Control of plant species diversity and community invasibility by species immigration: seed richness versus seed density

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Immigration rates of species into communities are widely understood to influence community diversity, which in turn is widely expected to influence the susceptibility of ecosystems to species invasion. For a given community, however, immigration processes may impact diversity by means of two separable components: the number of species represented in seed inputs and the density of seed per species. The independent effects of these components on plant species diversity and consequent rates of invasion are poorly understood. We constructed experimental plant communities through repeated seed additions to independently measure the effects of seed richness and seed density on the trajectory of species diversity during the development of annual plant communities. Because we sowed species not found in the immediate study area, we were able to assess the invasibility of the resulting communities by recording the rate of establishment of species from adjacent vegetation. Early in community development when species only weakly interacted, seed richness had a strong effect on community diversity whereas seed density had little effect. After the plants became established, the effect of seed richness on measured diversity strongly depended on seed density, and disappeared at the highest level of seed density. The ability of surrounding vegetation to invade the experimental communities was decreased by seed density but not by seed richness, primarily because the individual effects of a few sown species could explain the observed invasion rates. These results suggest that seed density is just as important as seed richness in the control of species diversity, and perhaps a more important determinant of community invasibility than seed richness in dynamic plant assemblages.

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A major goal of ecologists has been to understand the factors that influence the structure and diversity of ecological communities. While much emphasis has been placed on understanding the factors that restrict communities to certain subsets of species, such as competition and disturbance (MacArthur and Levins 1967, MacArthur 1972, Connell 1978, Huston 1979, Tilman 1982) the role of species immigration in community assembly dynamics remains poorly understood (Tilman 1993, Loreau and Mouquet 1999, Hubbell 2001, Brown and Peet 2003). This is in part due to confusion over what "immigration" actually means in relation to species diversity. For example, in MacArthur and Wilson's (1967) classic theory of island biogeography, species diversity is in part determined by rates of immigration of new species, where, given a constant extinction rate, species diversity is increased by the richness of immigrants (Simberloff and Wilson 1970, Tilman et al. 1997b). On the other hand, species diversity may also be promoted by the density of arriving propagules,

wherein certain species persist in sites where they would not otherwise be self-maintaining, a phenomenon called "mass effect" (Shmida and Wilson 1985, Loreau and Mouquet 1999). The density of propagule influx is also important from the standpoint of recruitment limitation, where the inability of a particular species to be present in all favorable sites influences community structure (Grime 1973, Tilman 1993, Tilman et al. 1997b).

The relationship between immigration and species diversity is further complicated by the possibility that propagule richness and propagule density interact to control diversity in natural communities; these interactions have generally been ignored in immigration-driven diversity models and experiments. For example, propagule density may control the intensity and timing of interspecific interactions, which in turn control the sensitivity of species diversity to propagule richness. In experiments where seeded communities are assembled by random draws from a common species pool, propagule richness increases the probability of including particularly dominant species that may themselves decrease resident species diversity, a so-called "sampling effect" (Aarssen 1997, Huston 1997, Tilman 1997, Tilman et al. 1997a, Fridley 2001, Wardle 2001). The ability of such a species to establish, however, should depend in part on its sown density (Shmida and Ellner 1984, Kunin 1998). Thus, low or high levels of seed density may decrease species diversity for a given level of seed richness. To our knowledge, however, the interactive effects of seed richness and seed density on species diversity have not previously been investigated.

While understanding the factors that control diversity is an important step in understanding the structure of communities, diversity itself may influence the functioning of ecological communities. For example, species diversity may place further limits on immigration by decreasing the success of subsequent invaders (Elton 1958, MacArthur 1970, Levine and D'Antonio 1999), an observation supported by recent experimental studies (Tilman 1997, Knops et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000, Symstad 2000, Hector et al. 2001). Diversity may decrease invasion by means of complementary resource use, where more diverse assemblages use more total available resources, and thus preclude the establishment of new species (MacArthur 1970). When diversity is manipulated as seeded richness, however, as it has been in several experiments (Knops et al. 1999, Levine 2000, Naeem et al. 2000), the negative diversity–invasibility relationship may simply be the result of a sampling effect for a particularly invasion-resistant species (Wardle 2001). Because sampling effects should also depend on the ability of a dominant species to establish, the influence of seeded richness on invasibility should depend on seed density, whatever the mechanism of invasion resistance.

