Oecologia (2013) 172:1147–1157
DOI 10.1007/s00442-012-2568-5

COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Historic land use influences contemporary establishment of invasive plant species

W. Brett Mattingly · John L. Orrock

Received: 15 March 2012 / Accepted: 11 December 2012 / Published online: 1 January 2013

Abstract The legacy of agricultural land use can have widespread and persistent effects on contemporary landscapes. Although agriculture can lead to persistent changes in soil characteristics and plant communities, it remains unclear whether historic agricultural land use can alter the likelihood of contemporary biological invasions. To understand how agricultural land-use history might interact with well-known drivers of invasion, we conducted factorial manipulations of soil disturbance and resource additions within non-agricultural remnant sites and post-agricultural sites invaded by two non-native *Lespedeza* species. Our results reveal that variation in invader success can depend on the interplay of historic land use and contemporary processes: for both *Lespedeza* species, establishment was greater in remnant sites, but soil disturbance enhanced establishment irrespective of land-use history, demonstrating that contemporary processes can help to overcome legacy constraints on invader success. In contrast, additions of resources known to facilitate seedling recruitment (N and water) reduced invader establishment in post-agricultural but not in remnant sites, providing evidence that interactions between historic and contemporary processes can also limit invader success. Our findings thus illustrate that a consideration of historic land use may help to clarify the often contingent responses of invasive plants to known determinants of invasibility. Moreover, in finding significantly greater soil compaction at post-agricultural sites, our study provides a putative mechanism for historic land-use effects on contemporary invasive plant establishment. Our work suggests that an understanding of invasion dynamics requires knowledge of anthropogenic events that often occur decades before the introduction of invasive propagules.

Keywords Agriculture · Disturbance · *Lespedeza* · Longleaf pine savanna · Soil compaction

Introduction

The legacy of agricultural land use can shape many contemporary ecological patterns and processes (Foster et al. 2003; Flinn and Vellend 2005; Cramer et al. 2008). For example, post-agricultural lands often exhibit substantial reductions in plant diversity and abundance (Vellend 2004; Flinn and Vellend 2005; Hermy and Verheyen 2007; Vellend et al. 2007), altered soil microbial communities and nutrient availability (Fraterrigo et al. 2005, 2006), and lasting changes in soil properties, including reductions in organic matter and water-holding capacity (Foster et al. 2003; McLauchlan 2006). These effects of historic agriculture may be particularly relevant for understanding the forces that shape the success of non-native plant invasions because resident plant diversity and productivity (Knops et al. 1999; Levine 2000; Symstad 2000; Hector et al. 2001), microbial associates (Callaway et al. 2004; Mitchell

---

Communicated by Bryan Foster.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-012-2568-5) contains supplementary material, which is available to authorized users.

W. B. Mattingly · J. L. Orrock
Department of Zoology, University of Wisconsin,
Madison, WI 53706, USA

Present Address:
W. B. Mattingly (✉)
Department of Biology, Eastern Connecticut State University,
Willimantic, CT 06226, USA
e-mail: mattinglyw@easternct.edu

et al. 2006), and soil resources (Huenneke et al. 1990; Davis and Pelsor 2001; Maron and Marler 2007) can all be important determinants of invasion success. Indeed, the potential for the legacy of agricultural land use to affect plant invasions is underscored by recent observational studies documenting that post-agricultural lands often have a greater abundance and diversity of invasive non-native species (reviewed in Vila and Ibanez 2011).

While the patterns revealed by these observational studies (e.g., Von Holle and Motzkin 2007; Mosher et al. 2009) often reflect the culmination of a long history of invasive plant establishment and spread, the actual timing of invasive propagule arrival relative to the abandonment of agriculture may be a critical determinant of invasive plant success. For example, an immediate consequence of soil disturbances, such as those associated with agricultural activities, is the disruption of resident plant community structure, often resulting in decreased plant species richness and productivity at local scales (Sousa 1984). Because invasive plant performance is often negatively correlated with each of these community properties (Levine and D'Antonio 1999; Levine et al. 2004), soil disturbances that disrupt resident plant communities may facilitate invasive plant establishment in otherwise competitive environments. However, as the time since the disturbance event increases (e.g., as in the course of old-field succession), resident communities may change in ways that reduce the likelihood that newly arrived propagules will establish. Thus, soil disturbance, whether from a historic or contemporary event, can provide a window of opportunity for invasive plant establishment; however, if propagule arrival does not coincide with the disturbance event, then over time previously disturbed habitat could become more resistant to plant invasions. This dynamic requires evaluation.

Despite the potential for the legacy of agricultural land use to affect invasion success, there is no experimental confirmation of the link between historic land-use patterns and invasive plant performance, making it difficult to evaluate whether past agricultural disturbance is a definitive driver of contemporary invasions. Moreover, because land-use legacies may interact with other common anthropogenic factors that affect invasive plant performance (e.g., changes in resource addition rates and disturbance regimes), factorial experiments that couple land-use patterns with factors known to affect invader success are necessary to fully understand the relationship between past land use and contemporary invasions. For example, agricultural land use may affect invader success by increasing soil compaction (Kyle et al. 2007; Parker et al. 2010), but this legacy effect may be countered by contemporary soil disturbances. As such, the lack of an experimental approach that explicitly considers agricultural land-use history and other important determinants of invasion success is a primary impediment to understanding the potentially widespread effect of historic agricultural land use on biological invasions.

In this study, we use experimental additions of two invasive *Lespedeza* species (*Lespedeza bicolor* and *Lespedeza cuneata*) to evaluate how past agricultural land use affects the likelihood of contemporary plant invasions. Further, we explicitly examine how contemporary ecological correlates of invasion success (i.e., soil resource availability and localized disturbance) might interact with past land use in determining invasive plant performance. By coupling a mechanistic multifactor experiment with variation in underlying land-use history, we test the following predictions:

1. Post-agricultural lands, by virtue of historic disturbances, will be less resistant to invasion than habitat lacking an agricultural history.
2. Contemporary soil disturbances and resource additions, by lessening the competitive environment, will heighten invasive plant performance.
3. The effects of contemporary disturbances will be contingent on land-use history, whereby invader responses to disturbance will be more pronounced in habitats lacking an agricultural history.

