Ecosystem legacy of the introduced N₂-fixing tree *Robinia pseudoacacia* in a coastal forest

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Abstract Habitat invasibility has been found to increase dramatically following the alteration of ecosystem properties by a nonnative species. *Robinia pseudoacacia*, black locust, is a nitrogen-fixing, clonal tree species that aggressively invades open habitats and expands outside of plantations worldwide. *Robinia pseudoacacia* stands in Cape Cod National Seashore were particularly susceptible to a hurricane in 1991 that caused widespread blowdown and a dramatic reduction in *Robinia* in some stands. We used this change to investigate the lasting ecological effects of this nonnative species on this upland coastal ecosystem. We established replicate clusters of 20×20 m field plots within 50 m of each other that contained native pitch pine (*Pinus rigida*) and oak (*Quercus velutina*, *Q. alba*) forest, living *Robinia* stands, and stands in which *Robinia* was eliminated or reduced to less than 5 % cover by the hurricane. Net nitrification and extractable soil nitrate concentration differed significantly between stand types, in the order *Robinia* > former *Robinia* > pine-oak. Nonnative species cover differed significantly between each stand type, in the order *Robinia* > former *Robinia* > pine-oak. Invasion of *Robinia pseudoacacia* increased soil net nitrification and nitrogen availability and precipitated a change in forest species composition that favored nonnative species. The presence of elevated soil nitrogen and nonnative species persisted at least 14 years after the removal of the original invading tree species, suggesting that the invasion of a tree species left a legacy of altered soil biogeochemistry, a higher number of nonnative species, and greater nonnative species cover.

Keywords Black locust · Facilitation · Invasion ecology · Legacy effects · Nitrogen cycling

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Introduction

Nonnative species that alter ecosystem functions are considered to have the greatest impacts on native biodiversity (Mack and D'Antonio 1998; Parker et al. 1999; Vitousek 1990). Habitat invasibility has been found to increase dramatically following the alteration of ecosystem properties by a nonnative species (Mack and D'Antonio 1998). The ecosystems that nonnative plant species have invaded have experienced altered fire regimes (D'Antonio and Vitousek 1992), nutrient cycling (Ehrenfeld 2003), hydrology (Di Tomaso 1998), soil salinity (Kloot 1983; Vivrette and Muller 1977), and soil microbial communities (Liao et al. 2008; Rout and Callaway 2009; van der Putten et al. 2007), permanently altering ecosystems in ways that prevent or decrease native species' ability to persist under the new conditions (Maron and Jeffries 2001; Corbin and D'Antonio 2004). Plant species capable of fixing atmospheric nitrogen have lasting impacts when they invade ecosystems that are relatively poor in nutrients (Corbin and D'Antonio 2004; Ehrenfeld 2003). Additionally, species with ecological functions that are novel to the recipient ecosystem [e.g., fixing nitrogen (N_2) where N_2 fixation was previously low] can have the largest effects (Vitousek et al. 1987; Vitousek and Walker 1989). For example, the nonnative nitrogen-fixing tree *Myrica faya* increased soil nitrogen input to 23.5 kg/ha/yr from 5.5 kg/ha/yr in uninvaded areas of young Hawaiian volcanic soils (Vitousek et al. 1987). The successional legacy left by this species is an additional impact, with fast-growing nonnative understory grasses filling the gaps following the death of this nitrogen-fixing overstory species (Adler 1998).

The presence of individual tree species can influence the important ecosystem process of N cycling in forest ecosystems. For example, stands of sugar maple (*Acer saccharum* Marsh) have lower C:N, higher extractable soil NO_3^-, and higher rates of net nitrification compared with stands of other tree species in northeastern US forests (Finzi et al. 1998; Lovett et al. 2004; Venterea et al. 2003). These differences, which indicate more rapid N cycling in sugar maple stands, can lead to changes to ecosystem functions at larger scales, such as higher NO_3^- watershed export in stream water (Lovett et al. 2002). Changes in N availability can also cause differences in growth rates among forest tree species, potentially leading to long-term changes in forest species composition (Zaccherio and Finzi 2007). This potential role for individual tree species suggests that invasion by a nonnative tree species that triggers changes to N cycling could have wide-ranging implications for both ecosystem biogeochemistry and species composition.

Black locust (*Robinia pseudoacacia* L.), hereafter "*Robinia*," is considered to be one of the top 100 woody plant invaders worldwide (Cronk and Fuller 1995).

Its ability to fix N_2 and to reproduce clonally are two of the five characteristic traits of natural area invaders (Daehler 1998). *Robinia* is thought to pose a threat to native species because of its ability to form dense, monospecific stands that may crowd out native vegetation (Mehrhoff et al. 2003). For example, nonnative species richness under *Robinia* stands in the northeastern coastal US is ten times higher than under paired native stands 20 m away (Von Holle et al. 2006).

