Land use history alters the relationship between native and exotic plants: the rich don't always get richer

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Abstract Observational studies of diversity have consistently found positive correlations between native and exotic species, suggesting that the same environmental factors that drive native species richness also drive exotic species richness, i.e., "the rich get richer". We examined patterns of native and exotic plant species richness in temperate forests that have been undergoing reforestation since the turn of the twentieth century to test the influence of disturbance arising from land-use history on this relationship. Overall, we found no relationship between native and exotic plant species richness. Instead, we found a positive relationship between native and exotic richness in older but not younger-growth forests, suggesting that the same processes that drove exotic plant richness in older forests also facilitated native plants. In contrast, younger forests had similar numbers of native species relative to older forests, but 41% more exotic species and 24% more compacted soils. Moreover, exotic but not native species richness was positively correlated with increasing soil compaction across all sites. Overall, our results suggest that elevated exotic plant invasions in younger forests are a legacy of soil disturbance arising from agricultural practices at the turn of the century, and that native and exotic plants may respond differentially to disparate environmental drivers.

Keywords Soil compaction · Land use history

Introduction

Theory and experimental evidence suggest that biologically diverse native communities should limit the number and impact of alien invaders, e.g., "biotic resistance" (Case 1990; Naeem et al. 2000; Kennedy et al. 2002). Observational studies, however, have commonly found the opposite pattern, whereby native and exotic species are often positively correlated, e.g., "the rich get richer" (Stohlgren et al. 2003; Meiners et al. 2004; Gilbert and Lechowicz 2005; Fridley et al. 2007). One proposed explanation for the latter finding is that the same environmental factors that enhance alien species also enhance native species (Levine and D'Antonio 1999; Stohlgren et al. 1999). There have been few attempts, however, to distinguish whether native and exotic species respond similarly to gradients in environmental drivers across the landscape, thus generating the pattern of the "rich get richer."

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Disturbance is one of the principle factors widely linked to altered species diversity in general and to increased biological invasions in particular (Hobbs and Huenneke 1992; D'Antonio et al. 1999; Parks et al. 2005, Mosher et al. 2009). Sites with a recent history of disturbance, for example, often contain more exotic plant species than relatively undisturbed sites (Hobbs and Huenneke 1992; D'Antonio et al. 1999; Parks et al. 2005; Mosher et al. 2009). A predominant form of disturbance in today's natural ecosystems, however, is historical. Following a peak of agriculture in the early 1900s, increasing farm consolidation led to the widespread abandonment of small farmlands across much of eastern North America (Flinn and Vellend 2005), and these post-agricultural lands are often marked by distinctively different conditions than lands that have never been cultivated (Foster et al. 2003). Soils on historically cultivated sites, for example, are often more compacted, have greater bulk density, lower organic content, altered pH, and less microbial biomass than comparable non-cultivated sites (Burke et al. 1995; Compton and Boone 2000; Falkengren-Grerup et al. 2006; Maloney et al. 2008). The relationship between previous cultivation and soil nutrient availability is more variable and highly dependent on the type of agricultural regime followed (McLauchlan 2006), as well as the post-agricultural plant community (Knops and Tilman 2000; Kulmatiski et al. 2006). In addition to altered soil characteristics, post-agricultural lands often have dramatically different plant communities, including elevated numbers of exotic plants and altered plant community composition (Neill et al. 2007; McDonald et al. 2008; Mosher et al. 2009). Despite these patterns, no studies to date have examined whether native and exotic richness respond similarly to gradients of site disturbance arising from land-use history.

We examined patterns of native and exotic plant species richness in temperate forests that have been undergoing reforestation since the early twentieth century to ask the following questions: (1) Are exotic and native plant species richness in forest understory communities correlated, either positively or negatively? (2) Are these patterns influenced by land use history? (3) Do environmental variables associated with land use history differentially affect native and exotic plant communities and thus alter the relationship between native and exotic plant species?

Methods

Study area

The Smithsonian Environmental Research Center (SERC) lies along the western shore of the Chesapeake Bay in Edgewater, MD (38°53′ N, 76°33′ W) and is located in a semi-rural area comprised of approximately 1,200 hectares of research forests and croplands. SERC and the surrounding areas have long been inhabited by humans, but intensive modification of the landscape appears to have arisen only during the last few 100 years. From approximately 10,000 years BP to the early 1600s, Native Americans used the site in the spring and fall to access fishing and shellfish, but more permanent settlements were located further inland, and there is no evidence of extensive forest clearing (Higman 1968). Beginning in the mid-1600s, however, forests in the area were successively cleared to support colonial-era tobacco plantations. Soil-depleting tobacco gave way to wheat and grain production in the mid-1800s, followed by dairy farming in the early 1900s. Since the early 1960s, SERC has operated as a field research station and most of the croplands have been allowed to revert to forests (Higman 1968); thus the contemporary landscape is a mosaic of forest ages reflecting their successive abandonment following intensive agricultural use during Colonial times.

Typical of secondary forests along much of the eastern US, SERC forests contain about 40 common canopy species, including tulip poplar (*Liriodendron tulipifera*), oaks (*Quercus falcata, Q. coccinea, Q. velutina, Q. rubra, Q. alba*), hickories (*Carya* spp.), beech (*Fagus grandifolia*), sweetgum (*Liquidambar styraciflora*), and red maple (*Acer rubrum*) (Higman 1968). The understory community at SERC contains about 150 species and is highly invaded by several common introduced species including Japanese honeysuckle (*Lonicera japonica*), wineberry (*Rubus pheonicolasius*), and Japanese stiltgrass (*Microstegium vimineum*). Soils at SERC are generally considered mesic, fine loamy ultisols. Previous studies indicate that sites at SERC with a previous history of cultivation have surprisingly similar values for some soil properties when compared to sites that have never been farmed, including pH, nutrient composition, % mineral composition, and grain size (Pierce 1974).