Materials and methods

Study system and site selection

We conducted this study at Fort Bragg, a military installation that occupies more than 73,000 ha of longleaf pine savanna in the Sandhills region of North Carolina, USA (Sorrie et al. 2006). Fort Bragg encompasses a mosaic of upland habitat with distinct land-use histories, including areas that were formerly cultivated and areas that lack a history of agriculture, hereafter referred to as post-agricultural and remnant habitats, respectively. Agriculture was abandoned when the military installation was established in 1918 (Aragon 2004), and former agricultural fields were then naturally reforested. As such, post-agricultural habitat is nearly a century old and has mature longleaf overstories similar to those of remnant habitat. In our study, tree canopy cover did not differ between post-agricultural (48.3 ± 4.8 %) and remnant (54.3 ± 2.0 %) sites ($t = -1.16$, $P = 0.28$).

Sites were selected using a Geographic Information System that contained installation boundaries, a digitized historic topographical map depicting the perimeters of cultivated fields in 1919, USDA soil series information, and annual prescribed and wildfire records from 1991 to 2009. We used the historic map to identify the locations of remnant and post-agricultural habitat across the landscape. We then narrowed our selection of sites by standardizing for soil type and fire management. Across all selected sites, soils belonged to the Blaney-Gilead-Lakeland soil unit, which is noted for well-drained soils with a high sand content (Wyatt 1995). All sites have experienced a 2.7- to 4.8-year fire-return interval since 1991. For each post-agricultural site, we selected a nearby (<1.5 km) remnant stand that met the soil and fire management criteria. All study sites were located in upland longleaf pine savanna throughout the western half of Fort Bragg (35°8′21″N, 78°59′57″W; Moore and Hoke Counties, North Carolina, USA).

Experimental design

Within each remnant and post-agricultural stand, we imposed a soil-disturbance treatment, manipulated soil nutrient and water availabilities, and separately introduced two non-native N_2-fixing *Lespedeza* species (*L. bicolor* and *L. cuneata*) into the experimental plots in a fully factorial design (Online Resource 1). Although both of these species may be invasive in southern pine forests (Norden and Kirkman 2006), neither species was present at the study sites prior to experimental introductions. All treatment combinations were replicated 8 times, yielding 128 experimental units per *Lespedeza* species (2 land-use levels × 2 disturbance levels × 2 nutrient levels × 2 water levels × 8 replicates). Within our split–split-plot design, historic land use provided the largest experimental unit, soil disturbance was applied within the land-use treatment, and the nutrient × water factorial treatments were applied within the disturbance treatment. Plot assignments were randomly determined at each of the lower levels of the split–split-plot design.

At each site we established two 1.5 × 1.5-m plots, separated by a 1-m-wide buffer, randomly oriented, and positioned within the interior of the stand at least 100 m from the nearest road or drainage. In January 2010, we imposed a soil disturbance treatment at each site by excavating the soil from one of the paired plots to a depth of 15 cm, removing all coarse above- and belowground vegetation, and returning the homogenized soil to the plot. Soil within the adjacent plot remained undisturbed.

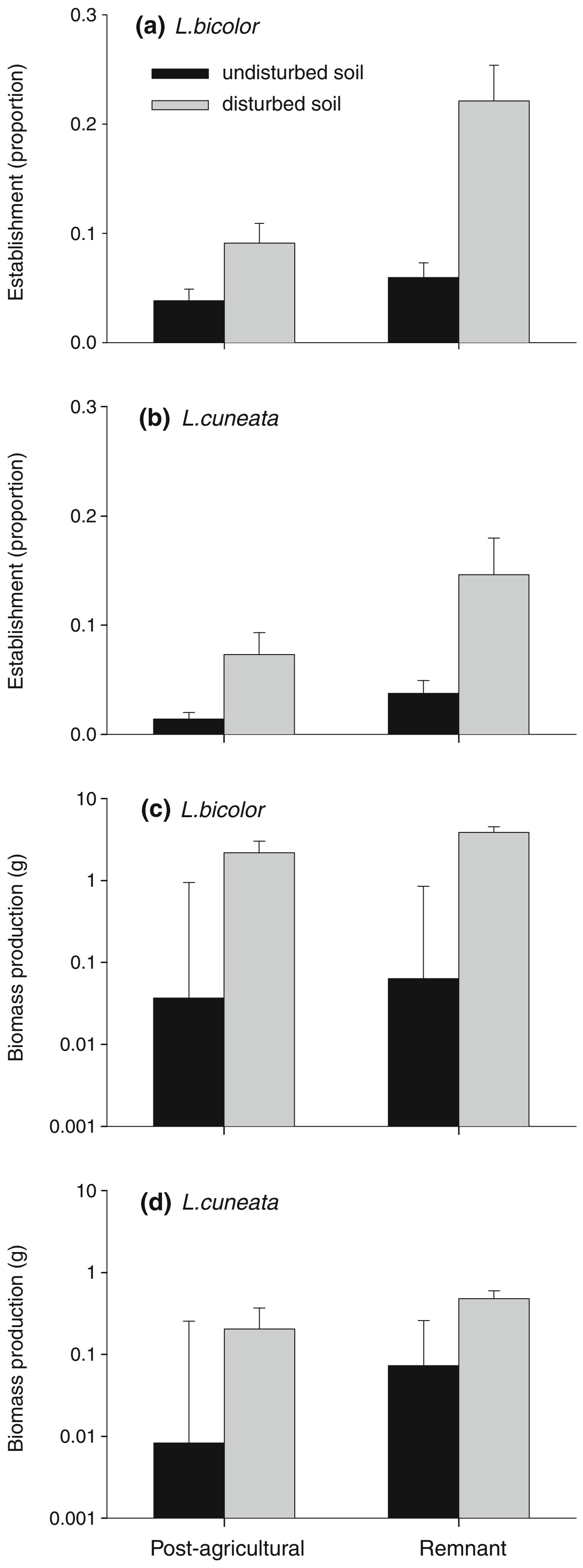
We split each 1.5 × 1.5-m plot into four 0.75 × 0.75-m experimental units, each of which received a unique combination of levels (i.e., ambient vs. enriched) of the soil nutrient and water treatments (Online Resource 1). In March 2010, two adjacent 0.75 × 0.75-m units were fertilized with slow-release fertilizer (N–P–K, 10–10–10) at a rate of 24 g N m^{-2} $year^{-1}$, a rate characteristic of the higher end of experimental nutrient gradients (Tilman 1993; Thompson et al. 2001). Two arenas were established within each experimental unit; we added 20 seeds of *L. bicolor* into one arena and 20 seeds of *L. cuneata* into the other. Each arena consisted of a clear plastic ring (21-cm diameter, 12-cm height) covered with hardware cloth and affixed to the ground with landscape staples. These arenas prevented seeds from washing out of the experimental units and minimized consumer pressure (all arenas were removed in May 2010). The water treatment was also initiated in March 2010, immediately following seed additions, wherein 15 mm of water was provided directly to the arenas twice a week for 10 weeks, totaling an additional 300 mm water $year^{-1}$ (i.e., a 25 % increase in mean annual precipitation) for those arenas assigned to the water-addition treatment level. We did not add water to arenas assigned to the ‘ambient water’ treatment level.

