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Properties of native plant communities do not determine exotic success during early forest succession

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Considerable research has been devoted to understanding how plant invasions are influenced by properties of the native community and to the traits of exotic species that contribute to successful invasion. Studies of invasibility are common in successionally stable grasslands, but rare in recently disturbed or seral forests. We used 16 yr of species richness and abundance data from 1 m^2 plots in a clearcut and burned forest in the Cascade Range of western Oregon to address the following questions: 1) is invasion success correlated with properties of the native community? Are correlations stronger among pools of functionally similar taxa (i.e. exotic and native annuals)? Do these relationships change over successional time? 2) Does exotic abundance increase with removal of potentially dominant native species? 3) Do the population dynamics of exotic and native species differ, suggesting that exotics are more successful colonists? Exotics were primarily annual and biennial species. Regardless of the measure of success (richness, cover, biomass, or density) or successional stage, most correlations between exotics and natives were non-significant. Exotic and native annuals showed positive correlations during mid-succession, but these were attributed to shared associations with bare ground rather than to direct biotic interactions. At peak abundance, neither cover nor density of exotics differed between controls and plots from which native, mid-successional dominants were removed. Tests comparing nine measures of population performance (representing the pace, magnitude, and duration of population growth) revealed no significant differences between native and exotic species. In this early successional system, local richness and abundance of exotics are not explained by properties of the native community, by the presence of dominant native species, or by superior colonizing ability among exotics species. Instead natives and exotics exhibit individualistic patterns of increase and decline suggesting similar sets of life-history traits leading to similar successional roles.

Plant invasions have become the focus of considerable societal concern and ecological research. This reflects the increasing impacts of invasions, both ecological (Vitousek et al. 1997) and economic (Pimentel et al. 2005), and the opportunity to use invasive species to explore fundamental questions in ecology (Sax et al. 2007). Considerable research has examined how invasibility is influenced by properties of the recipient community, and in particular, by the richness of native species (Tilman 1997, Levine and D'Antonio 1999, Stohlgren et al. 1999, Levine 2000). Elton (1958) first hypothesized that invasibility is inversely related to species richness, with species-rich communities better able to preempt resources. This view has been supported by subsequent theories (MacArthur 1970, Tilman 2004) that highlight the importance of resource competition in structuring natural communities. These posit that biodiversity should limit invasion of non-native species through competition for resources.

Field studies have generally documented negative relationships between richness of native and non-native species at small spatial scales (e.g. plots of one to several square meters), but positive relationships at larger scales (e.g. landscapes) (Stohlgren et al. 1999, Levine 2000). The consistency of empirical and theoretical studies at small, but not large spatial scales reflects the short distances over which plants compete for resources (Levine and D'Antonio 1999). Although resource competition is central to theories on non-native plant invasions, few studies have considered how community properties other than richness or evenness limit the success of invasive species. If resource availability varies with competition intensity (Davis et al. 1998), community properties related to resource preemption, such as plant cover or biomass, should exert strong controls on invasion.

In addition to the effects of native plant abundance, the traits of resident species may be critical to limiting invasions. Theoretical models (Tilman 2004) and field experiments (Fargione et al. 2003) suggest that invaders should be most limited by natives that share similar functional traits (e.g. timing of life-history events, responses to disturbance, and resource use). Thus, exotic annuals should be most responsive to the diversity or abundance of native annuals. At the same time, invasion success may be linked to the abundance of community dominants, regardless of their functional traits. Dominant species can suppress invaders because they are highly competitive (Fargione and Tilman 2005), or because they can modify other ecosystem processes or properties (e.g. herbivory, soil biota, or allelochemicals; Emery and Gross 2007).

An alternative line of research has explored how the life-history traits of exotic species contribute to successful colonization. Exotics could have an advantage over natives because they 1) are able to escape natural enemies outside of their native ranges (Keane and Crawley 2002), 2) have traits or combinations of traits that are not represented in the resident community (Vitousek et al. 1987b), or 3) are competitively superior to natives (Funk and Vitousek 2007). Alternatively, exotics and natives might not show consistent differences in functional traits (Thompson et al. 1995) but instead, both could be colonists with similar traits and processes leading to successful establishment (Davis et al. 2000, Meiners 2007).

An underlying assumption of most theoretical and empirical studies of invasibility is that recipient communities are stable systems. However, this assumption has limited application given the prevalence of disturbance in both natural and human-modified systems. Studies addressing invasibility in recently disturbed or successional communities are sparse (but see Meiners et al. 2002, 2004, Sax 2002, Belote et al. 2008), which is surprising because successional systems are globally common, exhibit enhanced resource availability, and commonly face strong invasion pressure, allowing comparison of native and non-native colonists (Meiners et al. 2002, 2004, Meiners 2007).