Exotic and native plant surveys

To determine the relationship between native and exotic plant species in contemporary forest communities, in June and July of 2008 we characterized the understory vegetation at 50 randomly selected sites within SERC research forests that were abandoned a minimum of 10 years ago and thus had a well developed understory. We focused on the understory plant community (<2 m in height) because the two non-native tree species at SERC, Tree-of-heaven (*Alianthus altissima*) and princess tree (*Paulownia tomentosa*) are not currently found as canopy species. At each site we followed protocols established by the Forest Inventory and Analysis program (U.S. Department of Agriculture, Forest Service 2002), sampling the vegetation within three 1.0 m^2 quadrats placed 4.7 m distant from the center of each site along transects placed at 30, 150, and 270° from due north. In each quadrat, we recorded the identity and percentage cover of all plant species shorter than 2 m tall. Cover measurements were estimated for each species separately and thus total cover within a quadrat could sum to greater than 100%.

Plot environmental traits

To assess environmental differences across our sites that might reflect various land use histories, we measured soil compaction, soil moisture, and light availability in each quadrat. Soil compaction was measured by taking the mean of five readings from a cone penetrometer (Fieldscout SC900, Spectrum Technologies, Plainview, IL) in the center of each quadrat, one reading from each 2.54 cm interval below the surface. Soil moisture was measured using a soil moisture probe (Fieldscout TDR 300 Spectrum Technologies, Plainview, IL) taken once in the center of each quadrat. Soil compaction and moisture readings were made on three consecutive days during which no precipitation occurred. Photosynthetically active radiation (PAR) was measured by placing a handheld ceptometer (AccuPar LP-80, Decagon Devices, Pullman, WA) above the understory vegetation (~2 m height) at each quadrat between the hours of 11am and 2 pm on cloudless days. A second reading obtained beneath the understory canopy provided an estimate of Leaf Area Index (LAI), a proxy for plant standing stock.

Land cover classification

We used aerial orthophotographs to identify historical land use of each site in 1938, the earliest available aerial photography for this area, and in 1952, 1974, and 1998. GPS locations for each site were superimposed onto aerial orthophotographs using ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA, U.S.A.). Color orthophotographs were available for 1998 (1:2400, VARGIS, 208 Elden St. Suite 204, Herndon, VA 20170) and 2005 (1:1200, EarthData International, Inc. Frederick MD, U.S.A.). Black and white aerial photographs were available for 1938 (1:20000), 1952 (1:63360), and 1974 (1:9600). These black and white photographs were georeferenced using ArcGIS to the more recent orthorectified aerial imagery (2005, by which time all sites were in closed canopy forest). For each time period, sites were then classified into one of the two predominant land covers, i.e., either forest or field. Sites were classified as forested if they had complete tree coverage. Croplands, pastures, and recently abandoned fields were all classified as fields because lower resolution of earlier black and white photographs prevented reliable discrimination among these three covers.

Statistical analysis

Species richness

All statistical analyses were conducted using R software (R Development Core Team 2008). The mean number of species and percent cover of three quadrats were used to generate species richness and cover of native and exotic species per site. We then used linear regression to determine whether there was a positive relationship between native and exotic species richness across all 50 sites ("the rich get richer" hypothesis), and whether there was a relationship between exotic species richness and native plant cover. We also separately examined these relationships within each land use classification from 1938, 1952, 1974, and 1998. Data in each regression model were examined for homogeneity of variance and normally distributed residuals, and no transformations were required to meet the assumptions of the model. We then used *t*-tests to determine whether native and exotic species richness and cover differed by land use history.

Plot environmental traits

We used a multivariate analysis of variance (MA-NOVA) to examine differences in environmental variables measured during the field survey (PAR, soil moisture, and soil compaction) relative to previous land use. Examining the response of the variables in aggregate allowed us to account for their covariance across plots. Data subjected to the MANOVA were examined for heterogeneity of variance and normally distributed residuals, and as a result PAR values were log-transformed to meet the assumptions of the model. We separately tested the effect of land use history on Leaf Area Index (LAI), an assessment of understory canopy density, because LAI is a derivative of light availability. Data were log-transformed to meet the assumptions of the model.

We then used linear regression to determine whether there was a positive relationship between native and exotic species richness and soil compaction, light availability, and soil moisture. Data in each regression model were examined for homogeneity of variance and normally distributed residuals, and PAR were log-transformed to meet the assumptions of the model.

Plant species composition

To examine species composition at each site, we used non-metric multidimensional scaling (NMDS) to ordinate plots in "plant space." The NMDS technique graphically depicts dissimilarity between plant communities based on values in a distance matrix. This distance matrix is in turn a summary of the difference in species composition (species identity and % cover) among sites. Because the depiction is based on rank difference, rather than numerical distance, NMDS is less susceptible than other ordination methods to outlying responses to underlying gradients (Clarke 1993). NMDS ordinations were constructed in R (package *vegan*, Oksanen et al. 2008) using Bray–Curtis distance based on the mean percent cover of plant species across the three quadrats at each site. We conducted three NMDS procedures, one each for all species together, only native species, and only exotic species.

To test the hypothesis that species assemblages differed by previous land use history, we used analysis of similarity (ANOSIM, Clarke 1993).