Data collection

In September 2010, seven months following seed additions, we evaluated the performance of each *Lespedeza* species both in terms of establishment and growth because the factors most crucial to invader success can vary across life history stages (Huston 2004). For each experimental unit, individuals were counted, clipped at the stem base, dried to a constant weight at 65 °C, and weighed. We defined invasive plant establishment as the proportion of individuals alive during this final census period and growth as the measure of per capita aboveground biomass per experimental unit (see also Gurevitch et al. 2008; Hooper and Dukes 2010). To evaluate the competitive environment localized within each experimental unit, we quantified the richness and aboveground biomass of the resident understory plant community within a 32-cm-diameter neighborhood centered on each sampling arena. All resident plants rooted within this area were grouped by species, clipped at the stem base, dried, and weighed. For each neighborhood, this census yielded measures of resident species richness and community productivity.

We measured several environmental variables that might contribute to differences in the success of invasive plant species between remnant and post-agricultural sites (Kirkman et al. 2001; Bassett et al. 2005; Walker and Silletti 2006). Forest canopy cover was quantified for each site by taking the mean of four measurements from a spherical crown densiometer (Forestry Suppliers, Jackson, MS) held at 1.37-m height. To further quantify forest structure, we measured the distance between study plots and the three nearest canopy trees at each site. We also measured the diameter of these trees at 1.37 m above the ground. Soil moisture holding capacity was quantified for each 1.5 × 1.5-m plot, wherein 12 soil cores (each 2.5 cm in diameter and 15 cm in depth) were collected, homogenized, and processed as in Brudvig and Damschen (2011).

Fig. 1 Effects of soil disturbance on **a, b** establishment and **c, d** ▶ biomass production of *Lespedeza bicolor* and *Lespedeza cuneata* in post-agricultural and remnant habitats. Establishment is defined as the proportion of individuals alive at the final census, and biomass production as the measure of per capita aboveground biomass per arena. Invasive plant responses are averaged across levels of the soil nutrient and water-addition treatments. Biomass data are presented on a log scale for readability, but analyses were conducted on non-transformed data. Data represent mean ± 1 SE



Soil compaction was quantified for each plot by taking the mean of six measurements from a cone penetrometer (Dickey-John, Auburn, IL) inserted to a 15-cm depth. Within the undisturbed plot at each site, we also measured the depth at which 2 MPa was attained, a level of soil compaction beyond which plant performance is generally constrained (Bassett et al. 2005).

Data analysis

To examine the proportion of added seeds that became established as plants, we used a generalized linear mixed model with a binomial response distribution (SAS version 9.1; SAS Institute, Cary, NC). We used a separate analysis for each *Lespedeza* species, treating land-use history, soil disturbance, nutrient addition, and water addition as fixed effects. We treated replicate sites as a random effect. Our model and subsequent significance tests explicitly incorporated the multi-level split-plot structure of our experimental design. We used the Kenward–Rogers approximation to estimate variance components and denominator *df*, as recommended by Littell et al. (2006). Because our hypotheses allow for multiple, interactive effects, we evaluated all possible interactions in our model.

We used linear mixed models to evaluate the following response variables: invader growth following establishment, resident species richness, and total resident biomass. The structure of these models with regard to fixed and random effects was identical to the model for invader establishment. Based on examination of residuals from preliminary analyses, a natural-log transformation was applied to the resident biomass data to improve normality. Examination of residuals following analyses suggested that residuals from all final models exhibited no patterns consistent with heteroscedasticity or non-normality.

To evaluate site-level environmental differences between land-use categories, we used *t*-tests that employed the Cochran and Cox approximation method to account for unequal group variances. To evaluate plot-level environmental differences, we used linear mixed models that treated land-use history and soil disturbance as fixed effects and replicate plots as a random effect. Finally, we used correlation analyses to evaluate relationships between

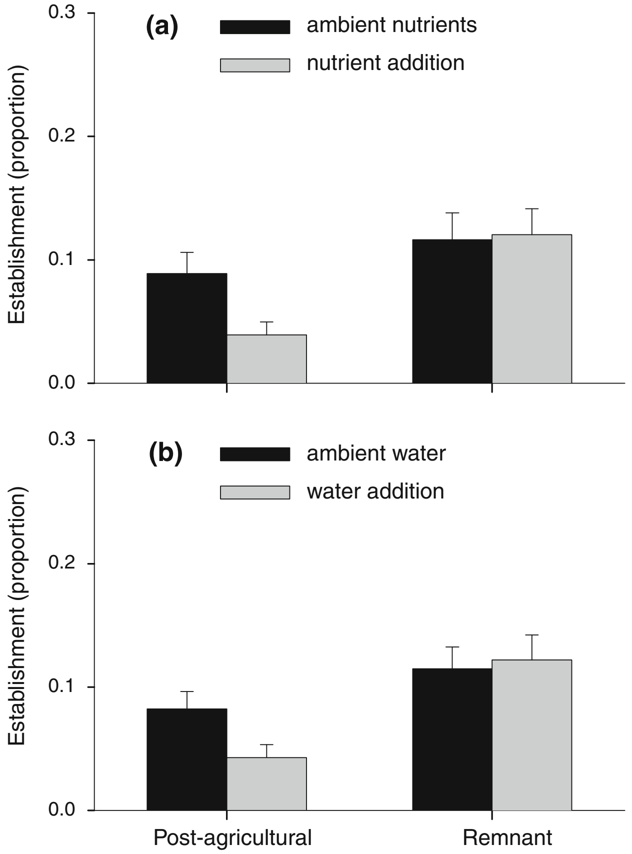


Fig. 2 Effects of land-use history on *L. bicolor* establishment in response to **a** soil nutrient and **b** water additions. Establishment is **a** averaged across levels of the soil-disturbance and water-addition treatments and **b** averaged across levels of the soil-disturbance and nutrient-addition treatments. Data represent mean ± 1 SE