We created experimental plant communities of common herbs to explicitly test the different effects of seed richness and seed density on community properties and thus clarify the role that the primary components of immigration play in structuring plant communities. By following community development through a growing season, we documented the changing interactions of seed richness and density through time. We also allowed surrounding vegetation to invade our experimental communities to test whether seed richness and density had interactive effects on rates of species invasion.

Methods

Experimental design

We constructed 100 75 × 75 cm experimental plots in an old field at Mason Farm Biological Preserve, Chapel Hill, North Carolina, USA. In these plots we constructed plant communities from seed with different levels of seeded richness and density of seed per species. We used three levels each of seed richness (3, 10, and 30 species) and density of seed per species (10, 100, and 1000 seeds), crossed in a fully factorial design. Each of these 9 treatments and a bare plot treatment (no sown seed) was replicated 10 times and randomly assigned to a plot in a 10 × 10 plot grid separated by 1 m walkways. Species composition for each seeded treatment was randomly selected from a pool of 30 grass and herb species (Table 1) that had been tested for seed viability and were not already present in the surrounding vegetation. Replicates were not compositional replicates; that is, no specific assemblage was grown more than once.

We established experimental communities on bare soil that had been plowed and disked five weeks prior to seeding. The experimental area was fenced in to prevent deer and rabbits from disturbing the plots; no herbivory was detected during the experiment. To minimize species growing into plots from the local seed bank, we allowed seed bank species to germinate in the open soil for 3 weeks after plowing, and then applied the short-lived, systemic herbicide Roundup (Monsanto Corp., St. Louis, MO, USA). Because immigration in natural systems is an ongoing process rather than a one-time event, we elected to reapply the seed treatments throughout the experiment such that each treatment represents a different rate of immigration with varied levels of seed richness and density. Thus, seeds were added to plots in four applications at three-week intervals, from June 1 to August 3, 1999, broadcasted into plots by hand while taking care to keep all broadcast seed within the target plot. Each reapplication of seeds had the same treatment number of species and seeds per species as the original application, but the species composition was randomly varied for each reap-

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Table 1. Experimental species. Botanical nomenclature follows Kartesz and Meacham (1999).

Species	Family	Seed wt (mg)*	Duration	Growth habit
Agastache foeniculum	Lamiaceae	0.47	Perennial	Forb
Amaranthus tricolor	Amaranthaceae	0.6	Annual	Forb
Anethum graveolens	Apiaceae	1.7	Annual	Forb
Artemisia absinthium	Asteraceae	0.2	Perennial	Forb
Artemisia vulgaris	Asteraceae	0.16	Perennial	Forb
Avena sativa	Poaceae	34.09	Annual	Graminoid
Chenopodium ambrosoides	Chenopodiaceae	0.1	Ann/Perennial	Forb
Chrysanthemum coronarium	Asteraceae	1.6	Annual	Forb
Fagopyrum esculentum	Polygonaceae	22.2	Annual	Forb
Festuca ovina	Poaceae	0.4	Perennial	Graminoid
Hypericum perforatum	Clusiaceae	0.25	Perennial	Forb
Lolium multiflorum	Poaceae	5.15	Ann/Bien/Peren	Graminoid
Matricaria recutita	Asteraceae	0.047	Annual	Forb
Medicago sativa	Fabaceae	2	Ann/Perennial	N-fixing forb
Nepeta cataria	Lamiaceae	0.5	Perennial	Forb
Nicotiana alata	Solanaceae	0.1	Perennial	Forb
Nicotiana sylvestris	Solanaceae	0.03	Perennial	Forb
Oenothera biennis	Onagraceae	0.4	Biennial	Forb
Panicum virgatum	Poaceae	1.28	Perennial	Graminoid
Papaver rhoeas	Papaveraceae	0.2	Annual	Forb
Papaver somniferum	Papaveraceae	0.32	Annual	Forb
Rudbeckia hirta	Asteraceae	0.3	Ann/Bien/Peren	Forb
Rumex acetosa	Polygonaceae	0.9	Perennial	Forb
Trifolium incarnatum	Fabaceae	3.2	Annual	N-fixing forb
Trifolium pratense	Fabaceae	1.8	Bien/Perennial	N-fixing forb
Trifolium repens	Fabaceae	0.8	Perennial	N-fixing forb
Urtica dioica	Urticaceae	0.17	Perennial	Forb
Verbascum thapsus	Scrophulariaceae	0.088	Biennial	Forb
Verbena hastata	Verbenaceae	0.2	Bien/Perennial	Forb
Vicia villosa	Fabaceae	35.7	Bien/Perennial	N-fixing forb