ANOSIM uses a bootstrap randomization (we used 999 bootstrap replicates) to determine the probability of group membership based on the within-stand versus between-stand variance in the community. Like NMDS, ANOSIM is based on rank distances between samples (we used the same Bray–Curtis distance matrices used for the NMDS). Within each grouping (all species, native species only, and exotic species only), we tested whether the species composition in newer-growth forests differed from sites that had been continuously forested since 1938.

Finally, to test whether our measured environmental variables influenced plant community composition, we used an indirect gradient approach to correlate the position of each site in the NMDS ordination with values of environmental variables found at each site. The strength and significance of the correlation between species composition and our measured environmental variables was tested with a randomization permutation procedure (999 permutations).

Results

Species richness and cover

We found 138 plant species, of which 110 were native and 28 were introduced (Appendix 1). The most common native species were Virginia creeper (*Parthenocissus quinquefolia*), spicebush (*Lindera benzoin*), Jack-in-the-pulpit (*Arisaema triphyllum*), and poison ivy (*Toxicodendron radicans*). Non-native plant species were also common and widespread, including Japanese honeysuckle (*Lonicera japonica*), Indian strawberry (*Duchesnea indica*), wineberry (*Rubus pheonicolasius*), Japanese stiltgrass (*Microstegium vimineum*), and multiflora rose (*Rosa multiflora*) (Appendix 1).

Overall across all 50 sites, there was no relationship between native and exotic species richness ($r^2 = 0.057$, $P = 0.094$). We found a significant pattern, however, when we separately examined sites with a different land use history in 1938, the earliest period for which we had aerial documentation of land use. When we looked specifically across the 22 sites that have been forested continuously since 1938, native and exotic plant richness were positively correlated (Fig. 1a, $r^2 = 0.255$, $P = 0.017$). In contrast, there was no relationship between native and exotic species

richness across the 28 sites that were fields in 1938 (Fig. 1b; $r^2 = 0.018$, $P = 0.496$). Results were qualitatively similar for land use history in 1952, 1974, and 1998 (Appendix 2). Overall, there was also a positive relationship between native species richness and native % cover that persisted across both land use categories (overall $r^2 = 0.548$, $P < 0.001$), and as a result, native cover and exotic species richness were also positively correlated across continuously forested sites ($r^2 = 0.254$, $P = 0.017$), but not in forests that were fields in 1938 ($r^2 = 0.024$, $P = 0.434$). These relationships were again similar when examined

across sites with differing land use histories in 1952, 1974, and 1998 (Appendix 3).

The pattern of the 'rich get richer' was altered because of differential invasions into younger forests. Forests that had been fields in 1938 had 41% more exotic species on average than continuously forested sites (Fig. 2, 1.47 m^{-2} ± 0.2 in old forests versus 2.07 m^2 ± 0.2 in new forests, $P = 0.029$). There was no difference in the mean number of native species in continuously forested versus younger forests (Fig. 2, $P = 0.748$), or in the % cover of native or exotic plants in continuously forested versus younger forests ($P \geq 0.251$, t-tests).

Plot environmental traits

Land use history affected the suite of environmental traits we measured (overall MANOVA, $P = 0.043$). Soil compaction in particular was 24% significantly higher in plots that had been fields versus forests in 1938 (Fig. 3, 88.0 kPa ± 6.4 in old forests versus 108.9 kPa ± 5.7 in new forests, $P = 0.018$), though soil moisture ($P = 0.095$) and light availability ($P = 0.319$) were not significantly affected by previous land use history (Fig. 3). An independent ANOVA of LAI showed no effect of land use history on the density of understory plant communities in continuously forested versus younger forests ($P = 0.140$). Across all sites, exotic but not native plant
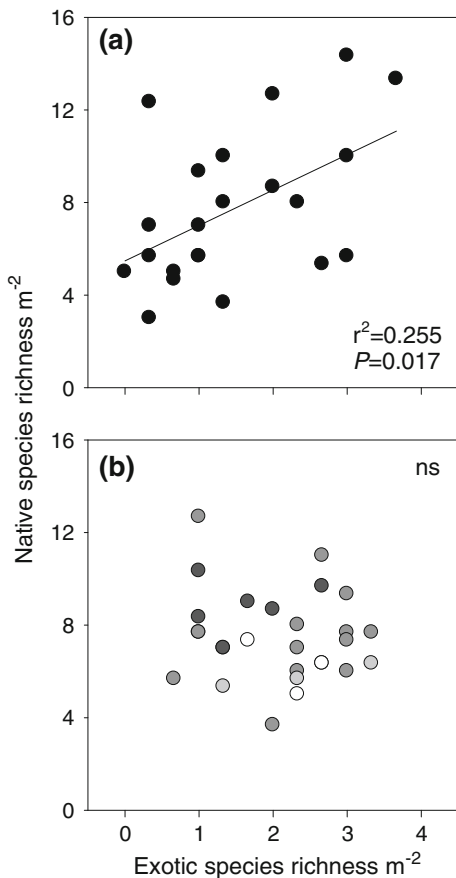

Fig. 1 We found a significant, positive relationship between exotic species richness and native species richness at the 22 sites that have been continuously forested since 1938 (the earliest aerial photographic evidence of land use; panel (**a**)), but no relationship between native and exotic plant species richness at the 28 sites that are currently forested but were fields in 1938 (**b**). In panel **b** the *symbol color* is indicative of stand age, with *dark* to *light symbol* gradations corresponding to sites becoming forested by 1952, 1974, 1998, and 2005, respectively
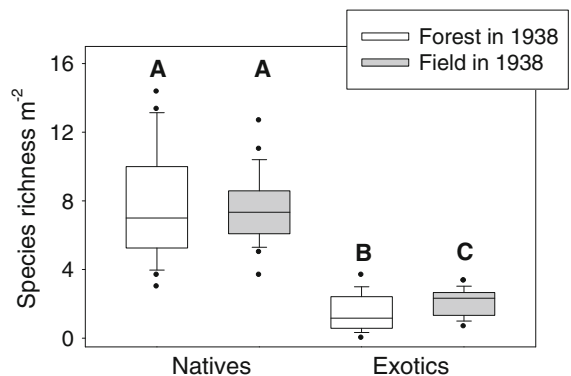