Robinia's large effect on species composition may be linked to its substantial effect on soil characteristics. In eastern forests, soils under *Robinia* have elevated levels of N, P, and Ca as well as increased net N mineralization and net nitrification rates compared with adjacent native pine-oak stands (Rice et al. 2004). In the southern Appalachians, soils under *Robinia* have greater total N, organic matter, and nitrate than uneven-aged mixed oak (primarily *Quercus prinus*) forests (Boring and Swank 1984). In a study of the effects of *Robinia* restoration on soil nitrogen in the pine-scrub oak barrens of New York, Malcolm et al. (2008) found that soil nitrogen concentrations and net N mineralization rates were reduced to levels similar to native stands two years after *Robinia* trees were physically removed from the sites and native plantings were established. Additionally, net nitrification rates were significantly reduced in the restored *Robinia* stands four years after restoration (Malcolm et al. 2008). In the study presented here, we aimed to examine the link between *Robinia*'s effect on soil characteristics and species composition and the potential for legacy effects by *Robinia*, following the loss of this species as the canopy dominant due to a hurricane disturbance.

Previous land use can also alter soil chemical characteristics and species composition across ecosystems, but the lengths of the legacies of these effects can vary. For example, widespread land tillage during the nineteenth century in the northeastern United States led to a forest tree and herb species composition that differs from that of old growth forests as well as secondary forests that developed on land previously used only as woodlots (Bellemare et al. 2002; Eberhardt et al. 2003; Motzkin et al. 1996). In some cases, the effects of previous tillage on soil characteristics and N cycling in reducing soil C:N, increasing soil N stocks and net N mineralization rates, and increasing nitrifying bacteria and net nitrification rates are ephemeral and do not persist beyond several decades (Compton et al. 1998; Neill et al. 2007). In other cases, however, changes to species composition, soil organic matter, and N cycling caused by alterations initiated by previous crop agriculture may be evident for a century or more (Compton and Boone 2000; Dupouey et al. 2002; Flinn and Vellend 2005; Koerner et al. 1997). While it is clear that previous land use can have long-lasting soil and species legacies, it is unclear

whether the invasion of a species that alters ecosystem properties can have long-lasting legacy effects. Important questions about these legacies include (1) do changes to soil N cycling alter forest species composition or facilitate invasion by nonnative species, and (2) how long will changes to soil biogeochemistry and species composition last in the absence of the original invader?

We investigated how the invasion and then subsequent decline in abundance of *Robinia* in the Cape Cod National Seashore (CCNS) in coastal Massachusetts (USA) influenced soil N biogeochemistry, forest species composition and the susceptibility of forests to invasion by nonnative plants. In addition, we investigated how the invasion of *Robinia* altered soil nitrogen biogeochemistry and forest species composition in pitch pine (*Pinus rigida*)-oak (*Quercus velutina*, *Q. alba*) forests. We also investigated the legacy of *Robinia* in areas that were previously invaded but in which live *Robinia* was no longer present because black locust stands were dramatically reduced by a hurricane in 1991.

We hypothesized that the *Robinia*-invaded stands would have elevated levels of soil N as compared to native pine-oak stands, and that N availability, N cycling rates, and the richness and density of nonnative species would decrease in stands that previously had *Robinia* but no current living *Robinia* trees. We tested these hypotheses by comparing indices of soil N availability and the understory vegetation of clusters of plots containing randomly selected *Robinia* stands, paired native pine-oak forest stands, and stands that formerly had *Robinia* but do not currently contain live *Robinia*.

Methods

In the northeastern United States, *Robinia* is an invasive tree species that has the potential to colonize open areas rapidly. Following establishment, it alters soil N cycling because it fixes N_2 through its association with *Rhizobium* soil bacteria and it spreads rapidly by clonal growth (Boring and Swank 1984). *Robinia* is an early successional, shade-intolerant tree species native to the central Appalachian and Ozark Mountains (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, resulting in a relatively short life span (Boring and Swank 1984). Historically, *Robinia* was selectively planted for its soil amendment properties, and as timber for fence posts, firewood, and insulator pins for telephone and transmission lines because of its characteristic strong, rot-resistant wood (Boring and Swank 1984; Cuno 1919; Ogden 1961). Today, *Robinia* stands are typically found near the sites of abandoned homes and farms within the matrix of native

pitch pine and oak forests across Cape Cod (Von Holle and Motzkin 2007).