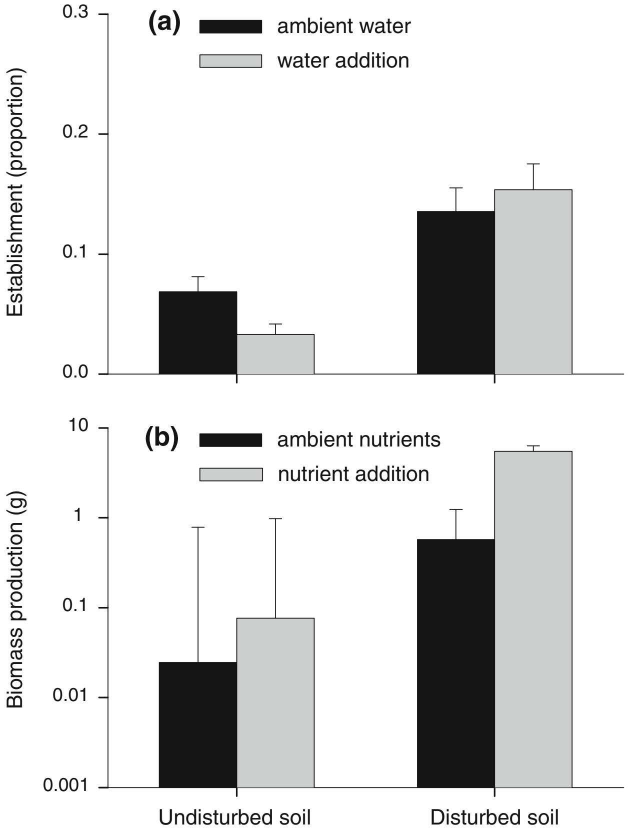


Fig. 3 Effects of soil disturbance on *L. bicolor* responses to **a** water and **b** soil nutrient addition. Establishment is averaged across land-use and nutrient-addition treatments, and biomass production is averaged across land-use and water-addition treatments. Biomass data are presented on a log scale for readability, but analyses were conducted on non-transformed data. Data represent mean ± 1 SE

invader performance, resident species richness and productivity, and environmental variables.

Results

Invasive plant establishment

For both species of *Lespedeza*, the proportion of seeds that established as plants was greater in remnant than in post-agricultural habitats (main effect of land use: *L. bicolor*, $F_{1,33.4} = 10.2$, $P = 0.003$, 100 % greater establishment in remnant plots, Fig. 1a; *L. cuneata*, $F_{1,18.8} = 6.3$, $P = 0.022$, 138 % greater establishment in remnant plots, Fig. 1b). Regardless of land-use history, soil disturbance promoted the establishment of both *Lespedeza* species (main effect of disturbance: *L. bicolor*, $F_{1,33.4} = 26.4$, $P < 0.001$, 200 % greater establishment in disturbed plots; *L. cuneata*, $F_{1,18.8} = 26.2$, $P < 0.001$, 352 % greater establishment in disturbed plots). For *L. bicolor*, responses to nutrient and water additions were contingent on land-use history (land use × nutrient, $F_{1,46.9} = 4.4$, $P = 0.042$; land use × water, $F_{1,112} = 5.2$, $P = 0.024$). In particular, nutrient and water additions both reduced *L. bicolor* establishment in post-agricultural habitats (linear contrasts: nutrient, $F_{1,65.5} = 6.7$, $P = 0.012$, 56 % reduction in establishment with nutrient addition; water, $F_{1,112} = 6.6$, $P = 0.012$, 48 % reduction in establishment with water addition) but not in remnant habitats (nutrient, $F_{1,31.2} < 0.1$, $P = 0.88$, Fig. 2a; water, $F_{1,112} = 0.1$, $P = 0.72$, Fig. 2b). Moreover, water addition and disturbance interacted to affect *L. bicolor* establishment (disturbance × water, $F_{1,112} = 7.5$, $P = 0.007$), such that water addition decreased *L. bicolor* establishment in undisturbed habitats only (linear contrasts: undisturbed, $F_{1,112} = 7.1$, $P = 0.009$; disturbed, $F_{1,112} = 0.7$, $P = 0.39$; 52 % reduction in establishment with water addition, Fig. 3a). *L. cuneata* establishment was reduced by nutrient addition (main effect of nutrient: $F_{1,53.6} = 7.3$, $P = 0.009$, 57 % reduction in establishment with nutrient addition) but not by water addition (main effect of water: $F_{1,112} = 3.2$, $P = 0.076$). The responses of *L. cuneata* to these resource additions were independent of land-use history and soil disturbance. For both species of *Lespedeza*, all other higher-order interactions describing the proportion of seeds establishing were non-significant (Online Resource 2). The proportions of individuals alive in May and September 2010 were highly correlated for both *L. bicolor* ($r = 0.68$, $P < 0.0001$) and *L. cuneata* ($r = 0.55$, $P < 0.0001$).

Invasive plant productivity

For both species of *Lespedeza*, average per capita biomass production was independent of land-use history (main effect of land use: *L. bicolor*, $F_{1,16.2} = 1.1$, $P = 0.31$, Fig. 1c; *L. cuneata*, $F_{1,12.2} = 0.8$, $P = 0.38$, Fig. 1d). Soil disturbance enhanced the growth of *L. bicolor* (main effect of disturbance: $F_{1,16.4} = 13.6$, $P = 0.002$, 200 % biomass increase in disturbed plots, Fig. 1c) but not of *L. cuneata* ($F_{1,11.1} = 2.8$, $P = 0.12$, Fig. 1d). For *L. bicolor*, nutrient addition enhanced productivity (main effect of nutrient: $F_{1,35.6} = 10.5$, $P = 0.003$), but this effect was detected only in disturbed habitats (disturbance × nutrient, $F_{1,35.6} = 10.0$, $P = 0.003$, 817 % biomass increase with nutrient additions, Fig. 3b; linear contrasts: undisturbed, $F_{1,40.4} < 0.1$, $P = 0.96$; disturbed, $F_{1,30.5} = 23.2$, $P < 0.001$). In contrast, resource additions did not affect *L. cuneata* productivity. For both species of *Lespedeza*, all other higher-order interactions describing per capita growth were non-significant (Online Resource 2).