Fig. 2 Forests that were fields in 1938 have the same number of native species, but more exotic species than continuously forested plots. Data are number of species per plot ($N_{field} = 28$, $N_{forest} = 22$). *Boxes* depict the median (*line* within the box), the 25th and 75th percentiles (*box boundaries*), and the 10th and 90th percentiles (*error bars*). *Symbols* depict values that were outside of the 10th and 90th percentiles. *Letters* represent significantly different means ($P < 0.05$, ANOVA)
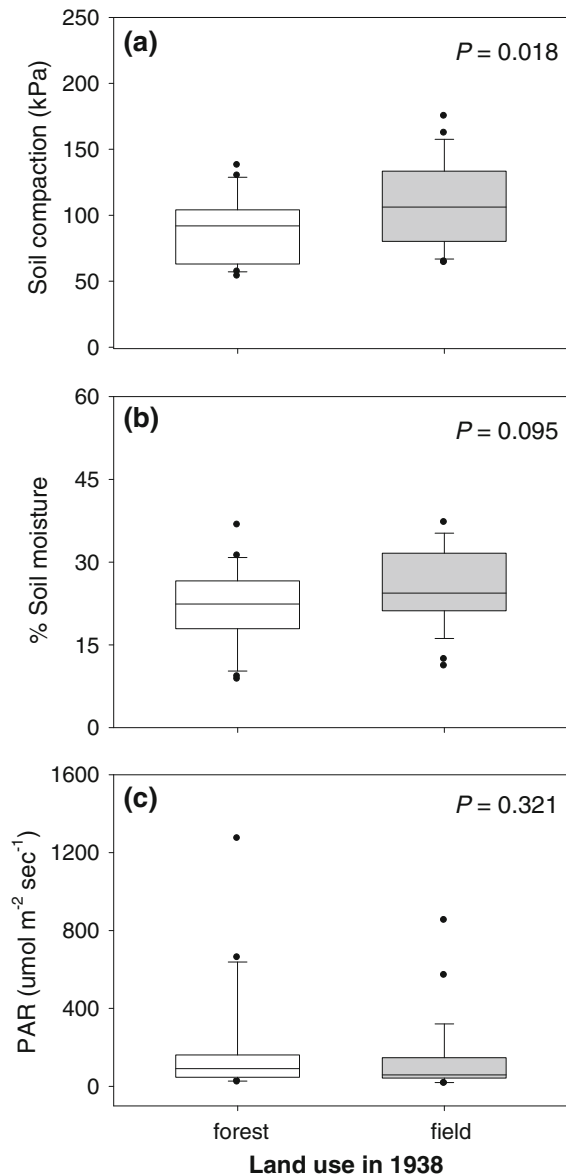
Fig. 3 Sites that were fields in 1938 have higher soil compaction (**a**) than plots that have been forested continuously since 1938. *Boxes* depict the median (*line* within the box), the 25th and 75th percentiles (*box boundaries*), and the 10th and 90th percentiles (*error bars*). *Symbols* depict values that were outside of the 10th and 90th percentiles. Soil moisture content and photosynthetically active radiation did not differ by land use history (**b**, **c**). Significance values are from a multivariate analysis of variance (MANOVA) using all environmental variables as a response to 1938 land use history

Fig. 4 Exotic (**a**) but not native (**b**) plant species richness is positively correlated with increasing soil compaction. *Filled symbols* were sites with continuous forest cover since 1938; *open symbols* were sites that were fields in 1938. Statistics are from linear regressions

availability or soil moisture ($P \geq 0.099$, linear regressions).

Plant species composition

Overall plant species composition differed across sites that had disparate land uses in 1938 (Fig. 5, $P = 0.020$), and soil compaction was the primary environmental variable that was significantly associated with these differences ($P < 0.001$). Compaction increased along an axis moving from plant species associated with plots that had been continuously forested towards plant species that were consistently associated with younger forests (Fig. 5).

When native species alone were ordinated using NMDS, there was a significant difference in plant species composition when grouped by land use

