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REPORT

Beyond biodiversity: individualistic controls of invasion in a self-assembled community

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Abstract

Recent experimental and simulation results, and competition-based ecological theory, predict a simple relationship between species richness and the invasibility of communities at small spatial scales – likelihood of invasion decreases with increasing richness. Here we show data from 42 continuous years of sampling old field succession that reveal quite different dynamics of plant invasion. Contrary to experimental studies, when richness was important in explaining invasion probability, it was typically positively associated with species invasion. Invasion of several species had a unimodal response to resident species richness, which appeared to be a mixture of compositional influences and a richness effect. Interestingly, invasions by native and exotic species did not fundamentally differ. Control of species invasion in this system is individualistic, caused by a variety of community-level mechanisms rather than a single prevailing richness effect.

Keywords

Biological invasion, community dynamics, diversity, individualistic responses, invasibility, long-term data, old fields, successional systems.

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INTRODUCTION

At small spatial scales, studies of invasibility in experimental systems (Tilman 1997; Knops *et al.* 1999; Stachowicz *et al.* 1999; Levine 2000; Prieur-Richard *et al.* 2000; Kennedy *et al.* 2002) and in simulation models (Case 1990; Tilman *et al.* 1997b), typically show a relatively simple relationship between species richness and the invasibility of communities – the likelihood of invasion decreases with increasing richness (Levine & D'Antonio 1999). However, studies of patterns in natural systems typically show that more diverse communities are more heavily invaded, particularly at larger spatial scales (Stohlgren *et al.* 1998; Wiser *et al.* 1998; Lonsdale 1999; Stohlgren *et al.* 1999). While there has been some attempt to reconcile these disparate results (Shea & Chesson 2002), the relative importance of diversity in regulating community invasibility is still unresolved for natural systems.

Experimental studies linking local diversity to community invasibility typically revolve around competitive mechanisms (Case 1991; Tilman *et al.* 1997a; Stachowicz *et al.* 1999; Kennedy *et al.* 2002). Species rich communities utilize available resources such as space (Stachowicz *et al.* 1999; Levine 2000) or soil nutrients (Tilman *et al.* 1997a; Loreau 1998; Knops *et al.* 1999) more completely, resulting in insufficient resources to support invading species (Knops *et al.* 1999; Stachowicz *et al.* 1999; Fargione *et al.* 2003). However, competition is not the only factor that structures communities (Tilman 1997; Davis *et al.* 2000; Levine 2000; Brown & Peet 2003; Bruno *et al.* 2003). Therefore, multiple factors may also control community invasibility. The focus on competitive interactions in experimental studies may be premature and could lead to an unwarranted generalization of community interactions controlling invasion (Bruno *et al.* 2003).

Our current understanding of controls on invasions is limited by several factors. Experimental studies of invasions are frequently short (Tilman 1997; Crawley *et al.* 1999; Knops *et al.* 1999; Stachowicz *et al.* 1999; Levine 2000; Prieur-Richard *et al.* 2000; Symstad 2000; Kennedy *et al.* 2002; Troumbis *et al.* 2002), while invasions occur over many years. Furthermore, experimental studies often utilize assembled communities detached from the factors that control diversity in natural systems, requiring continual manipulation. This limits their utility in understanding invasions in dynamic natural systems (Kennedy *et al.* 2002;

Troumbis *et al.* 2002). In addition, mathematical models of invasions frequently assume equilibrium interactions, a condition not often seen in natural systems (Levine & D'Antonio 1999). To overcome these limitations to our understanding of invasions, long-term experiments and monitoring in unaltered communities are needed to validate studies based on simplified or unrealistic conditions and to evaluate patterns derived from natural systems (Wiser *et al.* 1998; Blossey 1999; Byers *et al.* 2002).

Successional communities are model systems for the regulation of community invasibility because they are characterized by continuous species invasions, are frequently heavily invaded by exotic species and are typically invaded rapidly. We used permanent plot data from the Buell-Small Succession Study to determine controls on invasion in a self-assembling plant community over a 42-year time span for a number of native and exotic plant invaders. The aim of this study was to provide a crucial linkage between manipulative experimental studies and observational patterns by revealing long-term community dynamics associated with species invasions. To address this issue, we specifically address the following questions. (1) Can local species richness predict the probability of invasion? (2) Does the inclusion of other community data improve the ability to predict invasions? (3) Do controls of invasion vary between native and exotic invaders?