In this study, we use 16 yr of successional data from a study of competitive interactions among plant species following a stand-replacing disturbance in an old-growth coniferous forest (Halpern et al. 1997, Rozzell 2003). Annual observations made at small spatial scales (1 m^2 plots) in control and plant-removal treatments provide opportunities to test whether community properties related to resource preemption (or functional similarity) influence invasion success, whether these relationships change over successional time, whether community dominants limit success of non-natives, and whether natives and exotics differ in their colonizing abilities. We address the following questions: Q1a) is invasion success, as measured by the richness or abundance of exotics, correlated with properties of the native community? b) Are these correlations stronger among communities of functionally similar taxa (i.e. exotic and native annuals/biennials)? c) Do the directions or strengths of these relationships change over successional time? We hypothesized that competitive interactions would be minimal (non-significant relationships between natives and exotics) during the early stages of succession when plant cover and biomass were low (Grime 1974), but that with time, increasing competition for space or resources would yield significant negative relationships between natives and exotics. We also predicted that negative relationships would be strongest between annuals/biennials due to similarities in life history. Q2) Do the presence or abundance of exotics increase with the removal of potentially dominant native species? We hypothesized that exotic colonists would respond positively (i.e. increase in density and cover) with removal of potentially dominant native species. We expected these effects to be greatest at times when exotics achieved peak abundance in the unmanipulated community. Q3) Do the population dynamics of exotic and native species suggest that exotics are more successful colonists in this system? We hypothesized that greater colonizing abilities and growth rates would allow exotic species to increase more rapidly and to achieve greater density than native colonists.

Methods

Study area

The 4-ha study site is at 730 m elevation on a gentle, east-facing slope in the valley of the south fork of the McKenzie River in the Cascade Range of western Oregon. The surrounding landscape includes mature to old-growth forests and plantations originating from clearcut logging in 1970s and 1980s.

The climate is characterized by mild, wet winters and warm, dry summers. At the central meteorological station (450 m elevation) at the nearby H. J. Andrews Experimental Forest, annual precipitation averages ~2300 mm, with 6% falling between June and August (Bierlmaier and McKee 1989). Snowfall is common but does not persist at this elevation. Soils are deep (>1.5 m), loamy Andisols (frigid typic Hapludand) formed from weathering of andesite, breccia, and volcanic ash.

Prior to harvest, the site supported a mix of mature and old-growth forest dominated by *Pseudotsuga menziesii*, with *Tsuga heterophylla*, *Thuja plicata* and *Taxus brevifolia* in the subcanopy. Understories were dominated by woody species, primarily *Rhododendron macrophyllum*, *Gaultheria shallon*, and *Berberis nervosa* (nomenclature follows Hitchcock and Cronquist 1973). The site was clearcut logged in May and June 1991 and broadcast burned on 11 September 1991 in a moderate- to high-intensity fire (Halpern et al. 1997).

Experimental and sampling designs

The full experiment consists of a randomized complete-block design with a control and eight treatments in which one or more species with different life histories and population dynamics are removed (for details see Halpern et al. 1997). Treatments were assigned randomly to nine 2.5 × 2.5 m experimental units (treatment areas) replicated in each of 25 blocks. Within each block, treatment areas are arranged in a 3 × 3 array with 1 m spacing. For this study, we excluded one block due to its unusual species composition associated with a distinctly shallower, rockier soil.

Plots were established and sampled in June 1990, prior to timber harvest. Vegetation measurements were made in a 1 × 1 m plot centered within each treatment area. Cover (%) of ground surface conditions (e.g. bare ground, fine litter, and logs) and of each vascular plant species was recorded annually through 2007 (year 16). In addition, stems were counted and measured for height and/or basal diameter annually through year 8 (except for year 5). Above-ground biomass was estimated using species-specific allometric equations developed for this site (Halpern et al. 1996). For most species with distinct shoots, biomass was predicted from height and/or basal diameter. For species without distinct shoots or with a trailing growth form, biomass was estimated from cover or a combination of cover and height.

Removal treatments were initiated in June 1992, synchronous with the first post-disturbance measurement. For the first 7 yr, removals were done monthly between April and June to minimize competition; seedlings were pulled by hand and vegetative shoots were clipped at the ground surface. Subsequently, removals were conducted at the time of vegetation sampling.

Six of eight removal treatments were discontinued early in the study when removal or target species became uncommon (Halpern et al. 1997). We restrict the analyses to the control and the two removal treatments that were maintained continuously: removal of *Rubus ursinus* and combined removal of *Berberis nervosa* and *Gaultheria shallon*. These species were chosen because they represent potentially dominant taxa with distinctly different successional dynamics. *Rubus* is a subordinate forest subshrub with a trailing habit that responds rapidly to overstory removal and can achieve very high post-disturbance cover via stoloniferous growth (Halpern 1989). In contrast, *Berberis* and *Gaultheria* are low, evergreen shrubs that dominate the forest understory, but recover more slowly through vegetative resprouting from extensive rhizome systems (Halpern 1989).

Statistical analyses

Q1) Correlations between invasion success of exotics and properties of the native community

We ran a series of Pearson correlations and multiple linear regressions with data from the control plots to explore relationships between measures of exotic success and properties of the native community (Q1a, b) and whether these relationships changed over time (Q1c). We first examined exotic and native communities as a whole (Q1a), then limited the analyses to annuals and biennials (i.e. short-lived monocarpic species – "annuals" for simplicity) (Q1b). For each analysis we used data from four times (years 2, 4, 7, and 16; Q1c) that were chosen to represent successional stages with progressively greater cover and biomass of native plants (reflecting correspondingly greater resource competition).