richness was positively correlated with increasing soil compaction (Fig. 4). There were no relationships between exotic/native richness and either light
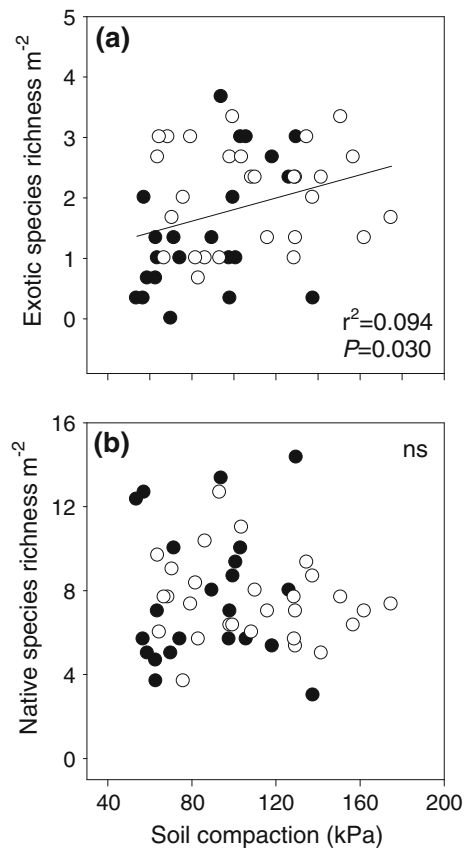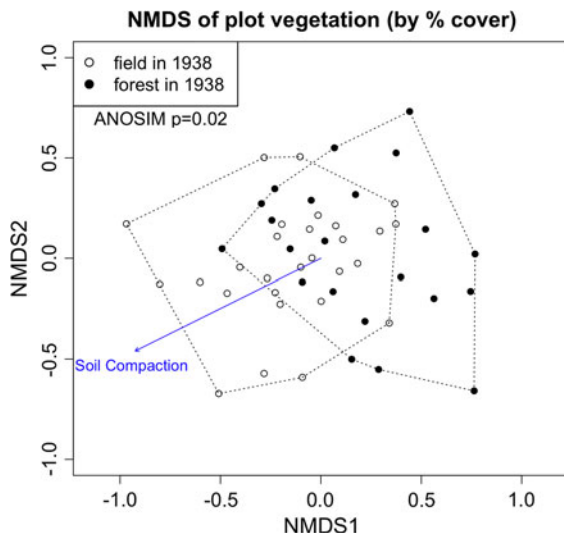
Fig. 5 Understory plant community composition in contemporary forests depends on land use in 1938. *Dashes* outline the maximum extent of each land use history in "plant community space" using non-metric multidimensional scaling (NMDS) of the rank Bray–Curtis similarity in percent cover (analysis of similarity, ANOSIM, $P = 0.02$). There was a strong association between increasing soil compaction and plant community composition in newer-growth forests (randomization tests, $P < 0.001$)

Fig. 6 Exotic plant community composition in contemporary forests depends on land use in 1938. *Dashes* outline the maximum extent of each land use history on "exotic plant community space" using non-metric multidimensional scaling (NMDS) of the rank Bray–Curtis similarity in percent cover (analysis of similarity, ANOSIM, $P = 0.008$). There were also significant associations between increasing light availability ($P = 0.034$, randomization tests), soil compaction ($P = 0.011$), and soil moisture ($P = 0.018$) and plant community composition. Species significantly ($P \leq 0.001$, randomization tests) associated with different vegetation types are plotted as the centroid of their mean abundance across all sites

history in 1938 ($P = 0.025$, ANOSIM). Particular species were consistently associated with older growth forests, including woody species such as red maple (*Acer rubrum*), ironwood (*Carpinus caroliniana*), and flowering dogwood (*Cornus florida*), as well as the perennial herb partridgeberry (*Mitchella repens*; all $P \leq 0.010$, randomization tests). In contrast, sites that had been fields in 1938 had higher cover of monocots, including sweet woodreed (*Cinna arundinacea*), nimblewill (*Muhlenbergia schreberi*) and poverty rush (*Juncus tenuis*), and forbs such as white avens (*Geum canadense*), and jumpseed (*Polygonum virginianum*; all $P \leq 0.010$, randomization tests). These differences in plant community composition appeared to be correlated with higher soil compaction ($P < 0.001$), which increased in sites that had been fields in 1938.

Considering only exotic species, plant species composition was again different according to land use history ($P = 0.008$, ANOSIM), but in this case differences were due to variance in the presence of particular species rather than variance in the relative abundance of the same species (Fig. 6). Sites that had
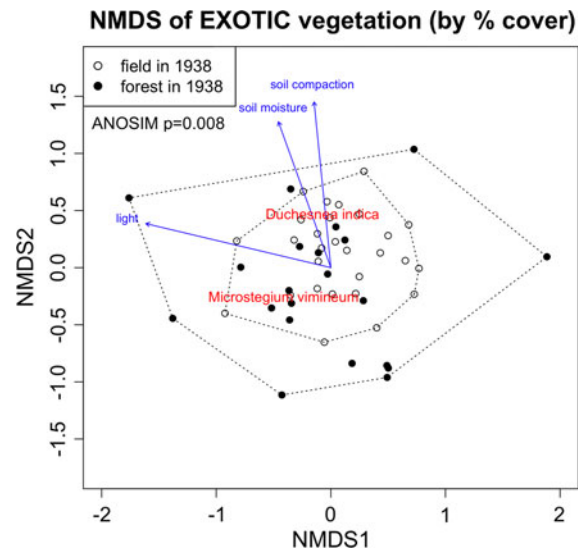
been fields in 1938 had highly similar exotic plant communities, dominated (in order of mean percent cover) by Japanese honeysuckle (*Lonicera japonica*), wineberry (*Rubus phoenicolasius*), indian strawberry (*Duschesnea indica*), redtop (*Agrostis alba*), and multiflora rose (*Rosa multiflora*). Sites that have been forested since at least 1938 varied more widely in terms of their exotic species composition; some resembled the historical field sites with an array of several exotic species, whereas others were dominated by one or two invasive species alone, including Japanese stilt grass (*Microstegium vimineum*), and mile-a-minute weed (*Persicaria perfoliata*). The position of sites within the NMDS ordination by exotic species composition was significantly correlated with all three measured environmental variables (Fig. 6). Along one NMDS axis, sites were separated by soil moisture ($P = 0.018$) and soil compaction ($P = 0.011$), whereas sites along the orthogonal axis were separated by light availability ($P = 0.034$).