METHODS

Study site and data collection

Invasion dynamics in abandoned agricultural land were studied from 1958 to 1999 at the Hutcheson Memorial Forest Center in the Piedmont of New Jersey, USA (40°30′N, 74°34′W) as part of the Buell-Small Succession Study (Pickett 1982). Within each of 10 fields, 48 permanently marked 0.5 m × 2.0 m plots were established immediately after abandonment and have been sampled since release. In each year (alternate years 1979–1999) the percent cover of all species present in each plot was recorded. These data represent the longest continuous data set on old field successional change known. Nomenclature follows Gleason & Cronquist (1991).

Exotic cover in the study site is highly variable over time and across fields, but typically exceeds 50%. While the proportion of exotic species has decreased over time, and field scale richness increased, species richness per plot has remained near 13 species per plot (Meiners *et al.* 2002).

Invasion dynamics

The temporal pattern of invasion was examined for each of the 26 most common invading species. These species included a range of life histories from many successional ages. The species examined included 14 native and 12 species exotic to North America. For each species, the period extending from the initiation of invasion (t_1) to peak cover (t_2) was identified. The time period was limited to a maximum of 10 years by setting t_2 to no more than $t_1 + 10$ to keep all invasions at a similar time scale. Initiation, t_1, was set when cover of the invading species was ≤5%, or at year 1 for species invading immediately after abandonment. When a species remained at ≤5% cover for extended periods, t_1 was set to when the species began to increase in cover. Plots already invaded at t_1 were dropped from the analyses. Only fields in which cover of the invading species at t_2 averaged ≥1% per plot were included in the analyses. The species analysed here represent all species within the study that were abundant enough to analyse statistically. Tree species increased in cover too slowly to be included in the study.

Statistical methods

Two analyses were conducted to assess influences on invasibility. To evaluate the general relationship between richness and invasibility, logistic regression was used to model the likelihood of invasion of a species at t_2 based on the species richness and richness^2 of the plot at t_1. The quadratic function (richness^2) was included to address the unimodal response found in some species. For all species in which richness was associated with likelihood of invasion in the first analysis, a second, mechanistic analysis was conducted. Multiple logistic regressions using forward model selection were used to evaluate the contribution of resident species composition, total cover and species richness on likelihood of invasion. The cover of the most abundant resident species, those with ≥5% cover at t_1, was included to evaluate the contribution of species composition to the previously described richness effects. In order to separate influences of overall community cover from compositional effects of individual species, total plot cover was also included in the analysis.

RESULTS

Of the 26 species analysed, 15 showed a relationship between initial plot richness and invasion (Figs 1 and 2). Species richness was positively associated with the likelihood of invasion in all but one species (Table 1). Five of these species showed significant unimodal relationships (Figs 1 and 2), shown by a positive slope estimate for richness and a negative slope for richness^2 (Table 1). Species analysed, but which did not show significant relationships with species richness were: natives – *Aster pilosus*, *Euthamia graminifolia*, *Parthenocissus quinquefolia*, *Potentilla simplex*, *Solidago*

