Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors

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Biological invasion is a widespread, but poorly understood phenomenon. Elton's hypothesis, supported by theory, experiment, and anecdotal evidence, suggests that an important determinant of invasion success is resident biodiversity, arguing that high diversity increases the competitive environment of communities and makes them more difficult to invade. Observational studies of plant invasions, however, find little support for this hypothesis and argue strongly against it. Lack of control of extrinsic factors (e.g., disturbance, climate, or soil fertility) that covary with biodiversity and invasion in observational studies makes it difficult to determine if their findings truly refute Elton's hypothesis. We examined performance of *Crepis tectorum* (an invasive, annual composite weed) in experimental prairie grassland plots and greenhouse plant assemblages in which resident species richness was directly manipulated. Under these conditions, unlike observational studies, no covarying extrinsic factors could interfere with interpreting results. We found a strong inverse association between resident diversity and invader performance as predicted by Elton's hypothesis. Higher resident diversity increased crowding, decreased available light, and decreased available nutrients all of which increased the competitive environment of diverse plant assemblages and reduced *C. tectorum* success. Examination of individual resident species impacts on *C. tectorum* performance demonstrated that this diversity effect was not due to the sampling effect. These results suggest that both Elton's hypothesis and its competitive mechanism may operate in nature, but covarying extrinsic factors may obscure the negative impact of diversity on invader success.

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The invasion of non-native species into assemblages of native plants is a pervasive and widespread phenomenon (e.g., Heywood 1989, Macdonald et al. 1991, Timmins and Williams 1991, D'Antonio and Vitousek 1992, Berger 1993, Hobbs and Humphries 1994, Cronk and Fuller 1995). With the increase of biological invasions due to the transport activities of a rapidly expanding and increasingly mobile human population, the ecological consequences of biological invasions has become a focal area of ecological study. Several volumes have surveyed the enormous literature on the subject (e.g., Mooney and Drake 1986, Drake et al. 1989, Hengeveld 1989, Ramakrishnan 1991, Cronk and Fuller 1995).

The diversity of native or resident species is a community characteristic that has been postulated by a number of authors since 1855 to be important in regulating invasion (Robinson et al. 1995, Planty-Tabacchi et al. 1996, Tilman et al. 1997a, Wiser et al. 1998), but considerable debate surrounds this hypothesis. Elton

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(1958), perhaps the most widely cited author of this postulate (Cronk and Fuller 1995, Levine and D'Antonio in press), hypothesized that lower resident diversity favors invasions and offered six lines of indirect evidence. Cronk and Fuller (1995) referred to Elton's hypothesis as the *Balance of Nature Hypothesis* and identified it as one of seven distinct hypotheses that currently predict plant invasion. Although a compelling and influential idea, current evidence supporting Elton's hypothesis is equivocal (Crawley et al. 1999, Levine and D'Antonio in press). Although theoretical studies (Case 1990, Drake 1990, Luh and Pimm 1993, Law and Morton 1996, Lockwood et al. 1997), microcosm studies (Robinson and Dickerson 1984, Robinson and Edgemon 1988, McGrady-Steed et al. 1997), and anecdotal accounts (Elton 1958, Knops et al. 1994) support Elton's hypothesis, observational studies find negative or no relationship (Robinson et al. 1995, Planty-Tabacchi et al. 1996, Wiser et al. 1998, Stohlgren et al. 1999, Levine and D'Antonio in press). Resolving this debate is the motivation for this study.

The most likely explanation for these conflicting results may be the covariation of extrinsic factors with resident plant diversity and invasion in observational studies (Fig. 1). Such covarying factors include disturbance (e.g., Ramakrishnan and Vitousek 1989, Rejmánek 1989, Hobbs and Huenneke 1992, McIntyre and Lavorel 1994a, b, Wiser et al. 1998), fire frequency (D'Antonio and Vitousek 1992, Leach and Givnish 1996), grazing (Mack 1989), water and nutrient levels (e.g., Tilman 1993, Milchunas and Lauenroth 1995, Burke and Grime 1996), percent open canopy or bare ground (e.g., Cavers and Harper 1967), proximity to human populations (e.g., Timmins and Williams 1991) and climate (e.g., Lindsay 1953, Lodge 1993, Ullmann et al. 1995).

Experimental studies can remove such covariation, but few have been conducted (Crawley et al. 1999, Levine and D'Antonio in press). To remove extrinsic factors that covary with plant diversity, we measured invasion success as a response variable to experimentally manipulated levels of resident plant species richness in experimental grassland plots in Minnesota, USA. By directly manipulating resident plant diversity we were able to determine how variation in diversity affects invasion success without interference from covariates of biodiversity. Success of an invader was measured as biomass of an invasive plant at its time of flowering, and not biomass of seedlings pulled from these plots as reported elsewhere (Knops et al. 1999). Note that flowering is seasonally regulated in *Crepis tectorum* and *Digitaria ischaemum*, thus small and large plants flowered at similar times.

We specifically focused on testing the competition-based mechanism proposed by Elton and others that high levels of resident diversity reduce invasibility because they generate a greater competitive environment

(Elton 1958, MacArthur and Wilson 1967, Turelli 1981, Post and Pimm 1983). That is, higher levels of diversity lead to communities that represent stronger competitive environments that are more difficult for non-resident species to invade unless disturbance or local extinction creates opportunities for invasion (Elton 1958, Case 1990, Drake et al. 1993, Law and Morton 1996).