Discussion

Observational studies (Stohlgren et al. 1999; Stohlgren et al. 2003; Meiners et al. 2004; Gilbert and Lechowicz 2005; Fridley et al. 2007) have routinely shown that native and exotic plant species richness are positively correlated, i.e., "the rich get richer." Our study partially supports this relationship. We found a positive relationship between native and exotic species in older growth forests (i.e., forested since 1938, Fig. 1a) but not younger forests (i.e., fields in 1938, Fig. 1b). This suggests that the same environmental factors that drive native species richness also drive exotic species richness, but only in older-growth forests.

In contrast, in younger forests we found 41% more exotic species (Fig. 2) and 24% greater soil compaction (Fig. 3a). Moreover, increasing soil compaction was positively correlated with exotic but not native species richness (Fig. 4), and soil compaction was further associated with changes in plant community composition (Figs. 5, 6). Thus, we hypothesize that soil compaction arising from agricultural history disrupted the rich-get-richer effect by facilitating exotic but not native plant establishment (e.g., Burke and Grime 1996; Woitke and Dietz 2002; Kulmatiski et al. 2006). Notably, in a study following the same plant survey methodology and measuring 26 variables at local scales, Huebner et al. (2009) also found elevated numbers of exotic plant species in younger forests. Similarly, Mosher et al. (2009) and Lilley and Vellend (2009) demonstrated that aspects of land use, including time since agricultural abandonment and proximity to human activities, respectively, can differentially alter the abundance of native and exotic species, in one case reversing the relationship between native and exotic plant richness (Lilley and Vellend 2009). Overall, these results suggest that native and exotic species may be responding to different environmental gradients across the landscape, in some cases weakening, eliminating, or even reversing the pattern of the 'rich get richer'.

Soil disturbance in general can disproportionately favor exotic species over native species (D'Antonio et al. 1999; Woitke and Dietz 2002; Kulmatiski et al. 2006), but few studies have examined whether native and exotic species differ in their responses to increased soil compaction. Soil compaction is commonly associated with agricultural practices (Raper 2005), can persist for years following agricultural

abandonment (Standish et al. 2006), and can influence plant establishment through increased soil resistance to plant roots, reduced porosity, reduced nutrient mineralization rates, decreased oxygen availability, and changes in water availability (Bassett et al. 2005). Higher soil compaction in younger forests may result from their longer association with mechanized equipment, grazing animals, and other human activities, or to changes in these practices over time (Prosser et al. 2000; Greenwood and McKenzie 2001; Hamza and Anderson 2004). In our study, younger forests at our sites had 24% greater soil compaction than older forests (Fig. 3), and increasing soil compaction was positively associated with exotic but not native plant species richness (Fig. 4), both implicating soil compaction as an environmental legacy of agricultural history that can differentially increase exotic but not native species richness. In contrast, Kyle et al. (2007) found that the invasive grass *Bromus tectorum* performed poorly in compacted old field soils, whereas all other exotic and native species were not affected by soil compaction. One potential explanation for our finding is that the invaders at our sites might possess traits that allow them to thrive in compacted or disturbed soils. For example, the exotic stoloniferous forest herb *Duchesnea indica* was positively associated with increased soil compaction (Fig. 6) and is a common horticultural plant used as ground cover in high disturbance areas (e.g., rock pathways and rock gardens; Huxley and Griffiths 1999). Moreover, some of the common invasive plant species in our study were intentionally introduced (e.g., *Lonicera japonica*, *Rosa multiflora*, *Rubus phoenicolasius*), and it is possible that these and other introduced species thrive in more recently disturbed forests because they were intentionally selected for their ability to thrive in challenging environments (Martin et al. 2009).

Other factors may also explain the increased abundance of exotic species in younger forests. For example, younger forests that were recently cropland or pasture may also experience increased propagule pressure, particularly if there are greater numbers of viable exotic species present in the seed bank (Myster and Pickett 1990). Japanese stilt grass (*Microstegium vimineum*), for example, is an annual plant and thus completely reliant on annual seed set to maintain populations. Furthermore, younger and more disturbed forests at SERC and elsewhere are also more

highly invaded by exotic earthworms (Gundale et al. 2005; Crow et al. 2009), and the intensive grazing of surface organic material by earthworms can also contribute to increased soil compaction (Hale et al. 2005) and thus potentially to exotic plant invasions.

It is also possible that differences in soil compaction were pre-existing and thus the cause and not the consequence of differential land use. However, our sites were broadly dispersed over a landscape comprised of similar topographies, they possess some similar soil characteristics, including soil type (fine loamy ultisols), grain size composition and mineralogy (Pierce 1974), and our results are consistent with numerous studies documenting higher soil compaction on previously cultivated versus uncultivated land (Compton et al. 1998; Lemenih et al. 2005; Maloney et al. 2008), suggesting that the observed differences are the result of previous land use.

Our result that older forests (i.e., forested in 1938) had lower exotic species richness than younger forests also supports other studies finding that less disturbed, older forests may be less susceptible to invasion by exotic plants (Jenkins and Parker 2001; McCarthy et al. 2001; Lundgren et al. 2004; Mosher et al. 2009; but see Martin et al. 2009). The resistance of older forests to exotic invasions has been attributed to low light availability, limited propagule dispersal, and reduced disturbance (Brothers and Spingarn 1992, but see Martin et al. 2009). In support of this hypothesis, the abundance of the noxious invaders Japanese stilt grass (*Microstegium vimineum*) and mile-a-minute weed (*Persicaria perfoliata*) were positively associated with increasing light availability in both younger and older forests (Fig. 6). Both species are often considered light-gap or edge species that can thrive in high light (Winter et al. 1982; Mountain 1989), thus exotic invaders may colonize and persist as long as disturbance (e.g., tree-falls, road cuts, etc.) maintains adequate light environments regardless of forest age (Brothers and Spingarn 1992; Martin et al. 2009).