Resident richness and productivity

Resident species richness and productivity differed among undisturbed post-agricultural and remnant plots (land use × disturbance interaction: species richness, $F_{1,14} = 11.8$, $P = 0.004$; productivity, $F_{1,14} = 19.3$, $P < 0.001$; Online Resource 2). In particular, post-agricultural habitats had fewer resident species than remnant habitats in undisturbed plots (linear contrast: $F_{1,20.5} = 9.7$, $P = 0.005$) but not in disturbed plots ($F_{1,20.5} < 0.1$, $P = 0.95$). Similarly, post-agricultural habitats were less productive than remnant habitats in undisturbed plots (linear contrast: $F_{1,21.5} = 19.9$, $P < 0.001$) but not in disturbed plots ($F_{1,21.5} = 0.1$, $P = 0.78$). Soil disturbance reduced resident species richness and productivity in remnant plots only (Online Resource 3). Neither resident species richness nor productivity was correlated with the establishment or productivity of either non-native *Lespedeza* species (Online Resource 4).

Environmental characteristics

Fire-return intervals were similar between remnant and post-agricultural plots (3.7 ± 0.3 years in remnant plots vs. 3.8 ± 0.2 years in post-agricultural plots, $t = 0.22$, $P = 0.83$). Proximity of canopy trees to study plots was independent of land-use history (5.4 ± 0.3 m in post-agricultural plots vs. 5.4 ± 0.5 m in remnant plots, $t = 0.04$, $P = 0.97$). These neighboring trees were also similar in diameter between the land-use categories (41.4 ± 1.4 cm in post-agricultural plots vs. 37.7 ± 2.4 cm in remnant plots, $t = 1.31$, $P = 0.21$). Soil moisture-holding capacity was independent of land-use history, although there was a trend of greater moisture-holding capacity in remnant plots (0.386 ± 0.014 in post-agricultural plots vs. 0.438 ± 0.015 in remnant plots, main effect of land use: $F_{1,14} = 3.8$, $P = 0.072$). Disturbance reduced soil moisture holding capacity independent of land-use history (0.434 ± 0.014 in undisturbed plots vs. 0.390 ± 0.016 in disturbed plots, main effect of disturbance: $F_{1,14} = 24.9$, $P < 0.001$). The upper soil horizons were more compacted at post-agricultural than at remnant sites (depth at which 2 MPa was attained: 8.3 ± 2.9 cm at post-agricultural sites vs. 40.1 ± 9.6 cm at remnant sites, $t = -3.17$, $P = 0.016$). Despite this difference, soil disturbance reduced compaction to similar levels in both post-agricultural and remnant plots (land use × disturbance, $F_{1,14} = 14.4$, $P = 0.002$, Fig. 4a; linear contrasts: undisturbed, $F_{1,25.9} = 20.5$, $P < 0.001$; disturbed, $F_{1,25.9} < 0.1$, $P = 0.99$). For each *Lespedeza* species, measures of both establishment (*L. bicolor*, $r = -0.62$, $P < 0.001$, Fig. 4b; *L. cuneata*, $r = -0.65$, $P < 0.001$; Fig. 4c) and productivity (*L. bicolor*, $r = -0.50$, $P = 0.004$; *L. cuneata*, $r = -0.43$, $P = 0.013$) were negatively correlated with soil compaction; invader performance was not correlated with the other environmental variables measured in our study (Online Resource 4).

Discussion

In a recent review, Gurevitch et al. (2011) surmise that 'different mechanisms may contribute to the invasion of different species, or to the same species in different places or at different times.' Our results illustrate that historic land use can provide an important lens through which to view this contingency in biological invasions because agricultural legacies consistently affected the establishment of two invasive species in our study. Our results also demonstrate that historic and contemporary disturbance regimes can have additive and complementary effects on invasion success. Further, our study points to soil compaction as a putative mechanism capable of creating persistent land-use effects on invasion success (see also Kyle et al. 2007; Parker et al. 2010) and mediating interactions between historic land use and contemporary disturbance: soil compaction was significantly greater in post-agricultural sites relative to remnant sites, but this difference was eliminated by contemporary soil disturbances (Fig. 4a).

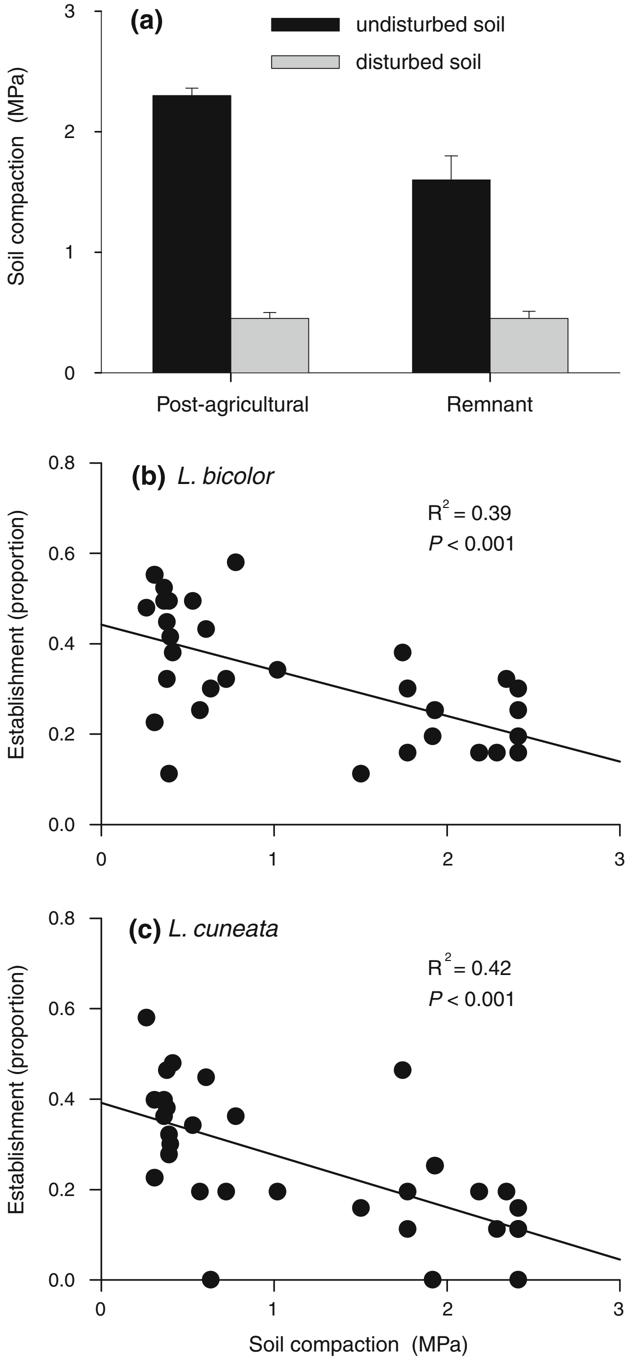


Fig. 4 **a** Effects of soil disturbance on soil compaction in post-agricultural and remnant sites. Data represent mean ± 1 SE. The relationships between soil compaction and the establishment of **b** *L. bicolor* and **c** *L. cuneata*. Plant performance is generally constrained when soil compaction exceeds 2 MPa (Bassett et al. 2005)