In July 2005 we identified twenty stands containing live *Robinia* and fifteen native forest stands comprising predominantly pitch pine (*Pinus rigida*), black oak (*Quercus velutina*), and white oak (*Quercus alba*)—hereafter "pine-oak" stands—in the towns of Eastham, Wellfleet, and Truro in the CCNS. We defined living *Robinia* stands as having >25 % living canopy cover of *Robinia*. Pine-oak forest stands had <5 % *Robinia* canopy cover. We also identified ten "former *Robinia*" stands that were dominated by *Robinia* prior to the August 19, 1991 passage of Hurricane Bob, which had sustained winds of 120–160 km/h, knocked down trees and utility poles (Vallee and Dion 1998), and severely damaged many *R. pseudoacacia* stands (CN, personal observation). These hurricane-affected stands contained less than 5 % canopy of living *Robinia* at the time of sampling. These formed ten clusters that contained all three stand types and five additional clusters that contained only pairs of pine-oak and *Robinia* stands. All pine-oak and *Robinia* stands were separated by no more than 20 m, and the *Robinia* and former *Robinia* stands were separated by no more than 50 m, with an average distance of 18 m. We sampled fewer former *Robinia* stands because they were not present in close proximity to current *Robinia* and native stands in all cases. All stands had similar proximity to roads. We used historical aerial photographs to identify the date of canopy death for the former *Robinia* stands (Fig. 1). Surficial geological deposits in the study stands were Wisconsin outwash plains with gently sloping kame and kettle topography. Soils were Typic Quartzipsamments of the Carver series (Fletcher 1993).

All *Robinia*, former *Robinia*, and pine-oak stands were located within land classified as "open" in the mid-nineteenth century (Hall et al. 2002). This land-use category comprises historically plowed or pastured land (Eberhardt et al. 2003). All *Robinia* and former *Robinia* stands had two or more of the six species strongly associated with past tillage (Eberhardt et al. 2003), indicating that they were formerly plowed. These proxy associations of historical land use were used because direct methods of determining land-use history were not permitted in the stands due to regulations prohibiting soil disturbance on US National Park Service lands (National Trust for Historic Preservation 1999). In addition to our proxy associations of historical land use, we had direct evidence of plowing and observed soil plow horizons in eight pine-oak, five *Robinia*, and seven former *Robinia* stands.

Soil sampling and analysis

We characterized the soil properties of all stands in July and August 2005 by systematically taking four soil cores
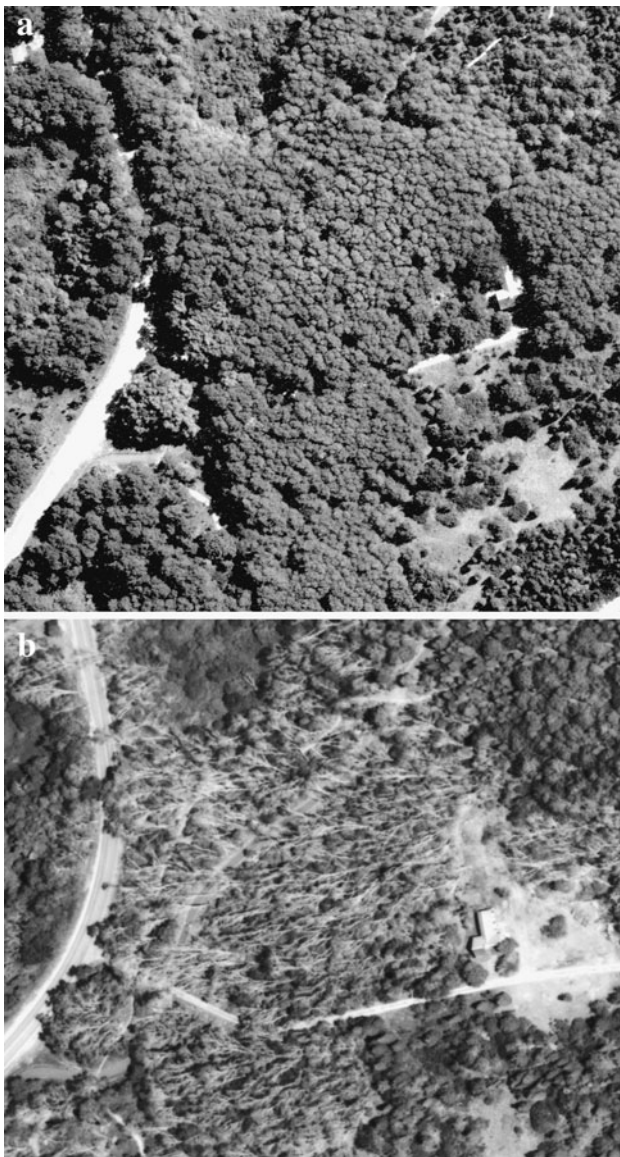
Fig. 1 Aerial photographs of a representative former *Robinia* stand (salt pond site) taken before and after Hurricane Bob, which hit Cape Cod on August 19, 1991. **a** Photograph taken on September 15, 1987. *Robinia* trees appear clumped, with healthy, full crowns. **b** Photograph of the same stand taken on September 8, 1991, four years after the original photo and 20 days after Hurricane Bob. The majority of the downed trees are *Robinia*, as identified in the field. As an aid to comparing the pictures, note the white house in the *middle right* of the image

approximately 10 cm deep along a randomized diagonal axis through a 20 × 20 m plot centered within each stand. Soil samples were pooled into one composite sample per plot. Samples were air dried and sieved (<2 mm). Soil pH (1:1 in water), percent organic matter (loss on ignition), total N (elemental analysis), and extractable P, Ca, Mg, K, Al, and Na (Melich III extraction) were analyzed by Brookside Labs, Inc. (New Knoxville, OH, USA).