Because competition is likely to be a scale-dependent process with different effects occurring at different levels (Crawley et al. 1999), we examined the relationship between diversity and community invasibility at two levels. The sedentary nature of plants suggests that the plant neighborhood is one appropriate scale at which to examine the consequences of interactions among plants (Harper 1977, Mack and Harper 1977, Waller 1981, Silander and Pacala 1985, Goldberg 1987, Armstrong 1993, Cain et al. 1995). In relatively homogeneous grassland plots, however, the effects of competition may be less localized and more diffuse and the effects of competition may vary across spatial and temporal scales (e.g., Goldberg and Scheiner 1993). Similarly, frequency of disturbance may affect competitive out-
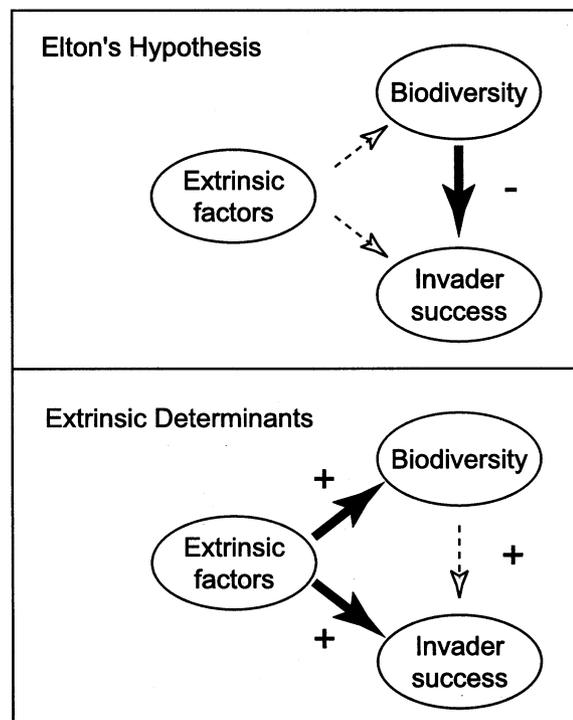

Fig. 1. Testing Elton's hypothesis and controlling for covarying extrinsic factors. Top: Elton's hypothesis explicitly predicts that variation in biodiversity affects invader success. A negative association is predicted because greater biodiversity leads to stronger competitive environments which in turn reduces invader success. Bottom: In nature, extrinsic factors, such as frequency of disturbance, soil fertility, and climate, often have similar effects on biodiversity and invader success. Such covariation may create apparent positive associations between biodiversity and invasion success.

comes (Collins 1987, Crawley 1987, Cronk and Fuller 1995), an effect often operating at the level of the plot or field. For this reason, we also examined the association at the level of the plot.

Our goal was to identify community characteristics that served as predictors of the success of an invasive plant. These community characteristics included species composition, crowding or competition for space and light, and nutrients. We focused primarily on *Crepis tectorum*, a weedy composite, but also examined *Digitaria ischaemum*, a weedy C_4 grass, both of which are common to all of the experimental plots.

Methods

The study system

The site is located at Cedar Creek Natural History Area (CCNHA), Anoka and Isanti Cos., Minnesota, USA. We conducted our study in the experimental grassland plots which are modeled after North American tall grass prairies. These plots consist of 147 9-m^2 plots varying in plant species richness from 1, 2, 4, 8, 12, to 24 (see Table 1 for list of species). These plots were arranged in a grid of 7×21 and randomly assigned treatment levels of diversity. Plots were established in 1994 and assigned levels of plant species richness were maintained by weeding. Further description of the experimental plots is available elsewhere (Tilman et al. 1996).

C. tectorum neighborhoods

Every plant within a 12.5-cm radius of each of the three flagged *C. tectorum* plants per plot was measured including its area and position within the 25-cm-diameter circle. This neighborhood size was chosen because *C. tectorum* plants in the plots were smaller than 25 cm in diameter. All plants in this 490.87-cm^2 area were operationally defined as being in the plant neighborhood for each *C. tectorum* plant. The central *C. tectorum* plant was considered the "target" plant. Maps were drawn by hand, scanned and analyzed using Image Pro software. The spatial coordinates and the area occupied by each plant were recorded.

Crowding of the target species was measured by use of an index that measured distance between the target and its neighbor and the size of its neighbor. The index consisted of measuring the angle (θ) described by two lines that connect the target plant to either side of the diameter of a circle that approximates the area of the neighboring plant (Fig. 2). The diameter is oriented such that it is perpendicular to the line connecting the midpoint of the diameter to the center of the target plant. The advantage of this index is that large, distant plants have values similar to small, close plants that may more closely reflect the relative impacts of plants of different sizes and different distances to the target plant.

We used an additional measure, $\theta_{adjusted}$, which equaled the product of θ and the Pearson correlation coefficient for the association between *C. tectorum* biomass and the area of all plants belonging to the species in the plot. This measure adjusts the index of a neighboring plant's presence (its size and distance from the invader) by its associative identity (the species-specific biomass correlation with the invader). Thus, if the species of an invader's neighbor typically shows strong negative associations with the invader outside the neighborhood, $\theta_{adjusted}$ provides a strong negative value for the neighbor. Likewise, if the species typically shows a positive association with the invader outside the neighborhood, then $\theta_{adjusted}$ provides a positive value for the invader's neighbor.

Measures of experimental plot production, N, and % cover

Plant biomass
Plant biomass in 1996 was calculated from three 10 cm by 1 m clipped strips taken three times (mid-June, July and August). Plant biomass was separated into live plants and litter, dried to constant weight, and weighed.

Root biomass
Root biomass was estimated by taking three 30-cm-deep and 5-cm-diameter cores per clipped strip for each of the three clipping periods. Samples were washed on a 1-mm screen and dried to constant dry weight. No attempt was made to separate dead and live roots. Soil was replaced with equal-sized cores from the edge of the plots.

Nitrate
Four 0–20-cm soil cores per plot were pooled and immediately extracted with 0.01 M KCl in mid-June, July and August. All samples were stored at 5°C and NO_3 was determined on a continuous flow RFA 300 Alpkem autoanalyzer (Alpkem Corporation, Clackamas, OR), following method A303-S170-04 within three days after collecting the samples.

Light
Light interception was measured with a sunfleck ceptometer (Decagon, Pullman, WA), as the percent light interception by the vegetation. This was measured at nine locations per plot in mid-June, July and August.

Cover
Percent cover was determined within two 0.5 by 1-m permanent quadrats at two time periods (mid-June and

Table 1. Effects of composition on invader performance and community ecosystem properties. This table lists the species planted in experimental plots and their contributions (measured as percent cover) to multiple regressions. The first regression examines *C. tectorum* performance as a function of its neighborhood composition. The following two regressions (columns) measure *C. tectorum* and *D. ischaemeum* performance as functions of plant composition of plots. The remaining regressions (columns) measures system or aggregate community properties (% transmittance light, above-ground biomass of all plants, root biomass of all plants, and NO_4) as functions of plant composition of the plots. "X" indicates presence in multiple regression models after backward, stepwise deletions. "(X)" means that this species was significantly correlated with another, so was not used in the regression. Measurements that were percents were arcsine-square-root transformed where this transformation improved linearity.