Changing competitive dynamics during secondary succession may also contribute to the pattern of reduced invasions in older forests. For example, older forests may lose exotic species over time as these sites undergo succession. In support of this hypothesis, only two of the exotic plants in the current study could be considered a canopy species, whereas many of the native understory plants that we observed do grow to be canopy species. Thus, following agricultural abandonment, succession of native understory species into a canopy layer could eventually outcompete and suppress exotics in older forests. In this scenario, time since abandonment may be more important than soil disturbance in explaining contemporary patterns of invasions, although these two key factors may often be linked.

This study highlights the importance of considering historical land use and soil disturbance when examining modern-day exotic-native plant relationships. In landscapes reverting from an agricultural to forested state, soil compaction caused by agricultural or pastoral land use during the early twentieth century was linked to increased exotic plant invasions. In contrast to assumptions that similar processes drive both native and exotic species richness across the landscape, this pattern of disturbance removed the pattern of the 'rich-get-richer' and led to increased invasions in younger, more recently disturbed forests.

Appendix 1

See Table 1.

Table 1 Frequency of occurrence for 138 plant species found in a survey of 50 forest sites located at the Smithsonian Environmental Research Center

Natives	Frequency	Exotics	Frequency
Parthenocissus quinquefolia	50	*Lonicera japonica*	49
Acer rubrum	47	*Rubus phoenicolasius*	34
Arisaema triphyllum	45	*Duchesnea indica*	32
Liquidambar styraciflua	45	*Rosa multiflora*	30
Lindera benzoin	44	*Microstegium vimineum*	23
Toxicodendron radicans	44	*Ligustrum sinense*	11

Table 1 continued

Natives	Frequency	Exotics	Frequency
Liriodendron tulipifera	40	*Allium vineale*	8
Viola papilionacea	35	*Alliaria petiolata*	5
Cinna arundinacea	32	*Rumex obtusifolius*	5
Smilax rotundifolia	32	*Commelina communis*	4
Polygonum virginianum	28	*Agrostis alba*	3
Sanicula canadensis	27	*Hedera helix*	3
Fagus grandifolia	26	*Rumex crispus*	3
Rubus occidentalis	26	*Trifolium repens*	3
Circaea lutetiana	25	*Berberis thunbergii*	2
Vitis labrusca	25	*Dactylis glomerata*	2
Galium circaezans	24	*Persicaria perfoliata*	2
Ilex opaca	24	*Polygonum convolvulus*	2
Botrychium virginianum	22	*Abutilon theophrasti*	1
Campsis radicans	22	*Ailanthus altissima*	1
Polystichum acrostichoides	22	*Albizia julibrissin*	1
Asimina triloba	21	*Glechoma hederacea*	1
Houstonia purpurea	21	*Medicago lupulina*	1
Prunus serotina	21	*Medicago sativa*	1
Poa autumnalis	17	*Mentha citrata*	1
Galium aparine	15	*Poa compressa*	1
Podophyllum peltatum	15	*Solanum physalifolium*	1
Solidago caesia	15	*Taraxacum officinale*	1
Carpinus caroliniana	14		
Ulmus americana	14		
Acer negundo	13		
Boehmeria cylindrica	13		
Carya alba	13		
Carex lurida	12		
Geum canadense	11		
Panicum clandestinum	11		
Onoclea sensibilis	10		
Viburnum prunifolium	10		
Carex vulpinoidea	9		
Viburnum acerifolium	8		
Mitchella repens	7		
Oxalis stricta	7		
Quercus alba	7		
Quercus velutina	7		
Apocynum cannabinum	6		
Carex swanii	6		
Impatiens capensis	6		
Juncus tenuis	6		
Osmorhiza longistylis	6		
Pinus virginiana	6		
Quercus falcata	6		

Table 1 continued

Natives	Frequency	Exotics	Frequency
Asplenium platyneuron	5		
Carex gracillima	5		
Cornus florida	5		
Fraxinus pennsylvanica	5		
Scutellaria saxatilis	5		
Wisteria frutescens	5		
Cynoglossum virginanum	4		
Elymus villosus	4		
Festuca rubra	4		
Phytolacca americana	4		
Salix nigra	4		
Solidago altissima	4		
Vaccinium corymbosum	4		
Verbesina occidentalis	4		
Carya glabra	3		
Dennstaedtia punctilobula	3		
Diospyros virginiana	3		
Eleocharis intermedia	3		
Muhlenbergia schreberi	3		
Platanus occidentalis	3		
Polygonatum biflorum	3		
Sassafras albidum	3		
Smilacina racemosa	3		
Acalypha rhomboidea	2		
Amphicarpaea bracteata	2		
Athyrium felix-femina	2		
Botrychium dissectum	2		
Erigeron annuus	2		
Euonymus americanus	2		
Juncus effusus	2		
Nyssa sylvatica	2		
Polygonum pensylvanicum	2		
Robinia pseudoacacia	2		
Acer spicatum	1		
Achillea millefolium	1		
Carex blanda	1		
Celtis occidentalis	1		
Chamaecyparis thyoides	1		
Crataegus sp.	1		
Desmodium nudiflorum	1		
Fraxinus profunda	1		
Helianthus tuberosus	1		
Hydrangea arborescens	1		
Iva frutescens	1		
Lycopodium digitatum	1		