We sampled the ten clusters that contained all three stand types (*Robinia*, former *Robinia*, and pine-oak) for soil nitrogen levels. We collected soil for extractable ammonium and nitrate and measured net N mineralization and net nitrification rates in each stand during both July and August 2005 to determine if there were differences in soil inorganic N pools and N transformation rates during the warmest summer months. We measured net N mineralization and net nitrification rates using the buried bag incubation method (Eno 1960). We collected 10 cm deep soil samples at ten points located uniformly along a randomized diagonal axis through each stand. We then collected ten paired core samples that were encased in one-quart plastic bags, buried to the same depth in the A horizon, and incubated for 30 days. All soil collections were performed and incubations initiated at least 24 h after the last rainfall. Soil cores clearly damaged by animals were discarded. All soil samples collected from the field were placed immediately on ice and processed within 8 h of collection. Soils were sieved through a 2 mm mesh sieve, and 10 g of soil was extracted in 50 ml of 2 M KCl for 24 h and then filtered through GFF filters. Ammonium concentrations in extracts were measured on a Lachat QuikChem FIA + 8000 series analyzer by phenol hypochlorite (Lachat method 12-107-06-1-A). Nitrate concentrations were measured by Cd reduction (Lachat method 12-107-04-1-B).

To investigate the possibility that natural patch-scale variation in soil nitrate (i.e., that native sites contain patches with high levels of soil nitrate that *Robinia* preferentially invades) is responsible for the higher levels of soil nitrate observed in the former *Robinia* and *Robinia* stands, we plotted a histogram of the nitrate soil values of the ten individual soil samples taken from each land-use type at the initial sampling period (Fig. 2). We used analysis of variance to test for differences in net N mineralization and net nitrification rates, and used stand type as the independent variable. We performed two-way analysis of variance to test for differences in NH_4^+ and NO_3^-, with stand type and month as the main effects. Data were log transformed where necessary to meet the assumptions of a normal distribution. We used Kruskal–Wallis tests to determine differences in soil pH, organic matter, total N, and extractable P, Ca, Mg, K, Al, and Na among stand types.

Vegetation sampling and analysis

To determine the effect of *Robinia* and former *Robinia* stands on native and nonnative species distribution and abundance, we surveyed a 20 × 20 m plot in the center of each stand from June–August of 2003 and July–August
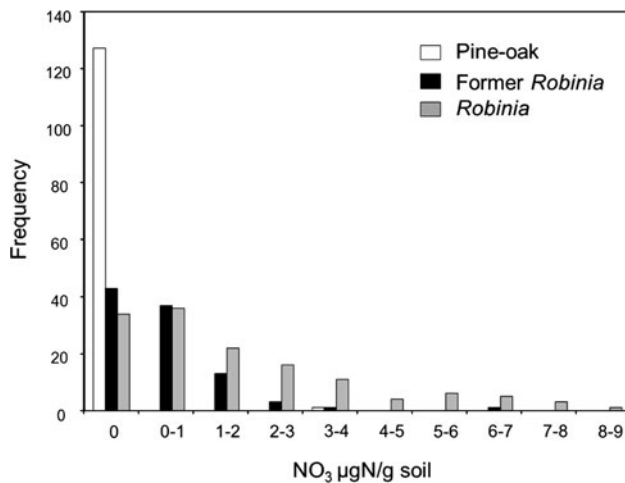
Fig. 2 Frequency distribution of NO_3 µgN/g soil (*x*-axis) for the ten individual samples taken from each plot and stand type: native pine-oak stands (*white bars*, paired *Robinia* stands (*gray bars*), and former *Robinia* stands (*black bars*)

of 2004. We compared the species cover and richness of twenty *Robinia* stands, nine former *Robinia* stands, and fifteen pine-oak stands. Total canopy cover of each canopy stratum was estimated visually. Percent cover of all herb, shrub, and tree species were estimated in eight cover–abundance classes using modified Braun–Blanquet cover classes (Mueller-Dombois and Ellenberg 1974), as in Von Holle and Motzkin (2007): <1, 13, 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. We summed subcanopy and canopy coverage for our visual estimation of total canopy cover for each plot. Species richness for each plot was determined from all strata of the canopy, canopy, subcanopy, shrub, and herbaceous layers. Nomenclature followed Gleason and Cronquist (1991) and plant origin (native or nonnative) followed Sorrie and Somers (1999). We conducted two-way analyses of variance for differences in species richness and cover, with plant origin (native, nonnative) and stand type as the main effects. We square-root transformed the data to meet the assumptions of a normal distribution (Zar 1999). We conducted Kruskal–Wallis tests to determine differences in canopy cover between stand types. To determine if the stand types differed in community composition, we conducted a nonmetric multidimensional scaling (NMS) analysis with six axes, forty runs of real data, fifty runs of randomized data, and an instability criterion of 0.00001 using PC-ORD, version 4.