At the community level, exotic success was measured by four variables: species richness (number of species per 1 m^2 plot), total cover, total biomass, and total density of stems (Q1a). At the population level, success of individual exotic species was measured by three variables: stem density, cover, and biomass. Population-level analyses were limited to species present in at least five (20%) of the control plots (*Crepis capillaris*, *Cirsium vulgare*, *Lactuca serriola*, and *Senecio sylvaticus*). Properties of the native community included species richness, total cover, and total biomass; density was not used because cover and biomass are better indicators of resource utilization by perennial species. For correlations between exotic and native annuals (Q1b), species richness was not considered because it varied minimally among plots.

For each of the selected dates, Pearson correlations were run ($\alpha = 0.05$) for combinations of variables representing exotic success and properties of the native community. However, analyses using biomass or stem density were limited to years 2, 4, and 7; analyses also were not conducted for years when natives and/or exotics were infrequent (present in $<20\%$ plots). This yielded a total of 153 correlations (134 for Q1a, 19 for Q1b).

Following correlation analyses, we used multiple linear regression (stepwise selection with a significance threshold of 0.05) to tease apart the contributions of native herb and shrub layers to exotic success. The herb layer included herbaceous and low woody species <1 m tall, and the shrub layer, taller woody species. Total cover or biomass of native plants within each layer served as predictors; native richness was not considered because the shrub layer consisted of only three species (*Arctostaphylos columbiana*, *Rhododendron macrophyllum*, and *Pseudotsuga menziesii*). We only analyzed data for years 7 and 16 because at earlier dates there were too few plots with cover in the shrub layer. In total, 23 regression models were run (13 predicting exotic success at the community level and 10 for individual exotic species).

All data were log transformed to meet the assumptions of normality. All tests were considered significant at $\alpha = 0.05$. Although analyses involved many non-independent tests with the possibility of spurious significance for a proportion of these, our objective was to identify general patterns of correlation and how they might change through time, rather than to test specific hypotheses about particular pairs of variables.

Q2) Consequences for exotics of removing key native species

To test whether exotic colonists responded positively to removal of potentially dominant native species, we used one-way analysis of variance (randomized complete-block design) to compare the total density (or total cover) of exotic species in the control and the two removal treatments. Comparisons were made for the years that exotics peaked in density (year 5) or cover (year 6). These dates coincided with near-peak cover of the removal species (*Rubus*: year 5, 7.4%, year 6, 11.9%; *Berberis* and *Gaultheria*: year 5, 12.6%, year 6, 13.6%). Data were log transformed to meet the assumptions of normality and homogeneity of variance.

Q3) Population dynamics of exotic vs native species

To assess whether exotics were more successful than natives as colonists, we compared nine measures of population performance with a series of Mann-Whitney tests. We used data from the control plots with individual exotic and native species as samples (Meiners 2007). We considered only those species present in at least 20% of the control plots. Thus, we used the same four exotics as in Q1 and five natives (*Collomia heterophylla*, *Conyza canadensis*, *Epilobium paniculatum*, *Madia gracilis* and *Lotus purshianus*); all are annuals or biennials. The nine measures of performance represent different aspects of the pace, magnitude, or duration of population growth: 1) maximum annual increase in frequency (percentage of plots occupied), 2) maximum annual increase in stem density, 3) average increase in frequency (computed between first appearance and peak frequency), 4) average increase in stem density (computed between first appearance and peak frequency), 5) maximum frequency, 6) maximum density, 7) years to peak frequency (number of years between first appearance and peak frequency), 8) years to peak density (number of years between first appearance and peak density) and 9) duration (number of years with frequency $>20\%$).

All statistical analyses were conducted using SPSS ver. 13.0 (SPSS, Chicago, IL, USA), except for Mann-Whitney tests conducted in R ver. 2.6.2 (R Foundation for Statistical Computing, Vienna, Austria).

Results

General successional trends

Logging and broadcast burning consumed most plant cover, but vegetation recovery was rapid. In control plots, total plant cover averaged 15% in year 1 and increased to $>70\%$ in year 2 due to rapid growth of species in the herb layer (Fig. 1a). Subsequent increases were more gradual reflecting continuous growth of species in the shrub layer. Total biomass (estimated through year 8) changed similarly to cover, averaging ~ 20 g m^{-2} in year 1, 145 g m^{-2} in year 2, and >300 g m^{-2} in year 8 (Fig. 1b).

In total, 78 species were observed. Of these, 60 were native and 18 were exotic (Supplementary material Table S1). Among natives, 17% were annuals; among exotics, 50% were annuals. Temporal trends in the richness of natives and exotics were similar, although natives were consistently more diverse (Fig. 2a, b). Mean values for both groups peaked early in succession, then declined slowly. In contrast to cover and biomass, the range of richness values changed little over time for either group. Natives were more abundant and persistent than exotics and showed a much wider range of abundance values among plots (Fig. 2c–f).