* Note: Most seed weights were obtained from Kew Botanical Garden (Tweddle et al. 2002); where a choice was given, we include seed weights measured using the orthodox method described in the database. *A. Foeniculum* and *N. sylvestris* seed weights were calculated from data distributed by Johnny's Seed Supply.

plication of seed. After the first sowing, ambient species from the surrounding vegetation were allowed to invade the experimental plots by purely natural means, including vegetative spread from plot edges and walkways (which were not cleared of vegetation), seed dispersal, and any late-emerging species from the soil seed bank. All recorded invading species are listed in Table 2. The experimental plots were watered as needed throughout the experiment to prevent desiccation.

For each plot we recorded the percent cover of each species at 3, 6, 9, and 12 weeks after first sowing. Maximum cover per species was 100%; thus, total cover and total richness were partly correlated.

Data analyses

To test the effect of seed richness and density on realized diversity (here defined as the number of species

Table 2. Invading species. Botanical nomenclature follows Kartesz and Meacham (1999).

Acalypha rhomboides	*Galinsoga ciliata*	*Phytolacca americana*
Acer rubrum	*Geranium carolinianum*	*Poa pratensis*
Allium vineale	*Geum canadense*	*Polygonum punctatum*
Amaranthus hybridis	*Helenium flexuosum*	*Portulaca oleracea*
Ambrosia artemisiifolia	*Hieraceum gronovii*	*Rhus glabra*
Barbarea vulgaris	*Ipomaea* sp.	*Robinia pseudoacacia*
Boehmeria cylindrica	*Juncus tenuis*	*Rosa multiflora*
Campsis radicans	*Lactuca biennis*	*Rubus* sp.
Chenapodium album	*Lespedeza cuneata*	*Rumex crispus*
Commelina communis	*Ligustrum sinense*	*Sida rhombifolia*
Cynodon dactylon	*Microstegium vimenium*	*Solanum americanum*
Cyperus sp.	*Mollugo verticillata*	*Solanum carolinense*
Datura stramonium	*Oxalis stricta*	*Sorghastrum nutans*
Digitaria ischaemum	*Paulownia tomentosa*	*Stellaria media*
Echinachloa crusgalli	*Phyllanthus amarus*	*Trifolium campestre*
Festuca sp.	*Physalis virginiana*	*Verbena urticifolia*
		Viola sp.

per plot) and invasibility over time, we performed a repeated measures analysis using the MIXED procedure of SAS version 8.0 (SAS Institute 1999). The repeated measures analysis used a mixed-model approach with unstructured covariance (i.e., no model for how data should covary with time). Denominator degrees of freedom were calculated using the general Satterthwaite approximation, which allows an accurate F approximation (Littell et al. 1996). Separate analyses were performed for two dependent variables: total cover of invasive species (representing "invasibility") and realized plot richness (representing "community diversity"). Realized plot richness included sown species and any invading species. These two statistical models initially included quadratic terms for seed richness and seed density and all possible two-way interaction terms (and 3-way for quadratic variables), which were subsequently evaluated using backward elimination. Sown seed richness and seed density were analyzed as quantitative (rather than class) variables in order to test for polynomial effects of seed richness and density on diversity and invasibility. An overall estimation of the effects of experimental treatments on invasibility was performed with an ANOVA using total cover of invaders at the final time period.

An important and uncontrolled covariate in our study was total seed density per plot, as we independently manipulated seed richness and density per species in an additive design. For example, treatments of 30 species and 10 seeds per species were sown with 300 total seeds per time period, whereas for 3 species/10 seed treatments only 30 seeds were sown. To control for this covariate post hoc, we partitioned the data into those 40 plots where overall seed density was either 300 or 3000 seeds per plot (i.e. plots of seeded richness of 3 or 30 combined with appropriate values of density per species – 10, 100, or 1000). We then used total seed density as a predictor variable alongside seed richness to predict total invasive cover in ANOVA.