To correct for multiple testing, we used the sequential Bonferroni technique (Rice 1989). With the exception of NMS analyses which used PC-ORD, version 4 (McCune and Mefford 1999), all statistical analyses were performed using SAS, version 8.

Results

Stand cover and *Robinia* mortality

There were no significant differences in total canopy cover between *Robinia*, former *Robinia*, and native pine-oak stands (Kruskal–Wallis test, $\chi^2 = 2.41$, $df = 2$, $p = 0.30$).

Each of the ten sampled former *Robinia* stands contained a canopy of living *Robinia* trees as of September 15, 1987. In addition, the *Robinia* trees in these stands were alive as of September 12, 1970 and April 23, 1978, as documented in aerial photographs. Photographs taken on September 8, 1991 indicated that eight of the stands had experienced substantial blowdowns (Fig. 1), and two of these stands had extremely low leaf cover. Hurricane Bob, which hit Cape Cod in August 1991 and caused widespread windthrow of trees, was most likely the cause for the extensive stand mortality. The majority of *Robinia* trees rooted inside all "former *Robinia*" stands were dead as of the time of sampling. Field surveys revealed that living *Robinia* trees comprised 25–60 % of the canopy of the *Robinia* stands, 0–5 % of the former *Robinia* stands, and never occurred in the canopies of the native pine-oak stands. The dominant canopy tree species of the *Robinia* stands was *Robinia*, with one stand containing *Pinus rigida*. The dominant canopy tree species in the former *Robinia* stands were *Pinus rigida*, *Quercus velutina*, and *Prunus serotina*. In the native pine-oak stands, the canopies were dominated by *Pinus rigida*, *Quercus alba*, and *Quercus velutina*. Interestingly, the subcanopies of the *Robinia* stands were dominated by *Prunus serotina*, *Juniperus virginiana*, and *Quercus velutina*, and the subcanopies of the former *Robinia* stands were dominated by *Prunus serotina*, *Quercus alba*, and *Quercus velutina*, whereas the subcanopies of the native pine-oak stand were dominated by *Quercus alba*, *Quercus velutina*, and *Juniperus virginiana*. With the exception of *Robinia*, none of these canopy or subcanopy tree species have the ability to fix nitrogen (USDA 2012).

Soil properties and soil N cycling

Total soil N, extractable soil P, and extractable soil Ca were higher in *Robinia* stands and former *Robinia* stands than in pine-oak forest stands (Table 1). Extractable soil ammonium and nitrate and rates of net mineralization and net nitrification did not differ by sample month (July and August 2005). Soils of both *Robinia* and former *Robinia* stands had significantly higher extractable ammonium compared with the pine-oak stands (Fig. 3b; $F = 18.76$, $p < 0.0001$). Extractable nitrate was significantly higher in *Robinia* stands than in former *Robinia* stands, and former *Robinia* stands had significantly higher extractable
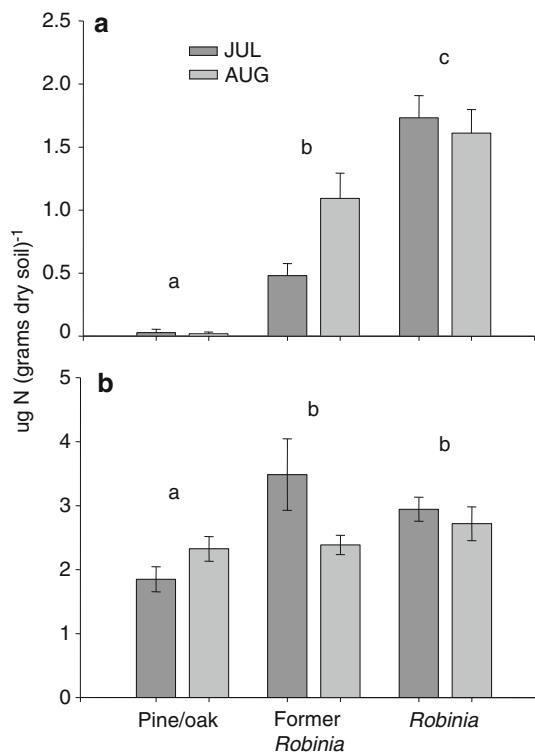
Fig. 3 Concentrations of extractable nitrate (**a**) and ammonium (**b**) in the soil of native pine-oak stands, former *Robinia* stands, and *Robinia* stands. Data are untransformed. *Different letters* denote statistically significant differences, as indicated by two-way analysis of variance, with month and stand type as the two classes. Soil nitrate and ammonium concentrations did not differ by month. Soil nitrate concentrations were significantly higher under *Robinia* stands than in former *Robinia* stands and pine-oak stands. Both former *Robinia* and *Robinia* stands had significantly elevated levels of ammonium compared with pine-oak stands