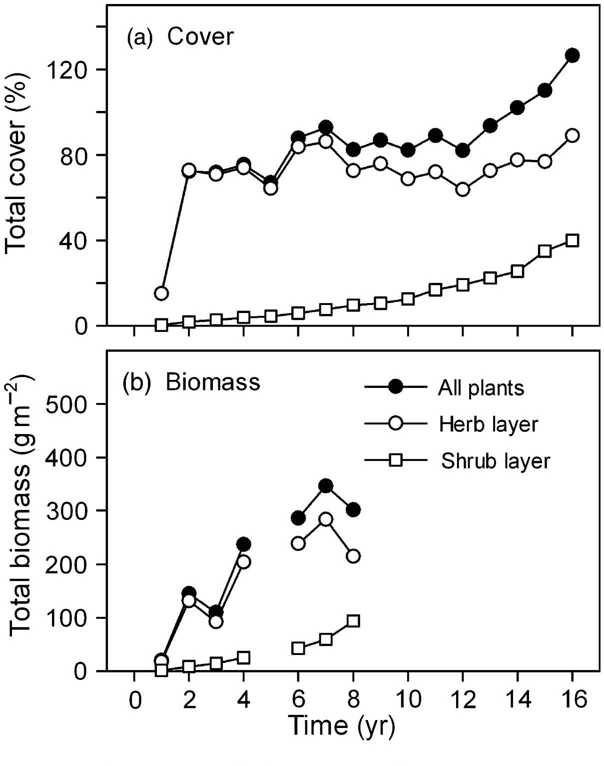

Figure 1. Changes in total plant cover and biomass over 16 yr of succession. Values are means of the control plots ($n = 24$). Biomass data were not collected in year 5 or after year 8.

Most native and exotic species selected for comparison of population trends showed rapid increases in abundance (Fig. 3). Species varied, however, in the timing of peak abundance and rate of disappearance from plots. Some were highly transient (e.g. *Senecio sylvaticus*, *Lactuca serriola*, and *Conyza canadensis*); others were more persistent (e.g. *Crepis capillaris*, *Epilobium paniculatum*, and *Collomia heterophylla*). *Lotus purshianus* (native) was unique in its invasion pattern, characterized by a continuous increase in frequency.

Relationships between native and exotic species

Q1) Correlation between success of exotics and properties of the native community

We hypothesized that natives and exotics, as groups, would show few correlations early in succession when plant cover was low, but significant negative correlations later in succession when resource competition became more intense. Temporal trends were only partly consistent with these predictions. In year 2, we detected only one marginally significant relationship between natives and exotics (Table 1, 2). In year 4, however, two (17%) of the community-level comparisons were significant (both negative correlations; Table 1) as were seven (19%) of the species-based tests (all negative correlations; Table 2). *Crepis capillaris* was the species most frequently correlated with properties of the native community (Table 2). After year 4, however, we detected few significant relationships between natives and exotics. Significant correlations were uncommon in year 7 and by year 16, only *Crepis* was present with sufficient frequency to include in the analyses (Table 2).

Multiple linear regressions designed to tease apart the contributions of native herb and shrub layers to exotic success also yielded few significant models. Two of 10 community-level models were significant, with negative relationships driven by the shrub layer (exotic density in year 7: $b = -0.65$, $p = 0.001$; exotic cover in year 16: $b = -0.46$, $p = 0.03$, respectively). Three of 13 species-level models were significant (all involving *Crepis capillaris*); these were also driven by negative relationships with the shrub layer (biomass in year 7: $b = -0.54$, $p = 0.007$; density in year 7: $b = -0.65$, $p = 0.001$; cover in year 16: $b = -0.56$, $p = 0.005$).

Patterns of correlation between native and exotic annuals were distinctly different from those of the broader plant community (cf. Table 3, 1) and did not support our hypothesis that negative relationships would be strongest between annual species because of their functional similarity. Early in succession (years 2 and 4), only one of 12 correlations yielded a significant result (negative in sign; Table 3). In years 7 and 16, however, all correlations were significant, but positive in sign. We tested whether this latter result could be explained by a shared positive association of natives and exotics with bare ground (which was not limiting early in succession). For cover (year 7 and 16) and biomass (year 7), only native annuals showed a