The potential for "sampling effects" (Wardle 2001) as the cause of a diversity–invasibility relationship in this experiment was high because seed richness treatments of 30 species were identical in species composition. If one species formed highly invasion-resistant stands, for example, this effect would be present in all 30-species treatments but only a small, random fraction of 3- and 10-species treatments. To determine whether this occurred for particular species, we examined the individual effects of each species on total final cover of invasives (measured in the last time period) in single factor ANOVAs conducted separately for each species (using all 90 plots). We then included a dummy variable for presence or absence of one species that proved particularly important in this analysis (*Fagopyrum esculentum*) in the full ANOVA model predicting invasibility (in which total density was controlled), and varied the order of listed terms in Type I SS to assess whether

seeded richness could significantly predict invasibility after the effects of *F. esculentum* had been accounted for, and vice-versa. For this analysis we noted the sum of squares of invasibility accounted for by each variable, also called a factor's "magnitude of effect" (Weldon and Slauson 1986).

We assessed the relationship between the total cover of invasives and the realized diversity of experimental species, and the realized abundance of experimental species (while controlling for total seed density per plot as a dummy variable by using the restricted dataset with 300 and 3000 seeds per plot) in the final time period using a linear regression model. Analyses (other than the repeated measures tests described above) were conducted using the PROC GLM procedure in SAS (SAS Institute 1999).

Results

Effects of seed richness and seed density per species on overall community diversity

Total community richness (seeded plus volunteer species) generally increased with time and with each level of seeded richness (Fig. 1A). A major exception was the decrease in diversity in plots of 30 sown species between 3 and 6 weeks after initial sowing, probably due to a filtering process of seedlings of species that successfully
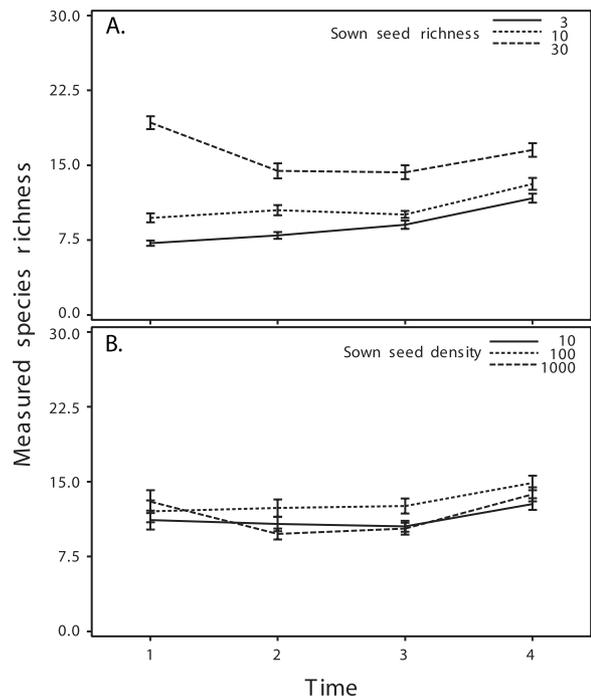

Fig. 1. Effects of seed richness (A) and seed density (B) on overall plot species richness over time. Bars represent means ± 1 s.e.

Table 3. Repeated measures results for the effects of seed density and richness on total species richness over time based on a mixed model approach with unstructured covariance. Degrees of freedom are calculated using the general Satterthwaite approximation (Littell et al. 1996). Type 3 tests of fixed effects shown.

Effect	Num. DF	Den. DF	F	Pr > F
Seed density	1	84	0.11	0.7403
Seed richness	1	86	57.14	<0.0001
Time	3	87	35.63	<0.0001
Seed density × seed richness	1	84	5.35	0.0231
Seed richness × time	3	87	35.99	<0.0001
Seed density × time	3	87	6.11	0.0008
Seed density^2	1	84	0.04	0.8403
Seed richness × seed density^2	1	84	6.42	0.0131

germinated but could not fully establish. The isolated effects of seed density per species were less apparent over time (Fig. 1B), but in general diversity was highest at the intermediate seed density. Repeated measures ANOVA revealed significant interactions between seed richness and density in the control of diversity, and of those variables over time (Table 3). Fig. 2 demonstrates this interaction and the unimodal nature of the seed density effect on diversity, and how this unimodal relationship was affected by seed richness (last term in model in Table 3). Seed density per species had little effect on diversity in the first time period when plants were small; as the communities developed, the effect of density depended on seed richness, where intermediate seed densities promoted diversity at all but the lowest richness level.