Land-use legacies and the greater success of invasive species in remnant habitats

By coupling a multifactor experiment with variation in underlying land-use history, our results reveal that the establishment of both invasive *Lespedeza* species is greater in habitats that lack an agricultural history. In contrast to our results, the patterns revealed in recent observational studies reflect the culmination of a long history of invasive plant establishment and spread following agricultural abandonment in the nineteenth century (e.g., DeGasperis and Motzkin 2007; Von Holle and Motzkin 2007; McDonald et al. 2008; Mosher et al. 2009), where it is likely that the disturbance associated with former agricultural practices initially facilitated the establishment of invasive plants which then persisted in the landscape during the course of old-field succession. In our study, the resistance of post-agricultural habitats to invasive plant establishment ~90 years after agricultural abandonment suggests that timing of propagule introduction is important, especially relative to the timing of agricultural activities. Supporting this notion, studies have also shown that non-native species richness and abundance in post-agricultural lands can vary with the time since introduction (Aragon and Morales 2003; Wilson et al. 2007), demonstrating in some cases that the relative abundance of non-native plants declines over time (e.g., Meiners et al. 2002). As with our study location, the abandonment and subsequent reforestation of former agricultural fields has widely occurred throughout Europe and eastern North America (Flinn and Vellend 2005). As such, understanding the influence of historic land use may provide insight into contemporary invasion dynamics in a broad range of human-modified landscapes.

Additionally, the relative absence of invasive plants in remnant forests, as documented by observational studies, may reflect inherent differences in propagule pressure between remnant and post-agricultural habitats (Martin et al. 2009) and the tendency for non-native species to be seed-limited in undisturbed habitats (Clark et al. 2007), differences that we overcame with our experimental approach. Indeed, by imposing an experimental framework over a historic landscape, our study demonstrates that contemporary disturbance can set the stage for the invasion of otherwise resistant post-agricultural habitats, thereby helping to reconcile the seemingly conflicting results of our experimental study with those of observational studies.

Historic and contemporary processes generate contingency in invasion success

Our study highlights the importance of considering historic land use as well as contemporary disturbances as determinants of invasive plant success. The general importance of soil disturbance in facilitating invasions is widely recognized and may operate through several pathways, including changes to the physical, chemical, and biological properties of disturbed soil (Lozon and MacIsaac 1997; D'Antonio et al. 1999). In post-agricultural landscapes, however, disturbance-induced changes in soil compaction may be of particular relevance to invasive plant performance. Increased soil compaction is indeed a persistent legacy of historic agriculture (Compton et al. 1998; Maloney et al. 2008; Parker et al. 2010) and one that has been shown to constrain plant performance through a variety of mechanisms, including reductions in porosity, nutrient mineralization rates, and oxygen and water availability (Unger and Kaspar 1994; Bassett et al. 2005). Soil compaction levels that exceed 2 MPa are generally considered to limit plant performance (Bassett et al. 2005). In our study, soil compaction was 44 % greater in post-agricultural (2.30 MPa) than in remnant (1.60 MPa) habitats. This considerable difference in soil compaction, combined with the positive invader responses elicited by disturbance-induced decreases in soil compaction and the strong negative relationship between soil compaction and invader establishment (Fig. 4) all suggest that an agricultural legacy effect on soil compaction is a probable cause for the observed differences in the proportion of seeds establishing for invasive *Lespedeza* plants between post-agricultural and remnant habitats.

Few studies have explicitly examined the influence of soil compaction on invasion success. As with our study, Kyle et al. (2007) use experimental seed additions and demonstrate that increased soil compaction reduces non-native plant performance. In contrast, Parker et al. (2010) reveal a positive correlation between compaction and non-native species richness. These equivocal results may be explained in part by the timing of analysis relative to propagule introductions: in contrast to seed-addition experiments, observational studies often evaluate the outcome of plant recruitment that occurred in the past and under conditions that may have differed from those observed at the time of the study. Nonetheless, the overarching importance of soil compaction in our study is suggested by the significant reductions in non-native plant establishment as well as in native richness and productivity on compacted soils of post-agricultural lands (Online Resource 3) as well as the negative relationships between soil compaction and both the establishment and growth of each non-native *Lespedeza* species. Although levels of soil compaction differed significantly between post-agricultural and remnant sites, other key environment characteristics that are known to affect plant performance in our study system (e.g., canopy cover, tree density, and soil water holding capacity) did not, nor were they significantly correlated with the performance of either invasive species (Online Resource 4). Further, the relative lack of understory vegetation in post-agricultural sites likely minimized competitive interactions between the invasive and resident plants, a factor that has otherwise been shown to constrain invasive species performance in more productive and diverse communities (Levine and D'Antonio 1999; Levine et al. 2004). Indeed, that invader performance was heightened in remnant habitats, which were more productive and diverse than post-agricultural habitats in our study, also suggests that factors other than competitive interactions, such as soil compaction, are driving patterns of invader success. Together, this evidence points to soil compaction as a likely mechanism for historic land-use effects on invasive plant establishment in contemporary landscapes. It is important to note, however, that even following disturbance-induced reductions in soil compaction, the performance of each non-native *Lespedeza* species was greater at remnant than at post-agricultural sites (Fig. 1). Our results thus show that the effects of agricultural legacies on plant establishment and growth extend beyond issues of soil compaction. A profitable area of future research would be to examine whether agricultural land use leads to persistent changes in soil pathogens and mutualists that may have detrimental effects on plant establishment and growth, even after compaction is alleviated by soil disturbances.

Although invader establishment was lower in post-agricultural than in remnant habitats, nutrient and water additions further reduced *L. bicolor* establishment in post-agricultural sites. This response was counterintuitive since the post-agricultural sites in our study provided a relatively competitor-free environment and since these resource additions have been shown to stimulate legume germination and facilitate seedling establishment (Williams et al. 2003; Van Klinken et al. 2008; Luna and Moreno 2009). However, in light of the considerable difference in soil compaction between remnant and post-agricultural sites, it is possible that *L. bicolor* establishment is reduced because land-use history and resource additions interact to produce an evolutionary trap (Schuler and Orrock 2012). In evolutionary time, resource-rich microsites were likely suitable for seedling establishment, but anthropogenic soil compaction uncouples the typical relationship between resources and establishment, where, to the detriment of the seedling, germination is prompted in an otherwise inhospitable microsite. Previous studies indeed demonstrate that seedlings are particularly vulnerable to the adverse effects of soil compaction (Smith et al. 2001; Bassett et al. 2005). Our results suggest that historic and contemporary processes can create evolutionary traps for seeds and that this effect may depend upon the plant species under consideration.