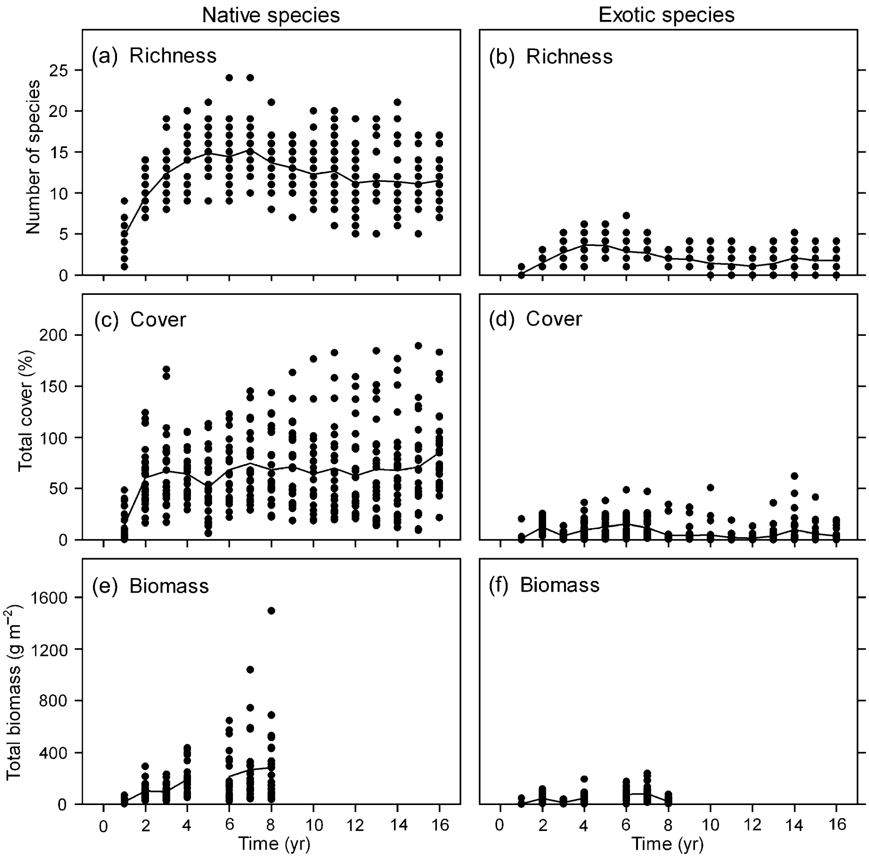

Figure 2. Changes in total richness, cover, and biomass of native and exotic species in control plots (n = 24) over 16 yr of succession. Points are individual plots illustrating the range of variation over time; solid lines are means. Biomass data were not collected in year 5 or after year 8.

positive correlation with bare ground; however, for density (year 7), both groups did.

Q2) Consequences for exotics of removing key native species

We hypothesized that exotics would respond positively to removal of native dominants. However, at peak cover (year 6) and stem density (year 5), abundance of exotics did not differ between controls and either removal treatment (non-significant main effects from one-way ANOVAs on exotic cover: $F_{2,69} = 0.015$, $p = 0.99$ and density: $F_{2,69} = 0.406$, $p = 0.67$).

Q3) Population dynamics of exotic vs native species

We hypothesized that greater colonizing abilities and growth rates would allow exotic species to exhibit more rapid invasion and achieve greater densities than native colonists. However, for none of the metrics considered did exotics and natives show a significant difference in performance (Table 4).

Discussion

On average, exotic species played a relatively minor and transient role in the post-disturbance vegetation. Most were annuals, biennials, or short-lived perennials that, at peak abundance, accounted for ~20% of local (plot-scale) richness and plant cover. This general result is consistent with previous studies of post-harvest succession in the Pacific Northwest, where exotics contribute minimally, or only briefly, to the post-disturbance flora (Halpern and Spies 1995, Tyler and Peterson 2006). It is also consistent with the roles of exotics in other forest ecosystems in western North America (Haeussler et al. 2004, Klinger et al. 2006, Sumners and Archibold 2007, Nelson et al. 2008), where they tend to be short-lived ruderals limited in time and space by their intolerance of shade (Meiners et al. 2002, but see Martin et al. in press). Despite low average abundance, exotics exhibited a wide range of richness and cover values among sample plots, providing an opportunity to explore the potential for interactions with native species at small spatial scales.

Correlations between success of exotics and properties of the native community

We hypothesized that relationships between natives and exotics would be non-significant early in succession, but significant and negative later in succession, reflecting increasing potential for competitive interactions over time. However, we observed few significant correlations for any of the metrics considered over the broad range of dates