Effects of seed richness and seed density on invasibility

Seed richness and seed density both negatively affected total cover of invasive species (Fig. 3, Table 4), and largely in additive fashion, but only after enough time had passed to allow species from the surrounding vegetation to invade. The cover of invasive species relative to that of native species increased over time with all treatments (Fig. 4). The highest cover of invaders occurred in the least species–rich plots where species were planted with only 10 seeds; the lowest cover of invaders occurred with maximum levels of seed richness (30) and seed density (1000 seeds per species; Fig. 3). Neither seed richness nor seed density was a very strong predictor of invasion, however; by the final time period, seed richness alone could account for 22% of the variance in invasive cover among plots, and seed density could account for 24%. As a more conservative estimate using the 40-plot data subset where the effects of total seed density per plot could be accounted for, seed richness could explain only 10% of the variation in invasive cover (although still significant, p < 0.05), whereas that for total seed density was 20% (p < 0.01).

The presence or absence of several species explained a large proportion of the variance of total invasive

cover that could otherwise be attributed to seed richness (Fig. 5), particularly that of *Avena sativa*, *F. esculentum*, *Trifolium pratense*, *T. incarnatum* and *Vicia villosa*. These five species had relatively large seed sizes and the last three species are, notably, nitrogen-fixers
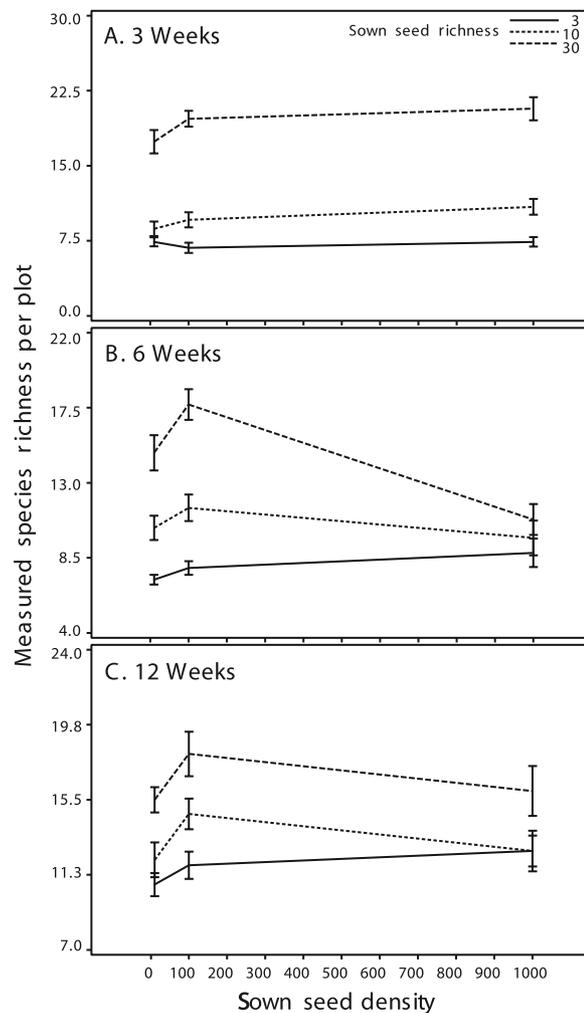