Species	*C. tectorum* (Neigh)	*C. tectorum* (Plots)	*D. isch.* (Plots)	% cover (Plots)	Light	Above biom.	Root biom.	NO_4
Non-leguminous forbs								
Achillea millefolium	X	X	X				X	X
Anemone cylindrica	X	X	X	X	X		X	
Asclepias tuberosa		X						X
Aster azureus	X		X					
Coreopsis palmata								
Euphorbia corollata	X							
Liatris aspera	(X)	X	X	X			X	
Rudbeckia hirta						X		
Solidago nemoralis						X		
Grasses (C_3)								
Agropyron smithii								
Elymus canadensis								
Koeleria cristata		X		X		X		X
Poa pratensis		X			X			X
Sporobolus cryptandrus	X		X	X	X	X		
Grasses (C_4)								
Andropogon gerardi	X	X	X	X	X		X	X
Bouteloua gracilis	X	X	X	X			X	
Buchloe dactyloides	X	X	X	X		X		X
Panicum virgatum		X						X
Schizachyrium scoparium	X			X	X		X	X
Sorghastrum nutans	X		X	X	X	X	X	
Legumes								
Astragalus canadensis								
Lespedeza capitata				X	X	X		
Petalostemum purpureum			X					X
Vicia villosa		X		X				
N	110	70	137	70	70	70	70	70
R^2	0.37	0.38	0.32	0.64	0.46	0.39	0.54	0.49
P	***	***	***	***	***	***	***	***

July) for species richness and three times (mid-June, July and August) for total plant cover. Percent cover was determined by visual comparison with pre-cut percent cover templates.

Greenhouse experiment

Greenhouse experiments were conducted to control recruitment variation, to confirm field patterns under more controlled environmental conditions, and to

provide additional measures of neighborhood impacts on invasive plants. *C. tectorum* plants in plots recruited naturally. Such uncontrolled recruitment could confound results (see Discussion). We therefore simultaneously established replicate potted plant neighborhoods with *C. tectorum* as the target plant. One hundred and forty round white flower pots, 14 cm diameter × 13 cm tall, were prepared with a bottom layer of paper toweling topped with 12 cm of steam-sterilized soil from CCNHA. Pots were placed on capillary matting and soil was kept moist throughout the experiment. Each pot was sprayed with an aqueous extract from unsterilized soil taken from CCNHA. This spray inoculated the soil with microbes, including *Rhizobium* spp. for nodularization of legumes, and bacteria and fungi for decomposition. All legumes produced nodules indicating success of the inoculation; however, it is unlikely that a full microbial community was reestablished. Given that all pots were uniformly inoculated, however, no treatment bias that might affect results was expected.

Each pot was seeded with *C. tectorum* (collected from CCNHA in 1996) as the target plant and with either *C. tectorum*, non-leguminous forbs (*Rudbeckia hirta*, *Achillea millefolium*), grasses (*Panicum virgatum* or *Bouteloua gracilis*), or legumes (*Astragalus canadensis*, *Vicia villosa*), obtained from Prairie Restoration, Inc., Princeton, MN and V and J Seed Farms, Woodstock, IL, as the neighborhood plants. These species were chosen to represent the four functional groups [i.e., C_3 grasses, C_4 grasses, legumes, and non-leguminous forbs (Tilman et al. 1996, 1997a)] used in the experimental grassland plots at CCNHA.
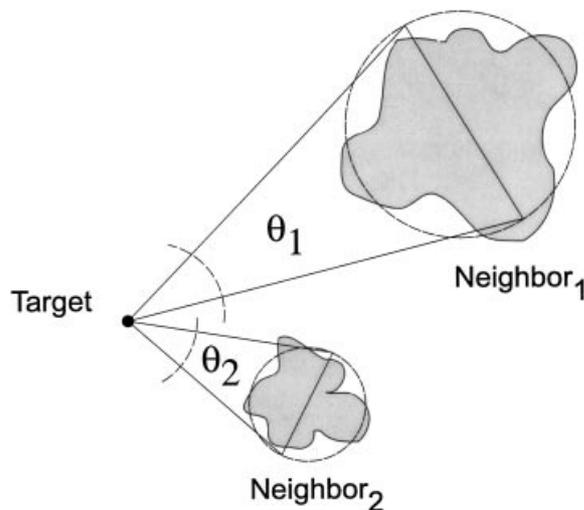
The following four kinds of neighborhoods were constructed, each containing a central target *C. tectorum* individual; (1) a single target plant of *C. tectorum* with no neighbors (five replicates); (2) monoculture neighborhoods of all seven species (five replicates for each species, 35 replicates total); (3) two-species polyculture neighborhoods (50 replicates) and (4) three species polycultures (50 replicates). Species in the two and three species polycultures were chosen at random from the pool of six possibilities.

Seeds (5–10) of each species were placed on the top layer using a template to ensure that the target species was in the center of the pot while neighboring species were equidistant (3.25 cm) from the center. Upon germination, seedlings were weeded to a final density of one seedling per position within each pot. Plants were staked to confine them to a limited region around the pot and to limit their effects on neighboring pots. To ensure constant photoperiod throughout the experiment's duration, ambient light was augmented by use of 400-W, high-pressure sodium lamps.

These greenhouse experiments would explicitly test if effects observed in the field could be produced in a small container under the controlled environmental conditions of a greenhouse. If patterns are similar, then support would be provided for the idea that a few individuals from a few species can create effects observed at the level of the plot.

Statistical analyses

Analyses consisted primarily of parametric statistic methods using SYSTAT (Wilkinson 1992). To identify associations between *C. tectorum* performance and the independent variables (measures of plot or community characteristics), we used multiple regressions with stepwise, backward deletions. All variables in multiple regressions were examined for colinearity (i.e., correlations, Bonferroni corrected probabilities < 0.05). Where two or more variables were correlated, only one variable was used thereby eliminating any correlations among independent variables.

Fig. 2. The index θ combines distance and size of neighbor in relation to a target plant. This figure illustrates how θ has similar values for a large neighbor that is far away (Neighbor 1) and a small neighbor that is close (Neighbor 2). See text for a definition of θ.