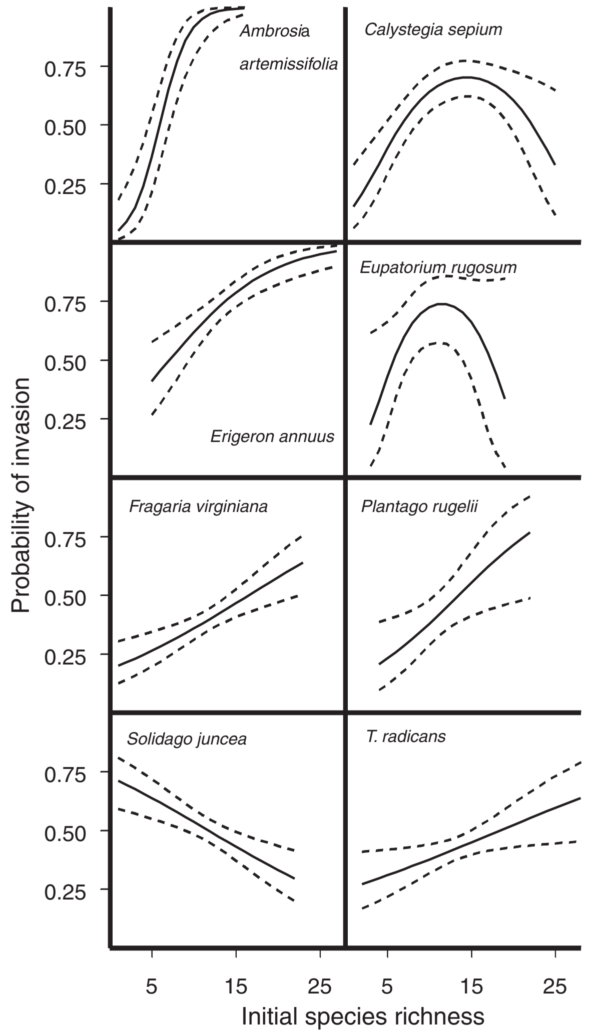

Figure 1 Influence of species richness on the invasion of native species. Predictions (—) and 95% confidence intervals (---) from logistic regression analysis of native species invasions are given. Life forms and invasion periods (years post-abandonment) for each species are: *Ambrosia artemissiifolia* (annual) years 1–5; *Calystegia sepium* (herbaceous vine) years 1–6; *Erigeron annuus* (annual) years 1–2; *Eupatorium rugosum* (perennial) years 30–40; *Euthamia graminifolia* (perennial) years 4–10; *Fragaria virginiana* (perennial) years 4–10; *Plantago rugelii* (perennial) years 1–3; *Solidago juncea* (perennial) years 5–15; *Toxicodendron radicans* (woody vine) years 10–20.

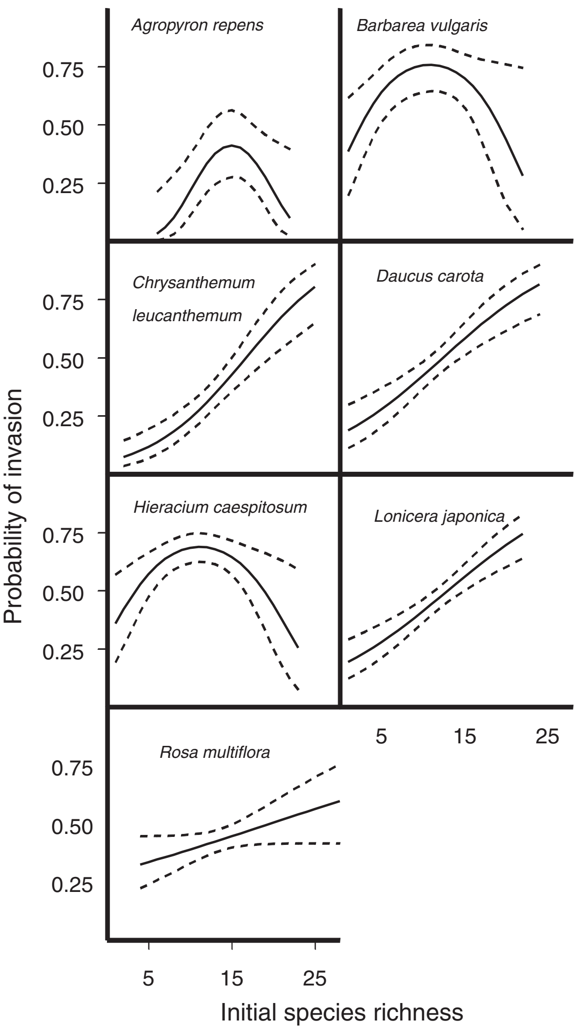

Figure 2 Influence of species richness on the invasion of exotic species. Predictions (—) and 95% confidence intervals (---) from logistic regression analysis of exotic species invasions are given. Life forms and invasion periods (years post-abandonment) for each species are: *Agropyron repens* (perennial grass) years 1–5; *Barbarea vulgaris* (biennial) years 1–2; *Chrysanthemum leucanthemum* (perennial) years 2–6; *Daucus carota* (biennial) years 1–4; *Hieracium caespitosum* (perennial) years 4–10; *Lonicera japonica* (woody vine) years 5–15; *Rosa multiflora* (shrub) years 10–20.

canadensis and *S. rugosa*; exotics – *Bromus racemosus*, *Poa pratensis*, *Rumex acetosella*, *Trifolium hybridum* and *T. pratense*.