Fig. 2. Effects of seed richness and seed density on overall plot species richness in three time periods. Bars represent means ± 1 s.e.
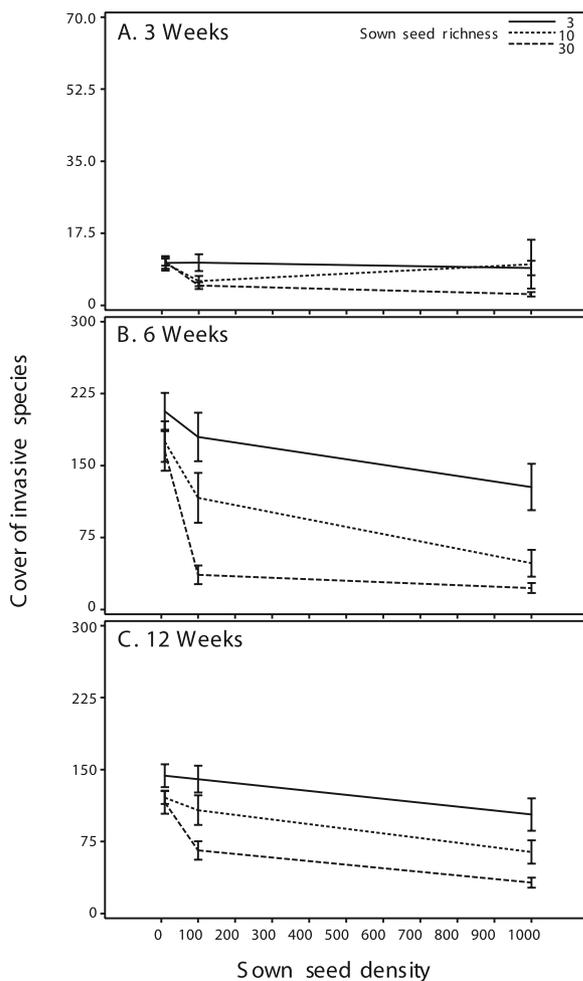
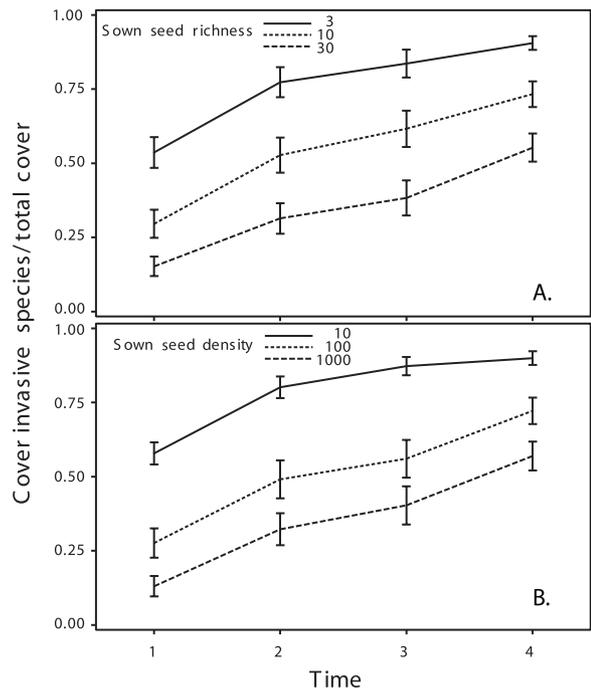Fig. 3. Effects of seed richness and seed density on cover of invaders in three time periods. Bars represent means ± 1 s.e.

Fig. 4. Effects of seed richness (A) and seed density (B) on relative cover of invasive species over time. Bars represent ± 1 s.e.

(Table 1). The effect of *A. sativa* is somewhat enigmatic because it never occurred at high relative abundance. The effect of *F. esculentum* was expected because of its large relative abundance in the plots in which it occurred. We therefore chose to compare the importance of seeded richness as a predictor of total invasive cover before and after accounting for the presence or absence of *F. esculentum* in experimental communities (note that p-value estimates are unwarranted here because of the reduction of statistical power associated with the factor listed last in the model, as richness and presence of any particular species were highly correlated). The 10% SS accounted for by seed richness (after total seed density) was reduced (6%) after accounting for *F. esculentum* (Table 5), suggesting that, even when only one species was included in this analysis, richness appeared to influence invasibility largely by sampling effects.

The regression of realized richness of experimental species on cover of invasive species (while controlling for total seed density) in the final time period provided further evidence that species richness did not have a significant effect on invasion. While the overall model is significant ($p < 0.05$, $R^2 = 0.25$), the realized richness of experimental species only explained 4.6% of the variation in invasive cover, and this was not a significant effect ($p > 0.10$; Table 6).

Table 4. Repeated measures analysis showing the effect of seed richness and density on the total cover of invasive species based in a mixed model approach with unstructured covariance. Degrees of freedom are calculated using the general Satterthwaite approximation (Littell et al. 1996). Type 3 tests of fixed effects shown.

Effect	Num. DF	Den. DF	F	Pr > F
Seed density	1	86	20.61	<0.0001
Seed richness	1	86	39.45	<0.0001
Time	3	86	119.25	<0.0001
Seed richness × time	3	86	14.17	<0.0001
Seed density × time	3	86	8.21	<0.0001
Seed density²	1	86	3.03	0.0851
Seed density² × time	3	86	6.93	0.0003

Discussion

Considered in isolation, community diversity (measured species richness per plot) was enhanced by seed richness, consistent with other experimental studies in which propagules were added in the form of increased