Results

Invader performance is associated with plot diversity
C. tectorum and *D. ischaemum* biomass showed a significant decline as resident plant diversity increased (Fig. 3). This result indicates that performance of both invasive species was lower when resident diversity was high. Reproductive, above-ground, and below-ground biomass were all strongly correlated (all pair-wise Pearson correlation coefficients > 0.942, all Ps < 0.001). Thus, for all analyses we used total biomass (the sum of
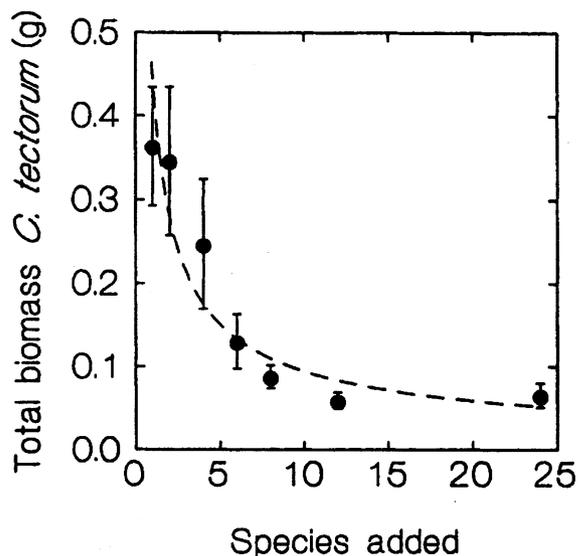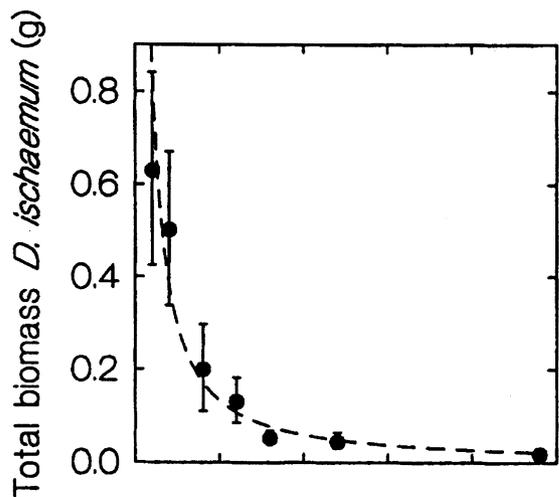
Fig. 4. Frequency distribution of θ in 25-cm-diameter plant neighborhoods surrounding target *C. tectorum* plants. Distribution is calculated for the entire set of 246 neighborhoods.

of a *C. tectorum* plant in the experimental plots had a mean of 39.86 (SD = 20.18, range = 2–113) plants. Of the 10086 plants recorded in the 253 neighborhoods, most had very low values of θ (median = 6.34, range = 0.76–157.66), indicating that most plants in a neighborhood were either small or distant (Fig. 4). That is, the distribution was amodal, with the majority of values left skewed. Neighborhoods had an average of 7–9 resident and non-resident (i.e. other invaders) species present (Fig. 5). The median species richness of a *C. tectorum* neighborhood, including invading plants, was 8 (mean = 8.82, range = 2–21), indicating that species richness of the neighborhood varied about the same as species richness of the plot (linear regression of species in neighborhood against species planted in plots in 1994; $N = 253$, $R^2 = 0.46$, $P < 0.001$), but the number of species within a neighborhood was lower than what

Fig. 3. Invading plant performance and species added to plots. Line represents fitted exponential curve using nonlinear regression. Filled circles represent means, and error bars are one SE. Top, regression parameter estimates; intercept = − 0.34 (SE = 0.10), exponent = − 0.40 (SE = 0.13), $R^2 = 0.15$, $P < 0.001$. Bottom, regression parameter estimates; intercept = − 0.61 (SE = 0.05), slope = − 0.14 (SE = 0.04), $R^2 = 0.45$, $P < 0.001$.

reproductive, below-, and above-ground biomass) as the dependent variable. A log transformation improved the linearity of most of the associations we examined, so we used the $\log_{10}$ (total biomass) as our measure of *C. tectorum* performance.

C. tectorum *neighborhood properties*

A *C. tectorum* neighborhood typically consisted of many plants, only a few of which were likely to have strong impacts on performance and representing only a subset of species in the plot. The average neighborhood
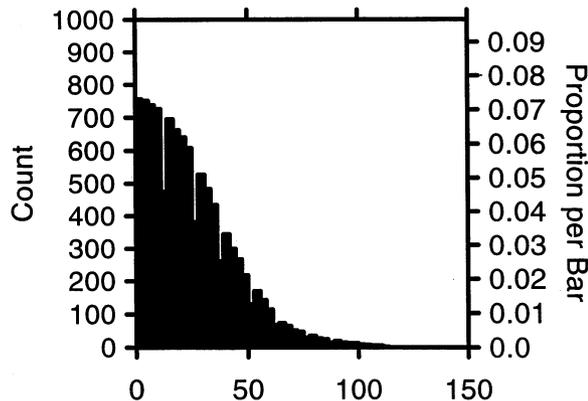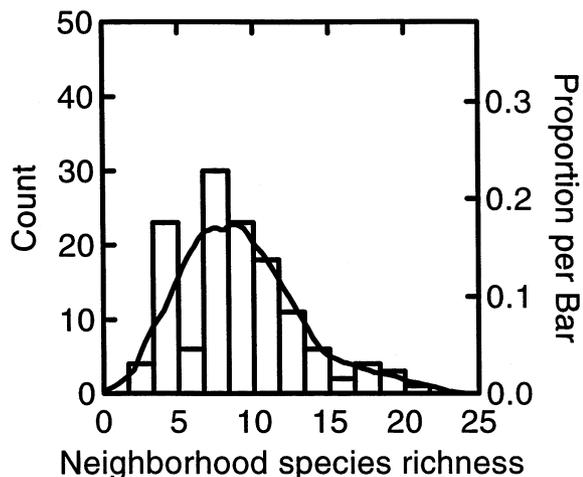

Fig. 5. Frequency distribution of neighborhoods with different numbers of species. Line represents DWLS smoothing function.

Table 2. Stepwise (backward deletion) multiple regression of total biomass of target *C. tectorum* (log$_{10}$-transformed) against neighborhood variables from 25-cm-diameter neighborhoods and plot variables. Final statistics for *C. tectorum* performance using neighborhood variables yielded $R^2 = 0.20$ and $P < 0.001$ ($N = 69$; $F = 7.03$; d.f. 3, 65). Final statistics for *C. tectorum* performance using plot variables yielded $R^2 = 0.33$ and $P < 0.01$ ($N = 70$; $F = 5.71$; d.f. 3, 66). Final statistics for *D. ischaemum* performance using plot variables yielded $R^2 = 0.29$ and $P < 0.001$ ($N = 137$; $F = 28.8$). "Species added" refers to the original species added to the plot (i.e. treatment level).