Historic land use had similar effects on both invasive *Lespedeza* species in our study: for *L. bicolor* and *L. cuneata*, the proportion of seeds establishing was greater in remnant than in post-agricultural habitats, but plant growth was independent of land-use history. However, the manner in which land-use history influenced invader responses to resource additions differed between these two *Lespedeza* species. Nutrient and water additions both reduced *L. bicolor* establishment in post-agricultural but not in remnant habitats, whereas these resources did not interact with land-use history in affecting *L. cuneata* success. These species-specific responses could be attributed to the fact that *L. bicolor*, a woody species with larger seeds than *L. cuneata*, exhibited greater establishment rates, was more productive, and thus achieved a greater range of variation in plant responses to resource additions. Our study only evaluated the responses of invasive non-native legumes, and thus it will be important to assess the manner in which historic land use influences the success of invasive plant species in other functional groups.

Implications for conservation and restoration

Remnant habitats often represent areas of conservation concern, particularly in the threatened longleaf pine ecosystem: these habitats typically exhibit high levels of plant diversity, contain endemic and otherwise rare species, and often provide the reference communities that are used to judge conservation and restoration goals (Frost 2006; Walker and Silletti 2006). Our results inform the management of invasive species in this threatened ecosystem: despite the low abundance of invasive plants currently in upland habitat at our study site (W. B. Mattingly and J. L. Orrock, unpublished data), our study demonstrates that remnant habitats are particularly suitable for invasive plant establishment. As a result, effective management to prevent invasion of these habitats will require special attention to the flow of propagules. In this system, dispersal limitation, at least in the case of invasive non-native *Lespedeza* species, seems the most likely explanation for their absence in remnant habitats. In support of this notion, Clark et al. (2007) find that non-native species are more likely to be dispersal-limited than native species in undisturbed habitats. In the longleaf pine ecosystem, in particular, research indicates that many species are indeed limited by seed availability (Myers and Harms 2009), suggesting that established plant communities in these highly diverse systems may not provide an effective barrier to the establishment of non-native *Lespedeza* species, a notion further supported by our study (Online Resource 3). Moreover, in light of the positive effects of soil disturbance on the success of invasive *Lespedeza* species, instances where increased propagule supply intersects with contemporary soil disturbance could increase community susceptibility to invasion, especially in remnant habitats. Importantly, processes that produce contemporary disturbance may also be associated with increased input of invasive propagules. For example, logging commonly creates soil disturbances, and vehicle traffic associated with logging machinery can provide a source of invasive plant propagules (Veldman and Putz 2010). Once invasive plant species colonize remnant habitats, the increased rates of establishment and growth that they experience in these areas may make eradication difficult.

In finding a role for historic land use in affecting invasive plant establishment, our study highlights the need for additional research into the mechanisms that create and maintain the effects of land-use legacies on biological invasions. For example, although multiple lines of evidence implicate soil compaction as being important in our system, other differences in soil conditions (e.g., microbial communities, Fraterrigo et al. 2006) could play an important role in affecting invasibility of post-agricultural lands, and future studies are needed to understand how agricultural land use may create long-lasting changes in soils that foster contemporary invasions. Moreover, we focus on N-fixing invasive species in this study, as they are often important in terrestrial systems (Richardson et al. 2000). However, future work that examines the degree to which other plant traits (e.g., seed size, dispersal ability, or growth form) contribute to invasibility in habitats that differ in their land-use history will also provide important information for fully characterizing the nature of biological invasions.

Acknowledgments We thank A. Powell for assistance in the field, J. Gray, L. Carnes-McNaughton, and J. Monroe for providing logistical support at Fort Bragg, and L. Brudvig and N. Reif for providing helpful comments on this manuscript. This study was supported by the Strategic Environmental Research and Development Program (project SI-1695) and complied with the current laws of the United States.

References

Aragon LV (2004) Sandhills families: early reminiscences of the Fort Bragg area. Environmental and Natural Resources Division, Cultural Resources Management Program, Fort Bragg

Aragon R, Morales JM (2003) Species composition and invasion in NW Argentinian secondary forests: effects of land use history, environment and landscape. J Veg Sci 14:195–204

Bassett IE, Simcock RC, Mitchell ND (2005) Consequences of soil compaction for seedling establishment: implications for natural regeneration and restoration. Austral Ecol 30:827–833

Brudvig LA, Damschen EI (2011) Land-use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34:257–266

Callaway RM, Thelen GC, Rodriguez A, Holben WE (2004) Soil biota and exotic plant invasions. Nature 427:731–733

Clark CJ, Poulsen JR, Levey DJ, Osenberg CW (2007) Are plant populations seed limited? A critique and meta-analysis of seed addition experiments. Am Nat 170:128–142

Compton JE, Boone RD, Motzkin G, Foster DR (1998) Soil carbon and nitrogen in a pine-oak sand plain in central Massachusetts: role of vegetation and land-use history. Oecologia 116:536–542

Cramer VA, Hobbs RJ, Standish RJ (2008) What's new about old fields? Land abandonment and ecosystem assembly. Trends Ecol Evol 23:104–112

D'Antonio CM, Dudley TD, Mack M (1999) Disturbance and biological invasions: direct effects and feedbacks. In: Walker LR (ed) Ecosystems of disturbed ground. Elsevier, New York

Davis MA, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasibility. Ecol Lett 4:421–428

DeGasperis BG, Motzkin G (2007) Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. Ecology 88:3115–3125

Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. Front Ecol Environ 3:243–250

Foster D, et al. (2003) The importance of land-use legacies to ecology and conservation. Bioscience 53:77–88

Fraterrigo JM, Turner MG, Pearson SM, Dixon P (2005) Effects of past land use on spatial heterogeneity of soil nutrients in southern Appalachian forests. Ecol Monogr 75:215–230

Fraterrigo JM, Balser TC, Turner MG (2006) Microbial community variation and its relationship with nitrogen mineralization in historically altered forests. Ecology 87:570–579