Table 1 continued

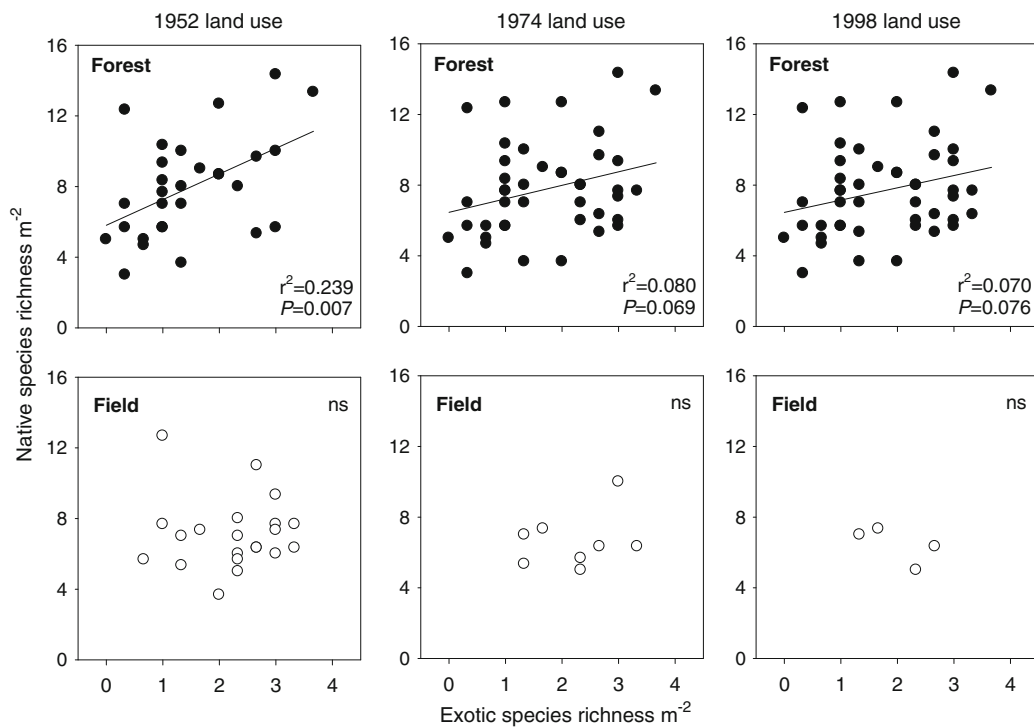| Natives	Frequency	Exotics	Frequency
Ophioglossum vulgatum	1		
Phalaris arundinacea	1		
Poa pratensis	1		
Polygonum arifolium	1		
Prenanthes altissima	1		
Prenanthes trifoliolata	1		
Quercus bicolor	1		
Quercus prinus	1		
Sambucus canadensis	1		
Saururus cernuus	1		
Solanum carolinense	1		
Solidago juncae	1		
Tridens flavus	1		
Uvularia grandiflora	1		

Appendix 2

See Fig. 7.

Fig. 7 We found a significant, positive relationship between exotic species richness and native species richness at the 29 sites that have been continuously forested since at least 1952 but at not at the 21 sites that were fields in 1952. The relationships were qualitatively similar but marginally non-significant for 1974 and 1998 land use histories. Statistics are from linear regressions
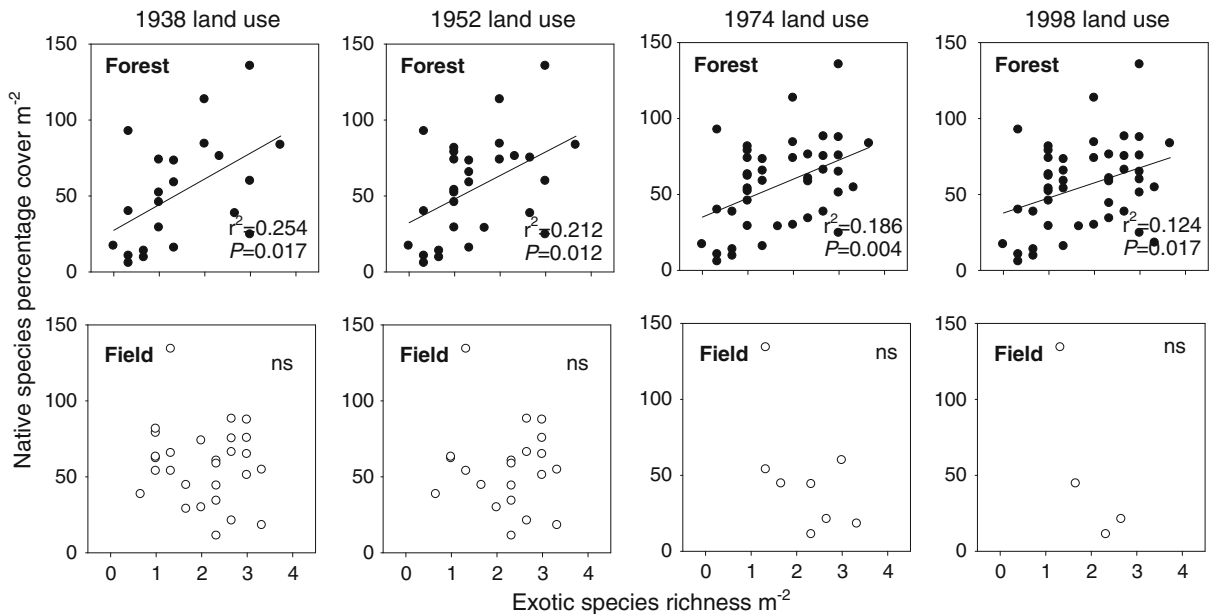
Appendix 3

See Fig. 8.

Fig. 8 We found significant, positive relationships between exotic species richness and native percentage cover across sites that had been continuously forested since at least 1938, 1952, 1974, and 1998. There were no relationships between native cover and exotic plant species richness at sites that were fields during each time period. Statistics are from linear regressions

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