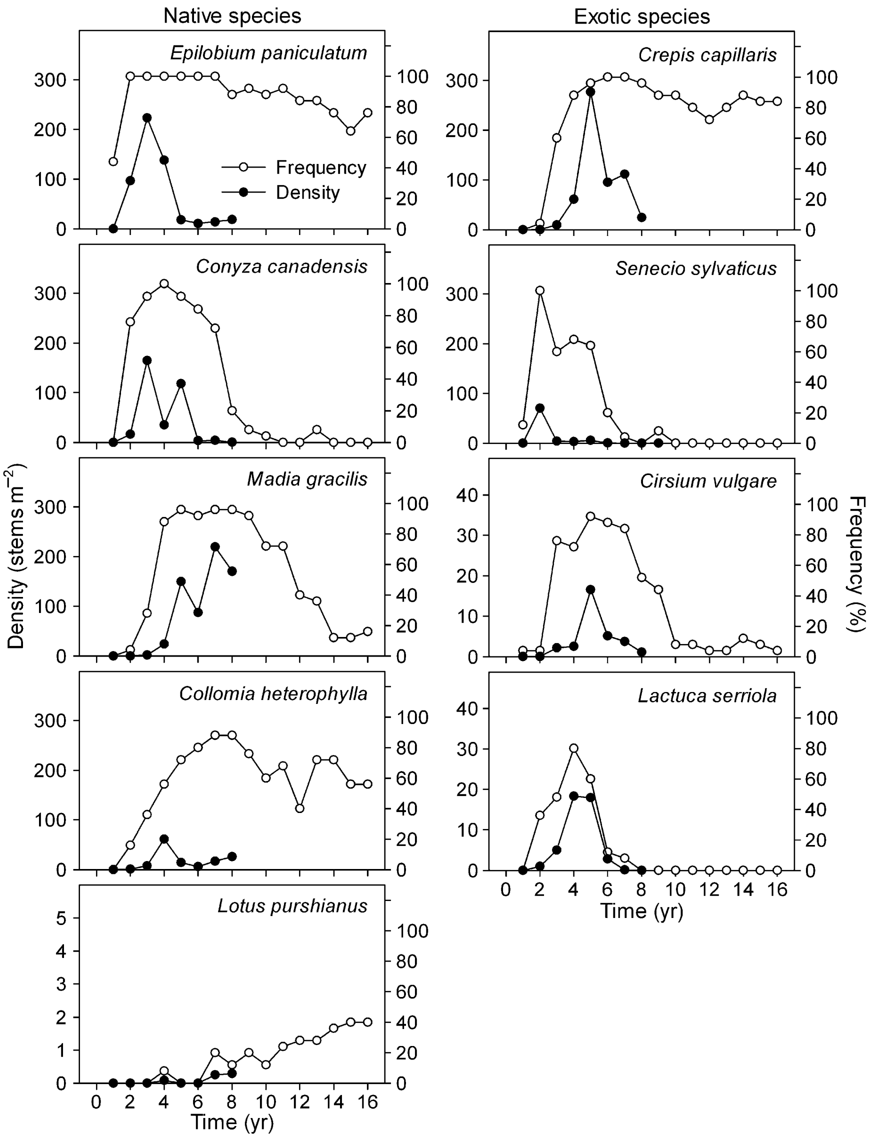

Figure 3. Changes in density and frequency of native and exotic species in control plots (n = 24) over 16 yr of succession. The species presented are those that occurred in at least 20% of plots. Density data were not collected after year 8. Note the variation in density scales among species.

Table 1. Pearson correlation coefficients between properties of native and exotic communities at different times during succession. All data were log transformed. Asterisks denote significant ($p \leq 0.05$) and plus marks denote marginally significant ($0.05 \leq p \leq 0.10$) relationships. Blank cells indicate that density and biomass were not sampled in year 16 (see Statistical analyses).

Native community	Exotic community	Year 2	Year 4	Year 7	Year 16
Species richness vs	Species richness	−0.14	−0.19	0.02	−0.13
	Total cover	0.16	−0.45*	−0.23	−0.19
	Total biomass	−0.19	−0.38^{+}	−0.23	
	Total density	0.22	−0.49*	−0.14	
Total cover vs	Species richness	0.07	0.05	0.03	−0.32
	Total cover	−0.25	−0.29	−0.35^{+}	−0.38^{+}
	Total biomass	−0.32	−0.22	−0.32	
	Total density	−0.14	−0.34	−0.12	
Total biomass vs	Species richness	−0.12	0.05	0.17	
	Total cover	−0.22	−0.40^{+}	−0.42*	
	Total biomass	−0.32	−0.15	−0.32	
	Total density	−0.15	−0.28	−0.26	

Table 2. Pearson correlation coefficients between properties of the native community and measures of invasion success for individual exotic species at different times during succession. All data were log transformed. Asterisks denote significant ($p \leq 0.05$) and plus marks denote marginally significant ($0.05 < p \leq 0.10$) relationships. Dashes indicate that correlations were not computed due to low frequency of exotics. Blank cells indicate that density and biomass were not sampled in year 16 (see Statistical analyses).

Native community	Exotic species	Metric	Year 2	Year 4	Year 7	Year 16
Species richness vs	*Crepis capillaris*	cover	–	−0.52*	−0.32	−0.32
		biomass	–	−0.55*	−0.26	
		density	–	−0.62*	−0.13	
	Cirsium vulgare	cover	–	0.07	0.12	–
		biomass	–	0.18	0.11	
		density	–	0.19	0.27	
	Senecio sylvaticus	cover	0.24	−0.04	–	–
		biomass	−0.15	−0.02	–	
		density	0.25	0.21	–	
	Lactuca serriola	cover	−0.28	0.00	–	–
		biomass	−0.28	−0.00	–	
		density	−0.34	−0.13	–	
Total cover vs	*Crepis capillaris*	cover	–	−0.50*	−0.14	−0.31
		biomass	–	−0.51*	−0.22	
		density	–	−0.54*	−0.12	
	Cirsium vulgare	cover	–	0.06	−0.22	–
		biomass	–	0.09	−0.17	
		density	–	0.05	−0.13	
	Senecio sylvaticus	cover	−0.28	−0.01	–	–
		biomass	−0.37^{+}	−0.06	–	
		density	−0.15	0.23	–	
	Lactuca serriola	cover	−0.10	0.13	–	–
		biomass	0.11	0.14	–	
		density	−0.02	−0.12	–	
Total biomass vs	*Crepis capillaris*	cover	–	−0.34^{+}	−0.49*	–
		biomass	–	−0.25	−0.45*	
		density	–	−0.24	−0.29	
	Cirsium vulgare	cover	–	0.11	0.03	–
		biomass	–	0.16	0.12	
		density	–	0.08	0.21	
	Senecio sylvaticus	cover	−0.22	−0.08	–	–
		biomass	−0.34	−0.20	–	
		density	−0.15	0.08	–	
	Lactuca serriola	cover	−0.13	−0.33	–	–
		biomass	0.04	−0.30	–	
		density	−0.08	−0.48*	–	