Variable	Coeff.	SE	t	P
C. tectorum neighborhood variables				
Constant	-0.680	0.099	-6.888	<0.001
Total cover	< -0.001	< -0.001	-1.650	0.104
Species added	-0.020	0.007	-3.030	<0.01
$\theta_{adjusted}$	0.001	0.001	1.590	0.117
C. tectorum plot variables				
Constant	-2.145	0.204	-10.498	<0.001
Root biomass	0.169	0.105	5.901	<0.001
D. ischaemum plot variables				
Constant	-3.203	0.247	-12.965	<0.001
Root biomass	0.869	0.149	5.835	<0.001
Nitrate	1.015	0.508	1.997	<0.05

was established in the plot; this was not surprising given its smaller size. Percent cover estimates (Table 1) indicated that relative abundances of resident species were very similar to relative abundances of species within *C. tectorum* neighborhoods ($N = 24$, Pearson correlation $= 0.766$, $P < 0.001$).

Of these 253 *C. tectorum* plants, 143 in 70 plots were recovered, with the others lost to senescence, accidental weeding, herbivory, or disease. This loss was not biased by treatment and appeared to be random (mean number of plots per species richness treatment was 10, minimum number for any treatment was 6 and maximum was 15).

Measured ecosystem properties are associated with plant composition

The composition (relative abundance) of resident species in plots showed significant associations with ecosystem properties. Each ecosystem property was treated as a dependent variable in a multiple regression using percent cover of each resident species as an independent variable. Although all five properties examined showed significant associations with composition ($P < 0.001$), the goodness of fit of the regression (R^2) varied. In order of best to poorest fit, the ecosystem properties were total percent cover ($R^2 = 0.64$), root biomass ($R^2 = 0.54$), nitrate available in the rooting zone ($R^2 = 0.49$), light transmittance ($R^2 = 0.46$), and above-ground biomass ($R^2 = 0.39$) (Table 1). In general, non leguminous forbs and C$_4$ grasses were consistently identified as important species associated with each ecosystem property (Table 1).

C. tectorum *performance is a function of plant composition*

The composition of resident species in plots could also significantly predict *C. tectorum* performance (Table 1). Analyses were conducted both at the level of the plot (using relative percent cover of resident species within the plot) and at the level of the neighborhood (using relative percent cover of resident species within the neighborhood). In general, as in the ecosystem properties, non leguminous forbs and C$_4$ grasses were consistently identified as important species associated with invader performance at the level of the plot (Table 1). Analyses at the level of the neighborhood showed similar patterns to that of the plot (Table 1).

Invader performance is associated with both community and ecosystem properties

Performance of *C. tectorum* and *D. ischaemum* could be significantly predicted by regression models that combined community as well as ecosystem properties. In these analyses, we used total cover, original resident species richness, and $\theta_{adjusted}$ as the variables representing community properties. We also used above-ground biomass, root biomass, and nitrate in the rooting zone as the ecosystem variables. Stepwise, backward elimination identified primarily community properties as predictors of *C. tectorum* at the level of the neighborhood, though only 20% of the variance was explained by the model (Table 2). At the level of the plot, however, ecosystem variables (root biomass and/or nitrates) were the principal variables identified as explaining close to 30% of the variance in invader performance (Table 2).

C. tectorum *performance in potted plant assemblages is a function of neighborhood species richness*

C. tectorum biomass showed a significant decline with the number of species per pot, irrespective of species identity (linear regression of log-transformed above-ground biomass of *C. tectorum* against number of neighborhood species, $N = 130$, $P < 0.001$, $R^2 = 0.10$) (Fig. 6). This result is similar to what was observed in the experimental grassland plots (compare Figs 6 and 3), suggesting that this greenhouse model exhibits patterns similar to what is observed under field conditions.
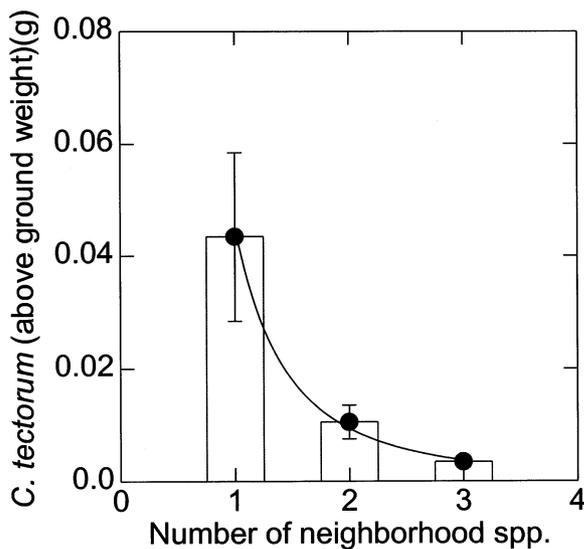
Fig. 6. Performance of *C. tectorum* (above-ground biomass) in potted plant assemblages. Number of species refers to number of plant species in neighborhood (pot). Bars represent means, and error bars are one SE. Line represents exponential curve using nonlinear regression to facilitate comparison with Fig. 3. Regression parameter estimates, intercept $= -0.96$ (SE $= 0.01$), exponent $= -0.04$ (SE $= 0.003$), $R^2 = 0.23$, $P < 0.001$.

Target *C. tectorum* biomass showed significant associations with above-ground biomass of neighborhoods ($N = 135$, $R^2 = 0.19$, $P < 0.001$), light transmittance ($N = 140$, $R^2 = 0.17$, $P < 0.001$), and below-ground biomass ($N = 140$, $R^2 = 0.31$, $P < 0.001$) (Fig. 7).

Neighborhood plants differed in above-ground production, below-ground production, and light interception (canopy). Fig. 8 shows that species with the highest mean values for one biomass or canopy variable do not necessarily have the highest values for others. For example, *A. millefolium* produced the most closed canopy, but is the second lowest ranking species in above-ground production and intermediate in below-

ground production. In contrast, *P. virgatum* produced the most open canopy, but is intermediate in above-ground production and has the highest below-ground production. Fig. 9 also shows that species in monoculture had relatively similar impacts on *C. tectorum* performance, with *A. canadensis* and *V. villosa* having the weakest effects. Thus, no single species strongly dominates in suppressing *C. tectorum* growth. Note also that interspecific competition was stronger than intraspecific competition (Fig. 9).