Fig. 5. An assessment of sampling effects. Percent variation in total abundance of invasive species during the final time period explained by factors when alone in the model divided by SS for the full model. Factors with a significant effect (p < 0.05) on invasibility when alone in the model are shown.
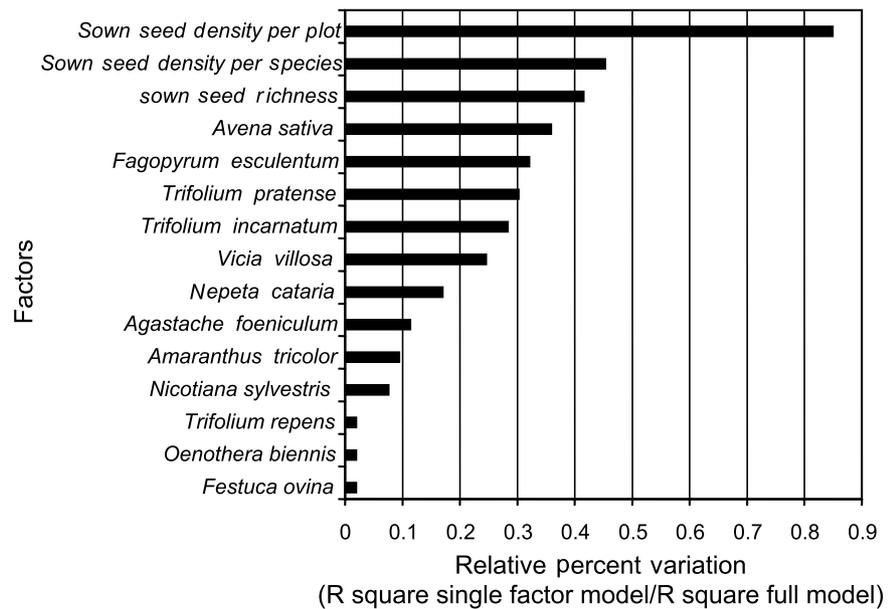

Table 5. ANOVA results (Type I SS) showing the effect of total seed density per plot (rather than seed density per species), seed richness and presence of *F. esculentum* on invasibility (total cover of invasives) in the last time period. Order 1 shows the results when *F. esculentum* is placed last in the model, while order 2 shows the results when seed richness is placed last in the model. The overall model error and R^2 are the same for both orders.

R^2	Coeff Var	Root MSE	Mean cover of invasives (%)		
0.32	39.61	42.10	106.30		

Source	DF	SS	Mean Square	F value	Pr > F
Model	3	29557.03	9852.34	5.56	0.003
Error	36	63809.37	1772.48		
Corrected Total	39	93366.40			

Order 1	DF	Type I SS	Mean Square	F value	Pr > F
Total seed density	1	18922.50	18922.50	10.68	0.002
Seed richness	1	9486.40	9486.40	5.35	0.03
Fagopyrum esculentum	1	1148.13	1148.13	0.65	0.43

Order 2	DF	Type I SS	Mean Square	F value	Pr > F
Total seed density	1	18922.50	18922.50	10.68	0.002
Fagopyrum esculentum	1	4605.78	4605.78	2.60	0.12
Seed richness	1	6028.75	6028.75	3.40	0.07

Table 6. Regression results for the relationship between invasibility (total cover of invasives) and the realized richness of experimental species (while controlling for total seed density) in the final time period. For the overall model $R^2 = 0.25$, $p < 0.05$, coefficient of variation = 40.96, root MSE = 43.54, and mean cover of invasives = 106.30%.

Parameter	Estimate	Error	t	Pr > |t|
Intercept	146.89	14.30	10.27	<.0001
Total seed density (dummy variable)	−0.01	0.006	−2.25	0.03
Realized richness of experimental species	−3.31	2.19	−1.51	0.14

species richness (Houle and Phillips 1989, Tilman 1997, Zobel et al. 2000). Considered jointly with the effects of seed density on community diversity, however, a more complex result emerges that demonstrates the importance of interactions between seed richness and seed density. Our seed richness and density treatments appeared to interact to influence diversity in two main ways. First, for any level of seed richness, a minimum threshold density of seed per species is required for each species to successfully establish with a high likelihood (given appropriate adaptations for a particular site). Some species may even be able to persist at a site with a high seed influx density even if they cannot be self-maintaining within the site (i.e. mass effects sensu Shmida and Ellner 1984). At these density levels, community diversity increases with seeded richness. Second, there is an upper threshold for seed density above which certain species dominate the assemblage and thus reduce diversity, similar to what is seen with plant assemblages in the hump-backed relationship between density and diversity described by Grime (1973, 1979). This explains the change in seed richness effect on diversity from linear to unimodal with increasing seed density (Fig. 2B). If the effects of seed density on realized richness were considered in isolation, ignoring interactions between seed richness and density, the importance of seed density as a determinant of community diversity would not be immediately apparent (Fig. 1B). Therefore, we strongly suggest that a full mechanistic analysis of how "immigration" processes affect species diversity in natural communities must include both richness and density components.