nitrate than native pine-oak stands (Fig. 3a; $F = 144.2$, $p < 0.0001$). In the pine-oak stands, 127 samples had zero nitrate in the soils, and one sample had 3.5 μg NO_3/g soil. For the *Robinia* stands, soil nitrate levels ranged from 34 samples with zero nitrate to one sample with over 8 μg NO_3/g soil (Fig. 2). Net N mineralization rates were not significantly different between the three stand types; pine-oak, former *Robinia*, and *Robinia* (see Table S1 of the Electronic supplementary material, ESM). However, net nitrification rates were 11.5 times greater in the *Robinia* stands than in the pine-oak stands. Furthermore, net nitrification rates were 1.5 times greater in the *Robinia* stands than in the former *Robinia* stands (Table S1 of the ESM).

Community effects

Species richness differed by stand type ($F = 14.9$, $p < 0.0001$), plant origin ($F = 229.5$, $p < 0.0001$), and their interaction (stand type × plant origin, $F = 27.8$, $p < 0.0001$), as indicated by two-way analysis of variance (Fig. 4a).

Nonnative species richness was significantly higher in *Robinia* and former *Robinia* stands than in pine-oak stands (Fig. 4a, mean ± SE: pine-oak 1.67 ± 0.50, former *Robinia* 7.22 ± 1.27, *Robinia* 9.4 ± 0.75). There were no differences in native species richness among stand types (Fig. 4a). Percent cover was significantly different by stand type ($F = 25.4$, $p < 0.0001$), plant origin ($F = 110.3$, $p < 0.0001$), and their interaction (stand type × plant origin, $F = 44.9$, $p < 0.0001$) (Fig. 4b). Pine-oak stands had significantly higher cover of native species than former *Robinia* stands, but native species cover in *Robinia* stands did not differ significantly between former *Robinia* or pine-oak stands. Cover of nonnative species under the
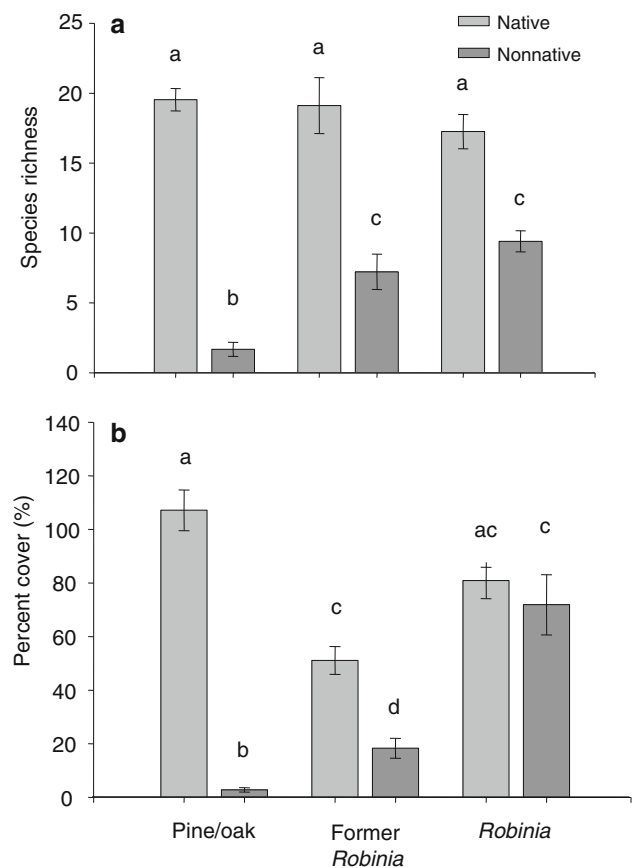
Fig. 4 Native and nonnative plant species richness (**a**) and percent cover (**b**) by stand type. Untransformed data are presented. *Different letters* denote statistically significant differences, as indicated by two-way analysis of variance with plant origin (native, nonnative) and stand type as the classes. **a** Nonnative species richness was significantly higher in *Robinia* and former *Robinia* stands than native pine-oak stands. There were no differences in native species richness between stand types. **b** Native stands had significantly higher percent cover of native species than former *Robinia* stands, but native species cover in *Robinia* stands did not differ between former *Robinia* and pine-oak stands. Nonnative species cover was highest in *Robinia* stands, followed by former *Robinia* and pine-oak stands. Cover was estimated for each species within a stand and can be more than 100 % because of overlapping forest strata

Robinia stands was 25 times higher than nonnative species cover in pine-oak stands and six times higher in the former *Robinia* stands than in the pine-oak stands (Fig. 4b, mean ± SE: *Robinia* 71.85 ± 11.25, former *Robinia* 18.3 ± 3.74, and native 2.8 ± .80).