tested. Later in succession, when it was possible to separate effects of herbaceous from taller woody plants, negative relationships suggested that any competition-induced declines were likely to have been driven by taller shrubs and regenerating trees, not by native herbs. Several factors may contribute to these declines: shading by taller growth forms (Kochy and Wilson 2000), root competition for soil resources (Coomes and Grubb 2000), and physical burial or inhibition of germination by leaf litter (Facelli and Pickett 1991). Litter effects may be particularly strong given dominance of the shrub layer by *Arctostaphylos* and *Rhododendron* which both produce sclerophyllous, highly recalcitrant leaves.

A number of factors may explain the absence of strong interactions between native and exotic herbs. First, despite considerable variation in development of exotics among plots, the range of richness and abundance values may have been inadequate to yield significant relationships with natives. Second, in a study of pairwise associations among individual species from the same experimental plots, Rozzell (2003) demonstrated that positive correlations were more common than negative ones (although the proportion of

Table 3. Pearson correlation coefficients between properties of native and exotic annual communities at different times during succession. All data were log transformed. Asterisks denote significant ($p \leq 0.05$) and plus marks denote marginally significant ($0.05 \leq p \leq 0.10$) relationships. Blank cells indicate that biomass and density were not sampled in year 16. Correlations between richness of natives and exotics were not computed because of the small range of richness values (see Statistical analyses).

Native annuals	Exotic annuals	Year 2	Year 4	Year 7	Year 16
Total cover vs	Total cover	−0.35^{+}	0.25	0.48*	0.45*
	Total biomass	−0.29	0.12	0.34*	
	Total density	−0.44*	0.14	0.62*	
Total biomass vs	Total cover	−0.16	0.11	0.55*	
	Total biomass	−0.18	0.06	0.44*	
	Total density	−0.30	0.05	0.67*	

Table 4. Results of Mann-Whitney tests comparing population metrics of native (n = 5) and exotic (n = 4) species present in at least 20% of control plots.

Population metric	Native species		Exotic species		
	Mean	SE	Mean	SE	p
Maximum annual increase in frequency (%)	48.8	10.1	63. 0	9.6	0.45
Maximum annual increase in density (no. m^{-2})	115.1	20.9	78.4	41.3	0.49
Average increase in frequency (%)	25.1	8.0	28.8	6.3	0.79
Average increase in density (no. m^{-2})	53.4	14.8	28.5	13.3	0.20
Maximum frequency (%)	84.8	11.4	93.0	4.1	0.87
Maximum density (no. m^{-2})	167.1	37.6	95.6	53.4	0.49
Years to peak frequency	5.4	1.8	3.7	0.6	0.70
Years to peak density	3.5	0.9	3.5	0.6	0.97
Duration (years with frequency >20%)	10.6	2.0	7.5	2.2	0.37

positive associations declined over time). Thus, competitive interactions between individual native and exotic species may be balanced, in part, by positive associations among other pairs of species. Both types of associations may contribute simultaneously to structuring plant communities (Callaway and Walker 1997, Holmgren et al. 1997). Third, individual exotic species may differ in their responses to natives (Meiners et al. 2004), thus reducing the potential for strong community-level patterns. Likewise, the pool of natives included species with a diversity of life-history and functional traits (short-lived ruderals to clonal, shade-tolerant herbs) – species that are likely to respond in diverse ways to disturbance, resource availability, and environmental stress. Variation in the abundance of these species among plots could lead to variation in the types and strengths of interactions with exotics (Meiners et al. 2004).

We attempted to distinguish among some of these possibilities by considering relationships between a functionally similar pool of natives and exotics (i.e. annuals), and the responses of individual exotic species. We expected negative relationships between native and exotic annuals to be stronger than those observed for the full community of species given similar life-history and resource-use strategies. However, we found few significant correlations early in succession (years 2 and 4), and consistently strong positive associations in later years (7 and 16). Positive associations among annuals later in succession could suggest facilitation of natives by exotics (or the reverse), however, this is unlikely. Facilitation would be more likely early in succession (soon after broadcast burning) when environmental stress was greater (Callaway and Walker 1997, Callaway et al. 2002). Moreover, densities of both native and exotic annuals were positively correlated with cover of bare ground in year 7. Positive associations at a time when germination sites are limiting suggests a shared affinity for this substrate rather than facilitation of one group by the other. A common response to environmental variation is often used to explain patterns of richness among natives and exotics (Levine 2000, Davies et al. 2005), but rarely patterns of abundance (but see Sax 2002).