Multiple logistic regression was used to examine each of the 15 species that showed a significant relationship between richness and probability of invasion. In this analysis, richness remained associated with probability of invasion in nine species (Table 2). Of these species, all but one showed a positive influence of initial richness or richness^2 on the likelihood of invasion. The exception to this was *Rosa multiflora*, which maintained a positive influence of richness and a negative influence of richness^2 on invasion. Invasion by most species (13/15) was associated with abundance of one or more resident species (Table 2). These influences were a mixture of positive and negative effects. Many species with negative quadratic effects of richness in the first analysis had negative associations with resident species; in some cases these effects replaced the earlier richness effects. Total plant

Table 1 Influence of species richness on the probability of invasion by native and exotic species

	Initial species richness		Richness^2	
	Slope	χ^2	Slope	χ^2
Native species				
Ambrosia artemisiifolia	0.59	24.67***	–	–
Calystegia sepium	0.41	15.13***	−0.01	11.49***
Erigeron annuus	0.17	18.86***	–	–
Eupatorium rugosum	0.72	4.26*	−0.03	3.67^{M}
Fragaria virginiana	0.09	13.50***		
Plantago rugelii	0.14	6.36*	–	–
Solidago juncea	−0.08	12.64***	–	–
Toxicodendron radicans	0.06	5.34*	–	–
Exotic species				
Agropyron repens	1.12	6.31*	−0.04	5.86*
Barbarea vulgaris	0.36	6.87**	−0.02	5.70*
Chrysanthemum leucanthemum	0.17	27.84***	–	–
Daucus carota	0.54	14.57***	−0.02	9.53**
Hieracium caespitosum	0.30	8.54**	−0.01	8.06**
Lonicera japonica	0.32	7.51**	−0.01	3.16^{M}
Rosa multiflora	0.03	4.62*	−0.01	3.42^{M}

M, marginally significant: $0.10 > P > 0.05$; $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Quadratic terms were only included in the model when $P \leq 0.10$. d.f. = 1 for species richness and richness^2.

Table 2 Factors controlling invasion success from simultaneous analyses of richness, cover and community composition

Invading species	Model effects
Agropyron repens (E)	*Ambrosia artemissifolia* (+)
Ambrosia artemissifolia (N)	Initial richness^2 (+); *Dactylis glomerata* (−)
Barbarea vulgaris (E)	*Chenopodium album* (+)
Calystegia sepium (N)	*Dactylis glomerata* (−); *Raphanus raphanastrum* (+)
Chrysanthemum lecucanthemum (E)	Initial richness^2 (+); Total plant cover (−); *Trifolium pratense* (+)
Daucus carota (E)	Initial richness (+); Initial richness^2 (+); Total plant cover (−); *Ambrosia artemissifolia* (−); *Dactylis glomerata* (−)
Erigeron annuus (N)	Initial richness (+); *Ambrosia artemissifolia* (−); *Chenopodium album* (−)
Eupatorium rugosum (N)	*Juniperus virginiana* (−)
Fragaria virginiana (N)	Total plant cover (+); *Agropyron repens* (−); *Aster pilosus* (+); *Daucus carota* (−); *Hieracium caespitosum* (+)
Hieracium caespitosum (E)	*Aster pilosus* (+)
Lonicera japonica (E)	Initial richness (+); *Aster pilosus* (+); *Chrysanthemum leucanthemum* (+)
Plantago rugellii (N)	Initial richness (+)
Rosa multiflora (E)	Initial richness (+); Initial richness^2 (−); *Euthamia graminifolia* (−); *Lonicera japonica* (+)
Solidago juncea (N)	Initial richness^2 (+); Total plant cover (+); *Aster pilosus* (−); *Dactylis glomerata* (−); *Hieracium caespitosum* (−)
Toxicodendron radicans (N)	Initial richness^2 (+)

Native (N) and exotic (E) indicated for each invading species. Symbols in parentheses indicate the nature of the effect.

cover was positively associated with invasion in two species and negatively associated with invasion in two others.

DISCUSSION

Resident species richness was a useful predictor of invasion in many of the species tested. However, in contrast to the majority of experimental studies and competition-based theory, species richness was positively associated with the likelihood of invasion in all but one of the species that showed an association. Five species had a significant unimodal relationship between initial richness and invasion rather than the monotonic relationship seen in many experimental systems. Most importantly, there is not a single characteristic that controls invasibility within this plant community, but instead a variety of individualistic controlling factors acting in concert. Therefore, it is impossible to make generalizations on the regulation of community invasibility. In addition, native and exotic species appear to respond to species richness and other invasion regulators similarly, indicating that these groups of species are not inherently different from each other (Thompson *et al.* 1995; Levine & D'Antonio 1999).

