lower than the age that would be expected, given that agricultural abandonment occurred in the 19th and early 20th centuries (Stone 1999). This discrepancy could owe to the short life span of this species or the susceptibility of older trees to windthrow. Many of the larger trees could not be cored because of heart rot or because they had fallen within the plot.

Discussion

The introduction of a novel functional type (leguminous nitrogen-fixing tree) into this upland forested ecosystem facilitates invasion by other nonnative species into this naturally invasion-resistant system (Von Holle et al. in preparation). Facilitations between nonnative species have been largely ignored in ecological studies, yet this type of interaction may have significant impacts on native ecosystems (Simberloff and Von Holle 1999). Black locust has been found to increase the cover and growth of both native and nonnative species in a variety of habitats. Nitrogen fixation in black locust stands in *Quercus velutina* savannas and woodland dune communities in northern Indiana led to increased establishment and spread of a nonnative grass, *Bromus tectorum* (Peloquin and Hiebert 1999). Likewise, Dzwonko and Loster (1997) reported higher cover of nitrophilous and ruderal species under black locust stands and greater cover of heathland species under Scots pine (*Pinus sylvestris*) stands in abandoned sandy grassland in a suburban landscape in southern Poland. They attributed this to the greater soil nitrogen availability and light under locust stands. The degree of nonnative plant invasion in pitch pine-dominated and hardwood forests of Long Island, NY, is positively related to higher rates of soil mineralization and nitrification and total soil content of calcium, magnesium and phosphorous (Howard et al. 2004). Our study demonstrates altered soil nutrients in addition to greater numbers and cover of nonnative species within locust stands as compared to native pine–oak and pine stands. Higher nutrient levels within black locust stands are most likely the cause for greater nonnative understory species richness and abundance levels. The added nutrients may allow nonnative plant species to persist within this xeric, nutrient poor, sandy, upland ecosystem. In this system, black locust stands serve as refuges for other non-native plants.

Despite the significant increase in nonnative species richness and cover within *Robinia* stands, this species does not appear to directly or indirectly affect native species richness or cover. However, *Robinia pseudoacacia* clearly changes the native and nonnative species composition. Native species that were less likely to be found within black locust stands include *Myrica pensylvanica*, *Gaylusaccia baccata*, *Arctostaphylos uva-ursi*, *Vaccinium angustifolium*, and *Pinus rigida*. With the exception of *P. rigida* and *M. pensylvanica*, these are ericaceous shrubs that may not be adapted to the rich soils found under the black locust stands or may not be able to compete with the species present within locust stands. It is unlikely that these species have not been able to disperse into these stands (Donohue et al. 2000), as all of these species have been able to successfully colonize historically plowed lands on the Cape, with the exception of *Gaylusaccia baccata* (Eberhardt et al. 2003).

The forest structure within black locust stands is markedly different than the structure found within native communities with similar land use histories. The existence of the nonnative species *Celastrus orbiculatus*, *Lonicera japonica*, *Rosa multiflora*, and *Lonicera morrowi* add a significant tall shrub and vine layer that is missing from the usually low-statured pine–bearberry, pine–hairgrass, and pine–oak–sedge understory communities associated with agricultural land use. As a result of the dense shrub community, native bird species appear to occur in greater abundances within the black locust communities than in other native forests (Von Holle, personal observation), and these birds may play a role in dispersal of the associated nonnative species. The linear decrease in nonnative animal-dispersed community similarity with distance from a focal stand mirrors the trend found for island bird community similarities with distance from the closest island to New Guinea (Diamond 1972). This suggests that, over time, animal dispersal of nonnative species between locust stands may have a significant long-term impact on nonnative species distributions. Control of nonnative bird-dispersed species within these stands may become a management priority. The lack of a relationship between nonnative wind-dispersed community similarity with stand distance is unsurprising, in view that the shortest distance between the randomly-selected study stands was 185 m. Stands within 100 m or less of each other may have greater overlap of wind-dispersed species. Likewise, the dispersal between stands via anthropogenic road disturbance does not appear to play a role in structuring these locust communities. Furthermore, the very low numbers and cover of nonnative species found within the native pitch pine and mixed pine and oak stands only 20 m from the edge of locust stands suggest that many nonnative species are unable to establish in this resistant forest matrix surrounding these highly invaded 'islands of invasion'.

The uneven age structure of the black locust study stands suggests that locust stands expanded across open areas following agricultural abandonment. Since the 1970's, black locust cover has declined across this landscape, most likely owing to its adaptation to open areas and the increase in forested area in Cape Cod since the early 20th century (Motzkin et al. 2002). Hurricane Hugo, which occurred in 1989, was most likely the cause of the significant decrease in landscape cover of this species from the 1970's to 2002. Windthrow of black locust was greater than that of native species from this event (W.A. Patterson, personal communication). The lack of regeneration of this species, combined with the significant natural decline in landscape cover makes it likely that this species will become a small part of this natural area in the future. Additionally, the increased numbers of native species within these stands over time indicates a slow colonization of these nitrogen-rich stands over time, which may result in eventual native species domination following the depletion of the unnaturally high nitrogen levels in the soils. Last, the presence of the canopy tree species *Prunus serotina*, *Quercus alba* and *Q. velutina* in 100%, 70%, and 85% of the black locust stands respectively, suggests eventual succession to native canopy species. We do not recommend control of black locust within Cape Cod National Seashore at this time, as it is in decline within the reforesting matrix. Removal of this overstory nonnative may result in nonnative understory species flourishing under conditions of an open canopy and enriched soils. However, in other locations where locust stands occur within open areas and where there is opportunity for expansion, the control of this species should be a priority, given its ability to facilitate other nonnative species.

Conservation implications

The natural decline of this species within the forested landscape of Cape Cod National Seashore should not alleviate concern regarding management of this species elsewhere. Ecosystem impacts of this species may change with anthropogenic atmospheric inputs. Elevated levels of atmospheric carbon dioxide increases *Robinia pseudoacacia* biomass production, nodulation, N and P content, and root N absorption (Olesniewicz and Thomas 1999), yet this species is sensitive to ozone (Porter 2003). However, the prediction of changes in tree species distribution and forest functioning in response to global climate change is difficult (Saxe et al. 2001). Forested areas that are becoming increasingly fragmented and cleared by development may experience increased cover of black locust. Xeric, nutrient-poor, and sandy ecosystems lacking in native leguminous nitrogen-fixing trees may be especially susceptible to facilitations between black locust and nonnative species that are not able to survive outside these stands. These black locust stands may, in turn, serve as sources for nonnative species dispersal, suggesting that co-occuring animal-dispersed nonnative species should be monitored for spread and controlled if necessary. The somewhat enriched soils and high levels of nonnative species accrued by the *Robinia pseudoacacia* presence may provide a long-lasting legacy across formerly agrarian landscapes, where many of these relic stands now persist. In sum, the complex interaction between soil composition, the nonnative species that exist within the invaded ecosystem, and the degree of fragmentation of the landscape is important to consider when making management decisions regarding this species.

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