It is likely that seed size played a role in determining community composition in our experiment, particularly in the densest treatments. In other studies, large seeded species have been shown to have a short-term competitive advantage over smaller seeded species (Burke and Grime 1996, Turnbull et al. 1999). In our experiment, the species with the greatest effect on invasibility typically had the largest seed size. We observed that these species (such as *Fagopyrum esculentum*) created dense canopies, particularly in plots with the highest seed density treatments. This was similar to the findings of Turnbull et al. (1999), who experimentally demonstrated that large seed mass species were the most successful in plots with high sown seed density (83% individuals), while in low seed density plots they comprised only 49% of individuals. In our experiment, large seeded species may have heightened the level of competition in high density treatments (reducing the measured richness) and allowed for a sampling effect wherein the richest plots may have had a higher likelihood of containing large seeded species.

The interaction between the immigration components of seed richness and seed density has consequences for community structure and composition, which themselves influence other ecosystem properties such as invasibility. By allowing the surrounding vegetation to invade our experimental plots over the course of the growing season, we were able to measure the indirect effects of seed richness and density on community invasibility as the total cover of invasive species at the conclusion of the experiment. Our results showed that the effects of seed richness and density appeared to operate in additive fashion to reduce invasion. If community diversity (represented by seeded richness) acts to repel species invasion, an increase in population densities should increase this effect, whether by intensifying the degree to which species complement each other in resource use (MacArthur 1970, Tilman 1997) or by enhancing the probability of a highly invasion-resistant species dominating (Wardle 2001). Our results appear more consistent with the latter, sampling effect explanation, for two major reasons. First, after the effect of the presence or absence of a single species (*F. esculentum*) on invasibility was accounted for, seed richness could explain very little of the variance in invasion success among plots (and indeed could only explain 10% of the variance even without accounting for *F. esculentum*). Second, there was no significant correlation between realized community diversity and invasion success after accounting for total seed density. Because such a "sampling"-type process could occur in natural systems when diversity is initially maintained by seed influx to a particular community (with a particularly successful competitor more likely to arrive in more diverse seed influx), this may be a legitimate means by which natural diversity could limit species invasion, at least for annual or highly unstable systems that are largely immigration–driven (Fridley 2001). For more extinction–driven systems in which disturbance and immigration rates exert less control over community structure, resource complementarity is expected to play a greater role in both community diversity and the community's susceptibility to invasion by new species.

Part of the importance of seed density to community diversity and invasibility in this experiment could be attributed to our short experimental duration, where the effects of large seeded species should be especially prominent. Dominance by these quick growing species might eventually give way to slower-growing perennial species and communities that are less structured by immigration than extinction processes. Therefore, our results are most immediately applicable to dynamic or less stable communities where recent immigrants are important contributors to community biomass. In addition, we did not account for variations in seed germination rates when calculating seed density, which may have influenced the outcome of the experiment by giving an advantage to species with high germination rates.

In conclusion, results of our experiment clearly highlight the need for separating the density and richness components of immigration processes as determinants

of community composition and structure. Several main points deserve emphasis. First, seed density and richness interact to control both diversity and invasibility. While seed richness influenced community diversity, seed density proved important in limiting both diversity and invasibility in our experiment. The influence of density on diversity and invasibility was related; there were high levels of competition in the densest plots which excluded both sown species and invaders. We strongly recommend that studies assessing the role of immigration processes on community diversity distinguish between richness and density of seed. Second, examined in isolation, seed richness appeared to have a negative effect on community invasibility, in agreement with several other experimental studies (Tilman 1997, Hector et al. 2001). However, this was largely due to a sampling effect resulting from the design of the experiment in which the plots of highest seed richness contained all species from the species pool, including the large seeded, competitive species such as *F. esculentum*. Third, we found that invasibility was strongly related to seed density (both total density and seed density per species) while the effect of seed richness on invasibility was less evident, suggesting that seed or propagule density is a more important determinant of community invasibility than seed richness in dynamic plant assemblages. Based on these observations, we agree with the general suggestion that the processes controlling species invasion in communities are ultimately determined by the processes that govern resident community composition and structure (Moore et al. 2001, Wardle 2001), and particularly whether communities are driven largely by immigration or extinction processes (Brown and Peet 2003).

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