Discussion

Elton's hypothesis

Plant invader success (total biomass at flowering of individual *D. ischaemum* and *C. tectorum* plants) showed a strong, inverse relationship with resident plant species richness of experimental grassland plots at Cedar Creek (Fig. 3). These results are in agreement with the pattern described by Elton (1958) and predicted by competition-based theory (e.g., Elton 1958, MacArthur and Wilson 1967, Turelli 1981, Post and Pimm 1983, Case 1990, Law and Morton 1996, Crawley et al. 1999, Levine and D'Antonio in press). Because extrinsic factors were not manipulated, these results are most likely attributable to factors associated with variation in resident plant diversity.

Both species are non-native invaders introduced from Eurasia (Gleason and Cronquist 1991) and not part of the experimental system. *C. tectorum* is a taprooted annual forb that persists as a rosette until flowering. It invades the plots early in spring before the majority of planted species leaf out. *D. ischaemum* is a late-season annual grass that appears in the plots in late July or August. Both species reproduce solely by seed. Additional invaders included grasses (*Digitaria ischaemum*, *D. sanguinalis*, *Cenchrus longispinus*, *Bromus inermis*, *Setaria glauca*, *Agrostis alba*, *Agropyron repens*,
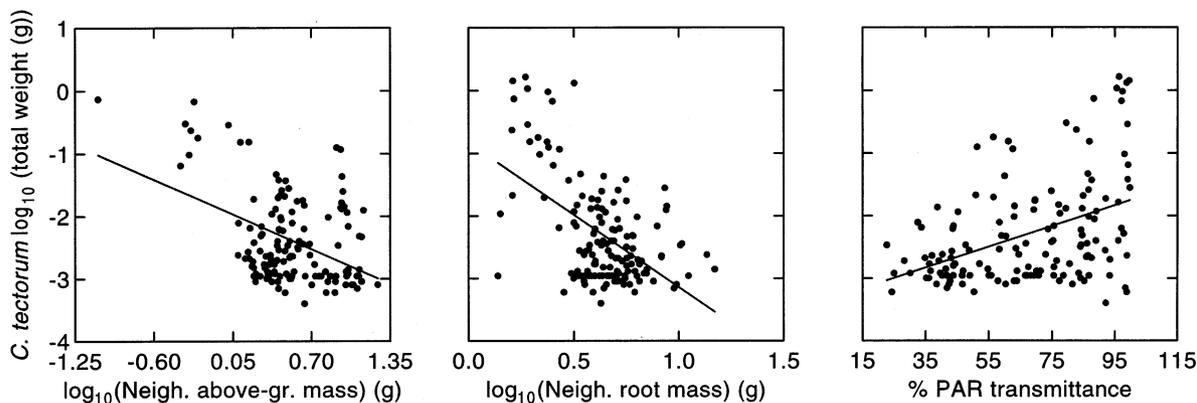

Fig. 7. Performance of *C. tectorum* and neighborhood properties in potted plant assemblages. Lines represent fitted least squares regression. Both above- (neighborhood) and below-ground (root) biomass have been $\log_{10}$ transformed to improve linearity.
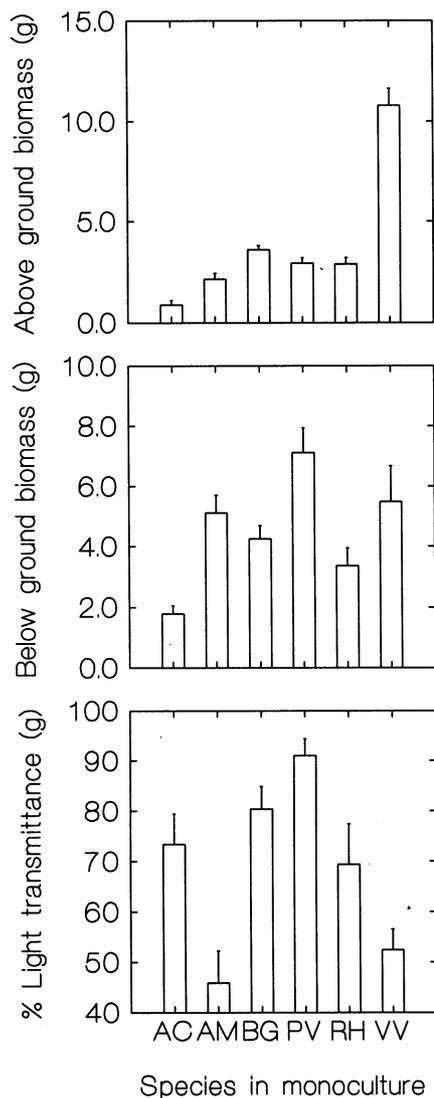
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Fig. 8. Monoculture neighborhood properties. Each pot contains three plants of species indicated by abbreviation. Bars represent means and errors are one SE. Top: Total above-ground biomass (dry weight) of monocultures with one central *C. tectorum* plant per pot. Middle: Total below-ground biomass (dry weight of roots). Bottom: Percent PAR transmittance. Monocultures are *Astragalus canadensis* (AC), *Achillea millefolium* (AM), *Bouteloua gracilis* (BG), *Panicum virgatum* (PV) *Rudbeckia hirta* (RH) and *Vicia villosa* (VV).

Panicum oligosanthes, *Aristida basiramea*, and *Cyperus* spp.) non-leguminous forbs (*Ambrosia artemisiifolia*, *Conyza canadensis*, *Erigeron annuus*, *Euphorbia glyptosperma*, *Chenopodium hybridum*, *Rumex acetosella*, *Taraxacum officinale*, *Cirsium arvense*, *Hedeoma hispida*, *Lepidium densiflorum*, *Berteroa incana*, *Silene antirrhina*, *Lychnis alba*, *Physalis virginiana*, *Polygonum tenua*, *P. convolvulus*, *Ambrosia cornopifolia*, *Mollugo verticillata*, *Oenothera biennis*, *Verbascum thapsus*, *Tragopogon major*, and *Solidago* spp.) and legumes

(*Trifolium arvense*, *T. repens*, *Medicago sativa*, *Melilotus officinale*). Some of these species are native, but were considered invaders. Although resources did not permit examining each of these species individually, total biomass of all invasive species showed a similar exponential decline with increasing resident diversity (Knops et al. 1999). Thus, these results may apply to many other invasive species in our study system.