Frost CC (2006) History and future of the longleaf pine ecosystem. In: Jose S, Jokela EJ, Miller DL (eds) The longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York, pp 9–42

Gurevitch J, Howard TG, Ashton IW, Leger EA, Howe KM, Woo E, Lerdau M (2008) Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. Biol Invasions 10:821–831

Gurevitch J, Fox GA, Wardle GM, Inderjit, Taub D (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. Ecol Lett 14:407–418

Hector A, Dobson K, Minns A, Bazeley-White E, Lawton JH (2001) Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. Ecol Res 16:819–831

Hermy M, Verheyen K (2007) Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversity. Ecol Res 22:361–371

Hooper DU, Dukes JS (2010) Functional composition controls invasion success in a California serpentine grassland. J Ecol 98:764–777

Huenneke LF, Hamburg SP, Koide R, Mooney HA, Vitousek PM (1990) Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. Ecology 71:478–491

Huston MA (2004) Management strategies for plant invasions: manipulating productivity, disturbance, and competition. Divers Distrib 10:167–178

Kirkman LK, Mitchell RJ, Helton RC, Drew MD (2001) Productivity and species richness across and environmental gradient in a fire-dependent ecosystem. Am J Bot 88:2119–2128

Knops JMH, et al. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. Ecol Lett 2:286–293

Kyle GP, Beard KH, Kulmatiski A (2007) Reduced soil compaction enhances establishment of non-native plant species. Plant Ecol 193:223–232

Levine JM (2000) Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Levine JM, Adler PB, Yelenik SG (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecol Lett 7:975–989

Littell RC, Milliken GA, Stroup WW, Wolfinger RD, Schabenberger O (2006) SAS for mixed models. SAS Institute, Cary, NC

Lozon JD, MacIsaac HJ (1997) Biological invasions: are they dependent on disturbance? Environ Rev 5:131–144

Luna B, Moreno JM (2009) Light and nitrate effects on seed germination of Mediterranean plant species of several functional groups. Plant Ecol 203:123–135

Maloney KO, Garten CT Jr, Ashwood TL (2008) Changes in soil properties following 55 years of secondary forest succession at Fort Benning, Georgia, USA. Restor Ecol 16:503–510

Maron J, Marler M (2007) Native plant diversity resists invasion at both low and high resource levels. Ecology 88:2651–2661

Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Front Ecol Environ 7:142–149

McDonald RI, Motzkin G, Foster DR (2008) Assessing the influence of historical factors, contemporary processes, and environmental conditions on the distribution of invasive species. J Torrey Bot Soc 135:260–271

McLauchlan K (2006) The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. Ecosystems 9:1364–1382

Meiners SJ, Pickett STA, Cadenasso ML (2002) Exotic plant invasions over 40 years of old field successions: community patterns and associations. Ecography 25:215–223

Mitchell CE, et al. (2006) Biotic interactions and plant invasions. Ecol Lett 9:726–740

Mosher ES, Silander JA Jr, Latimer AM (2009) The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. Biol Invasions 11:2317–2328

Myers JA, Harms KE (2009) Local immigration, competition from dominant guilds, and the ecological assembly of high-diversity pine savannas. Ecology 90:2745–2754

Norden H, Kirkman K (2006) Field guide to common legume species of the longleaf pine ecosystem. Joseph W Jones Ecological Research Center, National Fish and Wildlife Foundation, Georgia Native Plant Society

Parker JD, Richie LJ, Lind EM, Maloney KO (2010) Land use history alters the relationship between native and exotic plants: the rich don't always get richer. Biol Invasions 12:1557–1571

Richardson DM, Allsopp N, D'Antonio CM, Milton SJ, Rejmanek M (2000) Plant invasions—the role of mutualisms. Biol Rev 75:65–93

Schuler MS, Orrock JL (2012) The maladaptive significance of maternal effects for plants in anthropogenically modified environments. Evol Ecol 26:475–481

Smith KD, May PB, Moore GM (2001) The influence of compaction and soil strength on the establishment of four Australian landscape trees. J Arboric 27:1–7

Sorrie BA, Gray JB, Crutchfield PJ (2006) The vascular flora of the longleaf pine ecosystem of Fort Bragg and Weymouth Woods, North Carolina. Castanea 71:129–161

Sousa WP (1984) The role of disturbance in natural communities. Annu Rev Ecol Syst 15:353–391

Symstad AJ (2000) A test of the effects of functional group richness and composition on grassland invasibility. Ecology 81:99–109

Thompson K, Hodgson JG, Grime JP, Burke MJW (2001) Plant traits and temporal scale: evidence from a 5-year invasion experiment using native species. J Ecol 89:1054–1060

Tilman D (1993) Species richness of experimental productivity gradients: how important is colonization limitation? Ecology 74:2179–2191

Unger PW, Kaspar TC (1994) Soil compaction and root growth: a review. Agron J 86:759–766

Van Klinken RD, Lukitsch B, Cook C (2008) Interaction between seed dormancy-release mechanism, environment and seed bank strategy for a widely distributed perennial legume, *Parkinsonia aculeata* (Caesalpinaceae). Ann Bot 102:255–264

Veldman JW, Putz FE (2010) Long-distance dispersal of invasive grasses by logging vehicles in a tropical dry forest. Biotropica 42:697–703

Vellend M (2004) Parallel effects of land-use history on species diversity and genetic diversity of forest herbs. Ecology 85:3043–3055

Vellend M, et al. (2007) Homogenization of forest plant communities and weakening of species-environment relationships via agricultural land use. J Ecol 95:565–573

Vila M, Ibanez I (2011) Plant invasions in the landscape. Landscape Ecol 26:461–472

Von Holle B, Motzkin G (2007) Historical land use and environmental determinants of nonnative plant distribution in coastal southern New England. Biol Conserv 136:33–43

Walker JL, Silletti AM (2006) Restoring the ground layer of longleaf pine ecosystems. In: Jose S, Jokela EJ, Miller DL (eds) the longleaf pine ecosystem: ecology, silviculture, and restoration. Springer, New York

Williams PR, Congdon RA, Grice AC, Clarke PJ (2003) Fire-related cues break seed dormancy of six legumes of tropical eucalypt savannas in north-eastern Australia. Austral Ecol 28:507–514

Wilson JRU, et al. (2007) Residence time and potential range: crucial considerations in modelling plant invasions. Divers Distrib 13:11–22

Wyatt PW (1995) Soil survey of Moore County, North Carolina. US. Department of Agriculture. Soil Conservation Service, Washington, DC