Analyses of the role of diversity in ecosystem function is plagued with questions about whether observed patterns are the effects of diversity *per se* or caused by an ecological sampling effect (Huston 1997; Tilman *et al.* 1997b; Loreau 1998). For example, plots with higher species richness may be more likely to contain a resident species capable of influencing colonization by an invading species (Huston 1997; Tilman *et al.* 1997b; Loreau 1998; Crawley *et al.* 1999). Our mechanistic analysis simultaneously examined the role of species richness and resident species composition in influencing the likelihood of invasion for each of the 15 species. This analysis further showed individualistic variation among species in factors associated with likelihood of invasion, most of which retained richness effects.

Most invading species responded to one or more resident species, indicating the prevalence of compositional effects. Compositional effects were a mixture of positive and negative influences on the likelihood of invasion. Each invading species, even those invading during the same time period, had a different combination of species associated with their invasions and there were no clear distinctions between native and exotic invaders. The interaction between resident community composition and invader identity appears individualistic (Callaway & Aschehoug 2000; Fargione *et al.* 2003). For example, the perennial grass *Dactylis glomerata* consistently had negative influences on the invasion of other species. Other resident species did not consistently influence invasibility, showing the potential for both positive and negative influences on invading species. Controls on invasion are, therefore, specific to each combination of resident and invading species (Troumbis *et al.* 2002; Fargione *et al.* 2003).

The combination of mechanisms controlling invasions obscures one clear influence of richness in this system – species richness is positively associated with successful invasions. For example, *S. juncea* shows a general pattern of decreasing likelihood of invasion with increasing species richness in the first analysis (Fig. 1). However, multiple logistic regression found that initial richness was always positively associated with invasion, while several common plant species depressed the likelihood of invasion, suggesting that an ecological sampling effect generated the overall association with richness in this species (Huston 1997). Thus, observed patterns of invasion are a combination of both diversity and compositional effects. As richness is generally positively associated with invasion probability in this system, it appears that the same factors that regulate local diversity also determine the suitability of a habitat for invasion in general (Wiser *et al.* 1998; Bruno *et al.* 2003). As richness of the local community increases, competitive interactions may increase via the ecological sampling effect, decreasing the success of plant invasions (Huston 1997). Taken together, the net positive association between local richness and invasion coupled with net negative competitive influences at higher richness appear to generate the unimodal invasion response to richness seen in several species (Bruno *et al.* 2003).

Invasion patterns may also be explained by mechanisms other than influences of species richness and plot composition. For example, total plant cover influenced the invasion of four species – two positively and two negatively. Competitive interactions are likely greater in plots with higher cover or biomass, leading to decreased invasion success (Tilman 1997; Kennedy *et al.* 2002; Troumbis *et al.* 2002), while suitable microclimatic conditions for germination and establishment may be more likely in higher cover plots (Reader & Beisner 1991; Bruno *et al.* 2003), leading to increased invasion success in some species. Additionally, differences in local species richness may be the result of differential seed input rates (Tilman 1997; Levine 2000; Brown & Peet 2003). However, differential seed availability is unlikely in this system as most species in the analyses were either abundant enough that all plots were close to potential seed sources or were likely present in the seed bank prior to abandonment (Kennedy *et al.* 2002). Furthermore, despite high rates of turnover, species richness per plot does not change with successional development in this system (Meiners *et al.* 2002), suggesting internal rather than external controls on richness.

While the data presented here come from a highly disturbed subset of potential communities, we believe that these results have several implications for understanding community invasibility. First, while richness was often associated with invasion probability, observed patterns of invasion in self-assembled systems are much more complex than suggested by experimental systems and do not follow predictions of current competition models. Furthermore, invasions of many species do not appear to be restricted by local community diversity, in fact, invasion probability is strongly positively associated with richness. The range and prevalence of diversity effects on invasibility need to be addressed in experimental studies so that realistic models of invasion can be developed. Second, constraints on invasions are not different for native and exotic species. Therefore, studies focusing on the metapopulation dynamics of native species will also shed light on the spread of exotic species into new habitats. Third, controls on species invasion appear individualistic, combining positive and negative interspecific interactions with the influences of diversity. Thus, diversity alone is not the dominant control on invasion success, but only a part of a very complex community-level interaction.