The mechanism of competition
Our studies of *C. tectorum* suggest that the mechanism for the observed inverse association between invader performance and resident species richness is associated with interspecific competition for space, light, and nutrients with neighbors. Multiple regression analyses showed that *C. tectorum* performance was significantly associated with the relative abundance of resident species in neighborhoods (Table 1). Because relative abundance of resident species also showed significant associations with nitrates, above- and below-ground biomass, light interception (percent transmittance), and percent cover (Table 1), we infer that variation in plant diversity is responsible for variation in these factors which in turn affect invader success.

Invasion in the experimental plots occurred naturally, so it is possible that recruitment could somehow explain the results. For example, small *C. tectorum* seeds may recruit more successfully in low diversity plots and differences in adult biomass could be due to initial differences in recruitment success. Our greenhouse ex-
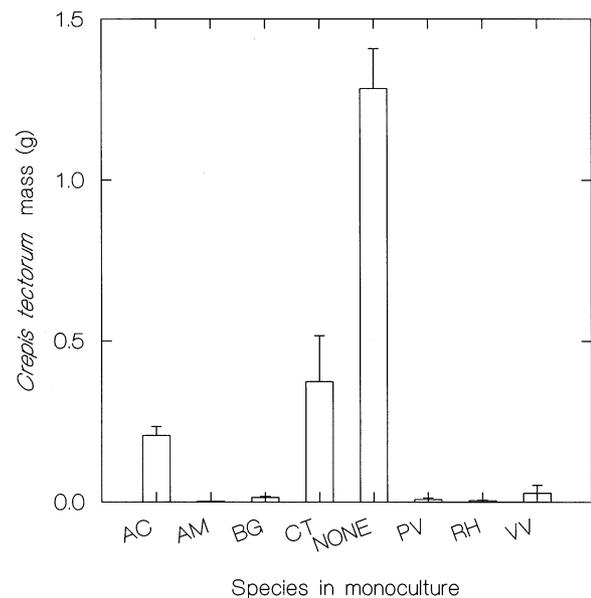

Fig. 9. Performance of *C. tectorum* biomass in potted monocultures of three neighbors. Biomass is estimated as dry weight of above-ground biomass. Assemblages were monocultures (see Fig. 8 for explanation of abbreviations), *Crepis tectorum* (CT), and "NONE" which indicates no neighbors (a single *C. tectorum* plant).

periments, however, suggest that the same pattern occurs when recruitment is controlled. *C. tectorum* seedlings in identical pots under identical initial conditions of space, water, light, and neighborhood density (three neighboring plants), grew poorly in high diversity neighborhoods as they did in plots (compare Figs 3 and 6). Light availability, above-ground biomass, and below-ground biomass also indicated that higher diversity communities in these pots represented more competitive environments (darker, more crowded conditions) (Fig. 7). The similarity between greenhouse and field experimental results support stronger competitive environments generated by more diverse plant communities as the mechanism that reduces invader success.

This mechanism most likely occurs at the level of the neighborhood. Greenhouse experiments showed that the same effect in the field could be produced in a small container under the controlled environmental conditions of a greenhouse (compare Figs 3 and 6), supporting the idea that it takes only a few individuals from a few species to create the effect observed at the level of the plot. Resident plant abundance and species richness in the grassland plots were both higher than in greenhouse assemblages, but analyses showed that plants with high θ values in *C. tectorum* neighborhoods were rare. That is, typically only a few plants are likely to have a significant presence (near the target or occupying a large space in the neighborhood) (Fig. 4). Thus, like the greenhouse assemblages and possibly in most plant neighborhoods, only a fraction of the species within a plot will be found in the neighborhood of an individual and only a few individuals will have strong effects. The effect of species richness therefore asymptotes at relatively low numbers (ca 10 spp.), as observed in Fig. 3.

Note that reductions in available space, light, and N due to greater exploitation efficiency in more diverse plant assemblages does not imply that average levels of interspecific competition are lower. The increased competitive environment of a diverse neighborhood results from resources being reduced to low levels due to niche complementarity (see below).

Mechanism of biodiversity effect

Biodiversity effects, such as observed in this study, are explained by two principal mechanisms, the sampling effect and niche partitioning or complementarity (Aarssen 1997, Hooper and Vitousek 1997, Huston 1997, Hector 1998, Hooper 1998, Loreau 1998a, Crawley et al. 1999). The sampling effect occurs when higher diversity communities randomly selected from a species pool ensure that species-rich plots have a higher probability of obtaining species with more pronounced impacts on ecosystem processes (Hector 1998, Loreau 1998a). This effect is likely to be most pronounced when competitive exclusion allows for dominant species to increase in biomass to the exclusion of other species

(Crawley et al. 1999). The niche partitioning effect occurs when higher diversity assemblages lead to more diverse and therefore more effective exploitation of local resources (Naeem et al. 1994, Hooper and Vitousek 1997, Tilman et al. 1997b, Hooper 1998, Loreau 1998b). This mechanism operates in young systems or in systems where diversity is either stable or changes slowly.

In this study, different resident species showed different abilities to use above- and below-ground resources both in plots (Table 1) and in the greenhouse study (Fig. 9). Mixed-species assemblages result in different species dominating use of space, light, or nutrients within a neighborhood. In the grassland plots, for example, 10 of the 24 species were identified by multiple regression as variables predicting *C. tectorum* performance at the level of the plot whereas 11 were identified at the level of the neighborhood (Table 1). Because the abundance of the resident species used in the analyses were not significantly correlated with one another and because species belonged to several functional groups (Table 1), no single species or single functional group accounts for the patterns observed. Given enough time, however, especially at high levels of nutrient inputs, should a single species come to dominate each plot, species identity is likely to be a better predictor of resistance to plant invasion than species richness (Crawley et al. 1999).

It is important to note that our plots are relatively young and species richness is low compared to "natural" prairie, thus it is difficult to be certain how well our findings might scale to older, larger systems. Prairie grasslands, however, are fire driven communities, thus average age of a grassland community since disturbance is likely to be small in natural systems as they are in our study system. Further, at the plot or neighborhood level, plant species richness is likely to be even higher than would be encountered in natural communities even if total species richness is much lower. Finally, the mechanisms which explain the results in our study are also likely to apply to most plant communities independent of scale.