A nonmetric multidimensional analysis (NMS) reveals disparate communities associated with *Robinia* and former *Robinia* communities, compared with the native pitch pine and pitch pine-oak communities (see Fig. S1 in the ESM). The cluster of native stands was clearly separate from that of the *Robinia* and former *Robinia* stands, indicating differences in species composition (see Table S1 in the ESM), which appear to be driven by the different edaphic conditions of the soils between the *Robinia*, former *Robinia*, and pine-oak communities. Increases in axis one and decreases in axis two of the NMDS were associated with increases in nitrate and potassium levels in the soil. Increases in axis one were also associated with increased total soil N.

Discussion

Legacy effects of *Robinia* invasion

Higher concentrations of extractable soil N and higher rates of net nitrification in *Robinia* stands and in former *Robinia* stands compared with native pine-oak stands suggest that the invasion by *Robinia* significantly altered soil N availability and patterns of N cycling. The vast majority (127 of 128) of the pine-oak soil samples analyzed in this study contained no detectable levels of nitrate, making it highly unlikely that native sites contain patches with high levels of soil nitrate that *Robinia* preferentially invades. The presence of *Robinia* left a legacy of changes to soil N cycling that lasted 14 years after *Robinia* trees were destroyed. The relatively high extractable ammonium, low extractable nitrate, and very low rates of net nitrification we observed in the native pine-oak forest soils were characteristic of coastal pine-oak forests and were consistent with low soil pH and modest rates of atmospheric N deposition in the Cape Cod region (Bowen and Valiela 2001; Lajtha et al. 1995; Neill et al. 2007). Invasion by *Robinia* increased the availability of soil inorganic N, presumably because of *Robinia*'s ability to fix N_2 by association with *Rhizobium*. The high nitrogen content of *Robinia* leaf litter and root and nodule tissues (Boring and Swank 1984) also speeds decomposition and further enhances inorganic N release (Melillo et al. 1982). These effects are qualitatively similar to those observed in other ecosystems invaded by plants associated with N_2 fixers (Vitousek et al. 1987). Increased supply of inorganic N favors nitrification and subsequent N export across a variety of forest ecosystems (Aber et al. 1989; Goodale et al. 2000).

Our findings were similar to those of Malcolm et al. (2008), who examined the effects of actively removing *Robinia* on soil N cycling in a low-nutrient central New York pine-oak forest. Malcolm et al. (2008) found that removing *Robinia* lowered net nitrification rates and that net nitrification rates of former *Robinia* stands remained higher than in the original uninvaded pine-oak forest. While Malcolm et al. (2008) found that *Robinia* removal significantly decreased total N-mineralization rates, we found that total N-mineralization rates remained high in former *Robinia* sites. Several factors could have contributed to this difference. These include the shorter time since *Robinia* removal and bulldozing, root raking, and seeding with grasses performed in the Malcolm et al. (2008) study. In the Malcolm et al. (2008) study, the roots were completely removed from the soil, whereas in our sites, large masses of nitrogen rich roots and associated *Rhizobium* bacteria were left behind in the soil to slowly decompose, likely enriching the soil. In addition, the Cape Cod pine-oak stands we studied had higher rates of net N mineralization (5 μgN/g/d compared with <0.5 μgN/g/d in New York), but this suggests that even on richer sites, the pattern of increased net nitrate production under *Robinia* and the decline in net nitrate production when *Robinia* are removed are similar between study systems.

In coastal forests on sandy soils, higher soil nitrate concentrations and nitrification rates may have important consequences for both forests and for adjacent coastal ecosystems because they have the potential to increase nitrate leaching and N loss to groundwater and streams in a region where anthropogenically driven increases in land-derived N inputs to coastal waters are linked to widespread eutrophication of coastal embayments (Seely et al. 1998; Valiela et al. 2000).

Previous land use can have effects on soil characteristics and stocks and turnover rates of soil organic matter that last many decades (Cambardella and Elliot 1994; Compton and Boone 2000; Jussy et al. 2002) or even centuries (Dupouey et al. 2002). In a New England coastal forest, Neill et al. (2007) found that subtle effects on soils of even relatively short periods of cultivation were still detectable 4–5 decades after cultivation ceased. Our study supports the growing recognition that a single plant species can exert a strong influence on N cycling (Hobbie 1992). Our findings indicate that the alteration of soil N cycling caused by *Robinia* was still apparent at least 14 years after the disappearance of the original invader. Similar legacy effects of species invasion even after the disappearance of the invader are rarely documented, and the ultimate durations of these changes are rarely known.