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REFERENCES

Blossey, B. (1999). Before, during and after: the need for long-term monitoring in invasive species management. *Biol. Invasion*, 1, 301–311.

Brown, R.L. & Peet, R.K. (2003). Diversity and invasibility of southern Appalachian plant communities. *Ecology*, 84, 32–39.

Bruno, J.F., Stachowicz, J.J. & Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.*, 18, 119–125.

Byers, J.E., Reichard, S., Randall, J.M., Parker, I.M., Smith, C.S., Lonsdale, W.M. *et al.* (2002). Directing research to reduce the impacts of nonindigenous species. *Conserv. Biol.*, 16, 630–640.

Callaway, R.M. & Aschehoug, E.T. (2000). Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, 290, 521–523.

Case, T.J. (1990). Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. Natl Acad. Sci.*, 87, 9610–9614.

Case, T.J. (1991). Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. *Biol. J. Linn. Soc.*, 42, 239–266.

Crawley, M.J., Brown, S.L., Heard, M.S. & Edwards, G.R. (1999). Invasion-resistance in experimental grassland communities: species richness of species identity? *Ecol. Lett.*, 2, 140–148.

Davis, M.A., Grime, P. & Thompson, K. (2000). Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.*, 88, 528–534.

Fargione, J., Brown, C.S. & Tilman, D. (2003). Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl Acad. Sci.*, 100, 8916–8920.

Gleason, H.A. & Cronquist, A. (1991). *Manual of Vascular Plants of Northeastern United States and Adjacent Canada*. New York Botanical Garden, Bronx, NY.

Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.

Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, 417, 636–638.

Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J. *et al.* (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.*, 2, 286–293.

Levine, J.M. (2000). Species diversity and biological invasions: relating local processes to community pattern. *Science*, 288, 852–854.

Levine, J.M. & D'Antonio, C.M. (1999). Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, 87, 15–26.

Lonsdale, W.M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology*, 80, 1522–1536.

Loreau, M. (1998). Biodiversity and ecosystem functioning: a mechanistic model. *Proc. Natl Acad. Sci.*, 95, 5632–5636.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2002). Exotic plant invasions over 40 years of old field succession: community patterns and associations. *Ecography*, 25, 215–223.

Pickett, S.T.A. (1982) Population patterns through twenty years of oldfield succession. *Vegetatio*, 49, 45–59.

Prieur-Richard, A.H., Lavorel, S., Grigulis, K. & Dos Santos, A. (2000). Plant community diversity and invasibility by exotics: invasion of Mediterranean old fields by *Conyza bonariensis* and *Conyza canadensis*. *Ecol. Lett.*, 3, 412–422.

Reader, R.J. & Beisner, B.E. (1991). Species-dependent effects of seed predation and ground cover on seedling emergence of old-field forbs. *Am. Midl. Nat.*, 126, 279–286.

Shea, K. & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.*, 17, 170–176.

Stachowicz, J.J., Whitlach, R.B. & Osman, R.W. (1999). Species diversity and invasion resistance in a marine ecosystem. *Science*, 286, 1577–1579.

Stohlgren, T.J., Bull, K.A., Otsuki, Y., Villa, C.A. & Lee, M. (1998). Riparian zones as havens for exotic plant species in the central grasslands. *Plant Ecol.*, 138, 113–125.

Stohlgren, T.J., Binkley, D., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A. *et al.* (1999). Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.*, 69, 25–46.

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

Thompson, K., Hodgson, J.G. & Rich, T.C.G. (1995). Native and alien invasive plants: more of the same? *Ecography*, 18, 390–402.

Tilman, D. (1997). Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, 78, 81–92.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997a). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.

Tilman, D., Lehman, C.L. & Thomson, K.T. (1997b). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl Acad. Sci.*, 94, 1857–1861.

Troumbis, A.Y., Galanidis, A. & Kokkoris, G.D. (2002). Components of short-term invasibility in experimental Mediterranean grasslands. *Oikos*, 98, 239–250.

Wiser, S.K., Allen, R.B., Clinton, P.W. & Platt, K.H. (1998). Community structure and forest invasion by an exotic herb over 23 years. *Ecology*, 79, 2071–2081.

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