Analyses at the population level suggest that the few negative correlations observed between natives and exotics were attributable to *Crepis capillaris*, the most abundant and persistent of the exotic species. Significant community-level correlations coincided with the timing of significant correlations with *Crepis*. The paucity of similar relationships among the remaining species suggests that controls on invasion may be highly individualistic and dependent on factors other than simple community traits (Troumbis et al. 2002, Meiners et al. 2004).

Consequences for exotics of removing key native species

Species-removal treatments provided an opportunity to test whether exotic species were inhibited by dominant species in the native community. Release of exotics would provide strong evidence for direct or indirect controls on invasion by these community dominants (Fargione and Tilman 2005, Emery and Gross 2007). However, neither removal treatment increased the cover or density of exotics. There are several possible explanations for the lack of response. First, resources unexploited by plant removals may have been preempted by species with similar successional roles rather than by exotic colonists; competition for resources should be more intense among species with similar functional traits (Fargione et al. 2003, Tilman 2004). Thus, native, mid-successional species may have benefited more than exotic annuals. This conclusion is supported by the non-significant differences in total cover of natives between controls and removals (ANOVAs on total native cover in year 5, $p = 0.957$; and year 6, $p = 0.254$), indicating that removal of dominants was compensated for by growth of other natives.

Another possible explanation for the lack of response to removals – one that is consistent with the results of correlation analyses – is that the successional dynamics of exotics are driven by factors other than interspecific interactions. In an earlier study in this experimental system, entire community removals (more extreme than the removal of dominants) did not prevent loss of the exotic, *Senecio sylvaticus*. Following peak density in year 2, *Senecio* declined abruptly and at comparable rates in both community removals and controls (Halpern et al. 1997). Thus, competitive interactions may not be responsible for displacement of early successional annuals. Instead, declines may be related to allelopathic effects, pathogens, litter accumulation, or changes in soils or ground-surface conditions (Jackson and Willemsen 1976, Vitousek et al. 1987a, Facelli and Pickett 1991, Davidson 1993, van der Putten et al. 1993). The availability of germination sites (mineral soil) may be critical for persistence of these species as populations are renewed annually or biannually from seed.

Increasing resource availability resulting from removals may thus offer minimal benefit if germination sites are limiting.

Population dynamics of exotic vs native species

Exotics could have an advantage over natives because of inherent differences in functional traits or competitive abilities, or in their ability to escape from natural enemies in new environments (Keane and Crawley 2002, Fargione et al. 2003, Funk and Vitousek 2007). The alternative proposition is that exotics and natives do not differ systematically in their traits (Thompson et al. 1995) or colonizing abilities (Davis et al. 2000).

A test of these competing theories in the current successional system revealed that natives and exotics did not differ consistently for any measure of colonizing ability or population success (i.e. rate of spread, rate or magnitude of increase in local density, or persistence). Clearly, our ability to demonstrate differences between groups is constrained by the small number of species with sufficient frequency to include in these tests. We were also unable to control for the proportions of species with differing modes of seed dispersal, a trait that could affect rates of spread. However, this cannot explain the absence of differences. All of the exotics were wind dispersed, whereas natives also included ''slower'' dispersers, i.e. species with adhesive (*Madia gracilis* and *Collomia heterophylla*) and ballistically dispersed seeds (*Lotus purshianus*). Moreover, species with similar modes of dispersal showed varying rates of spread or increase. In sum, population trends appeared as variable within as between groups. In a long-term study of old-field succession with a much larger sample of species ($n = 25$), Meiners (2007) also was unable to demonstrate a statistical difference in the population dynamics of native and exotic species, leading to a similar conclusion – that natives and exotics possess similar sets of traits and play similar ecological roles in early successional communities.

Conclusions

Studies of plant invasibility have been conducted primarily in grassland ecosystems (see review in Levine et al. 2004), but rarely in forests or successional communities (but see Sax 2002, Meiners et al. 2002, 2004, Meiners 2007). Long-term studies in disturbed forests, which are common globally, exhibit rapid successional dynamics, and host a broader diversity of plant functional types than do grasslands, broaden the scope of invasibility research.

In this early successional system, exotics behave as ''weak'' invaders, coexisting with natives as a minor component of the post-disturbance vegetation (Ortega and Pearson 2005). They are short-lived species (mostly annuals and biennials) that peak at relatively low abundance and decline rapidly during succession. Community-level analyses provide little evidence that, at small spatial scales (1 m^2), invasion success relates to properties of the native community or that relationships with natives change over time in predictable ways. The factors that promote establishment and increases among exotics appear similar to those that promote successful colonization of native ruderals: exposure of mineral soil by disturbance and local production of an abundance of seed by an initial cohort of recruits. Declines over time reflect changes in the biotic and abiotic environment that limit local seed production (e.g. shading by taller woody plants) and inhibit recruitment (e.g. loss of germination sites to accumulating litter). Comparable variation in population dynamics and individualistic patterns of increase and decline suggest that exotics and natives possess similar combinations of functional traits that lead to similar successional roles in these forests.

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