The mechanism behind the *Robinia* legacy is likely related to edaphic changes associated with this species, rather than to the physical disturbance to the soils caused

by the blowdown of overstory trees. An experimental hurricane blowdown conducted at the Harvard Forest, located approximately 270 km from our study sites, resulted in a doubling of potential net nitrification rates in blowdown areas compared to adjacent controls three years after the experimental manipulation (Carlton and Bazzaz 1998). If we assume that nitrification rates double after hurricane blowdown in the native pitch pine and oak forests adjacent to *Robinia* stands, the average nitrification rate found in native pine-oak stands (0.35 μg NO_3/g soil/day) would increase to 0.70 μg NO_3/g soil/day. This nitrification rate would still be significantly lower than the mean nitrification rates for the *Robinia* stands (4.6 μg NO_3/g soil/day) or the former *Robinia* stands (3.3 μg NO_3/g soil/day), so we assume that the legacy effect of increased nitrification rates and increased levels of soil nitrate in *Robinia* and former *Robinia* stands are from N_2 fixation effects associated with bacterial symbionts of *Robinia*, rather than the physical disturbance of blowdown. If changes to N cycling are more closely related to the quality of soil organic matter formed while *Robinia* was present than to the effects caused by changes to the composition of the vegetation initiated following *Robinia* invasion, the sandy soils and relatively short (~50 year) turnover time of organic matter in the soils of these coastal forests (Peterson et al. 2003) may limit the duration of these effects. While net nitrification levels were significantly higher in the former *Robinia* stands compared with native stands, they were also significantly lower (30 %) than in living *Robinia* stands, suggesting that if this trend continues, net nitrification levels might return to the low levels of native stands about 60 years following the death of the *Robinia* canopy.

We found that plant community composition differed significantly among stands, with characteristic species formations occurring under *Robinia* and former *Robinia* canopies that were distinct from those in native stands, and soil nitrate concentrations and net nitrification rates were closely associated with this pattern. Field surveys revealed that nonnative species richness was significantly higher in the *Robinia* and former *Robinia* stands, than in the pine-oak stands. Abundance of nonnative species was the highest in the living *Robinia* stands, followed by former *Robinia* and pine-oak stands. This is consistent with the observation that nonnative species richness levels were 80 and 85 % lower in the pine-oak stands than in the former *Robinia* and *Robinia* stands, respectively. In northern Indiana, cover of the high-impact nonnative species downy brome grass (*Bromus tectorum*) was found to be highest under mature *Robinia* trees, and to decrease in mean cover with decreasing *Robinia* age (Peloquin and Hiebert 1999). In our system, the very low levels of nonnative species in pine-oak stands is extraordinary, given that these stands

were less than 20 m from *Robinia* stands and not likely to be limited by propagule pressure.

Light availability is not likely to be the mechanism behind these high levels of nonnative understory species, as there were no significant differences in total canopy cover between *Robinia*, former *Robinia*, and native pine-oak stands. However, high light availability resulting immediately after the blowdown of *Robinia* trees in the former *Robinia* plots may have enabled the establishment of nonnative species which persist in the understory. Our results suggest that the high-nutrient conditions that occur in the soils of *Robinia* and former *Robinia* stands may foster high establishment and biomass of nonnative plant species, and that the low-nutrient conditions of the pine-oak soils may limit nonnative plant growth. The death of the canopy *Robinia* trees may lead to a slow decline in the richness and cover of understory nonnative species. Alternatively, the removal of the living *Robinia* overstory may have no effect on understory nonnative species, and the longer time period that the nitrogen-fixing *Robinia* remains as a canopy tree may allow greater nonnative species richness and (especially) cover, to increase over time. Furthermore, the invasion by *Robinia* may substantially alter the soil microbial community, which, in turn, could increase the nutrient dynamics and pools available for colonization by nonnatives (Liao et al. 2008). In a meta-analysis comparing invaded to native ecosystems, Liao et al. (2008) found that rates of soil net N mineralization and nitrification were significantly increased in invaded habitats relative to native ecosystems. Rout and Callaway (2009) suggest that these increases in soil N pools and rates of N cycling in invaded habitats may be due to the evolution of invasive plant traits that increase nitrogen cycling or, alternatively, the interaction of invasive plants and soil microbial communities to allow soil microbes to increase the nitrogen cycling of invading plants in recipient ecosystems (Callaway et al. 2004; Klironomos 2002). These varying hypotheses could be tested with research conducted over longer time periods, with stable N isotopes to differentiate between *Robinia* and non-*Robinia* derived N, or with manipulative experiments.

Conclusions

Soil alterations by nonnative species that lead to elevated nutrient levels appear to increase the likelihood that other nonnative species will invade these habitats. *Robinia* invasion is associated with highly altered soil biogeochemistry and plant community composition. These effects lasted for 14 years after the death of the original invader, suggesting the invasion of a tree species has lasting effects on soil biochemistry and forest species composition.

More generally, the ecological legacy of a nonnative plant will depend on the lifespan of the plant, its ability to resist successional development and shading, the rate of nutrient loss from the invaded soils once the invader has died, the associated microbial community, as well as whether the native species in the recipient ecosystem are adapted to low-nutrient conditions. At the landscape scale, we can think of these ecological legacies as high-nutrient, highly invaded patches, or "islands of invasion," shifting in nutrient levels and species composition over successional time (Von Holle et al. 2006).

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