Extrinsic biodiversity covariates versus direct biodiversity effects

These results clearly support Elton's hypothesis and his proposed competition-based mechanism, but they do not necessarily conflict with findings from studies which allow extrinsic factors to covary with biodiversity (Fig. 1). Observational studies cannot identify mechanisms responsible for patterns of association (Levine and D'Antonio in press) and cannot separate effects due to variation in resident plant diversity from effects due to extrinsic factors that covary with diversity (see, e.g., Manly 1992, Underwood 1997). Thus, there is no clear way to compare our findings with those of observational studies. For example, Wiser et al. (1998) exam-

ined invasion success of *Hieracium lepidulum*, an herbaceous plant, into mountain beech (*Nothofagus solandri* var. *cliffortoides*) habitats in New Zealand while Planty-Tabacchi et al. (1996) examined associations between percent alien species and resident diversity in riparian corridors of the Pacific Northwest and Southwestern France. Both these studies found positive rather than inverse associations with resident plant diversity and invasion success, but variation in resident plant diversity was often associated with other factors, such as soil fertility or disturbance.

In another example, Ullmann et al. (1995) showed a positive correlation between resident and invasive plant abundance and resident and invasive species richness in New Zealand. Both resident and invasive abundance and species richness, however, were associated with climatic factors. Given such covariation, a positive association between resident diversity and invader diversity is to be expected, thus the notion that "diversity begets diversity" (Palmer and Maurer 1997) may be commonly found in observational studies.

Finally, seed addition experiments are similar to observational studies because they do not manipulate extrinsic factors (Levine and D'Antonio in press, Turnbull et al. 2000). For example, Robinson et al. (1995) introduced seeds of *Eshscholzia californica*, the California poppy, to experimental California grassland plots which varied in resident diversity due to differences in disturbance and dominance of resident species among plots. Similarly, Tilman (1997) introduced seeds from 54 species of non-resident grassland species to prairie grassland plots which varied naturally in resident plant species richness. Although Robinson et al. (1995) found a positive association between diversity and invasion success and Tilman (1997) found a negative association, neither study directly manipulated resident plant diversity so it is not possible to derive from these studies whether in situ reductions in diversity would increase or decrease invasion success.

Our study demonstrates that it is inappropriate to infer that resident diversity *encourages* invasion because observational studies show positive correlations between resident diversity and invasion success. Observational studies may identify positive, negative, or no association depending on which covarying factor is associated with invasion and diversity. It is also inappropriate, however, to infer from our experimental studies that more diverse communities are more resistant to invasion if resident diversity and extrinsic factors, such as disturbance or nutrients, covary with resident diversity. The appropriate interpretation of our findings is that biodiversity loss within a community can lower its resistance to invasion. That this effect is due to changes in the competitive environment of the plant neighborhood supports Elton's hypothesis.

References

Aarssen, L. W. 1997. High productivity in grassland ecosystems: effected by species diversity or productive species? – Oikos 80: 183–184.

Armstrong, R. A. 1993. A comparison of index-based and pixel-based neighborhood simulations of forest growth. – Ecology 74: 1707–1712.

Berger, J. J. 1993. Ecological restoration and non-indigenous plant species: a review. – Restoration Ecol. 1: 74–82.

Burke, M. J. W. and Grime, J. P. 1996. An experimental study of plant community invasibility. – Ecology 77: 776–789.

Cain, M. L., Pacala, S. W., Silander, J. A., Jr. and Fortin, M.-J. 1995. Neighborhood models of clonal growth in the white clover *Trifolium repens*. – Am. Nat. 145: 888–917.

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

Cavers, P. B. and Harper, J. L. 1967. Studies in the dynamics of plant populations. 1. The fate of seed and transplants introduced into various habitats. – J. Ecol. 55: 59–71.

Collins, S. 1987. Interactions of disturbances in tallgrass prairie: a field experiment. – Ecology 68: 1243–1250.

Crawley, M. J. 1987. What makes a community invasible? – In: Gray, A. J., Crawley, M. J. and Edwards, P. J. (eds) Colonization, succession and stability. Blackwell Scientific, pp. 429–453.

Crawley, M. J., Brown, S. L., Heard, N. S. and Edwards, G. R. 1999. Invasion-resistance in experimental grassland communities: species richness or species identity? – Ecol. Lett. 2: 140–148.

Cronk, Q. C. B. and Fuller, J. L. 1995. Plant invaders. – Chapman and Hall.

D'Antonio, C. M. and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. – Annu. Rev. Ecol. Syst. 23: 63–87.

Drake, J. A. 1990. The mechanics of community assembly and succession. – J. Theor. Biol. 147: 213–233.

Drake, J. A., Mooney, H. A., di Castri, F. et al. 1989. Biological invasions: a global perspective. – John Wiley and Sons.

Drake, J. H., Flum, T. E., Witteman, G. J. et al. 1993. The construction and assembly of an ecological landscape. – J. Anim. Ecol. 62: 117–130.

Elton, C. S. 1958. The ecology of invasions by animals and plants. – Methuen.

Gleason, H. A. and Cronquist, A. 1991. Manual of vascular plants of northeastern United States and adjacent Canada. 2nd ed. – New York Botanical Garden.

Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. – Ecology 68: 1211–1223.

Goldberg, D. E. and Scheiner, S. M. 1993. ANOVA and ANCOVA: field competition experiments. – In: Scheiner, S. M. and Gurevitch, J. (eds) Design and analysis of ecological experiments. Chapman and Hall, pp. 69–93.

Harper, J. L. 1977. Population biology of plants. – Academic Press.

Hector, A. 1998. The effects of diversity on productivity: detecting the role of species complementarity. – Oikos 82: 597–599.

Hengeveld, R. 1989. Dynamics of biological invasions. – Chapman and Hall.

Heywood, V. H. 1989. Pattern, extent and modes of invasions by terrestrial plants. – In: Drake, J. A., Mooney, H. A., Castri, F. D. et al. (eds) Biological invasions: a global perspective. Wiley and Sons, pp. 31–60.

Hobbs, R. J. and Huenneke, L. F. 1992. Disturbance, diversity and invasion: implications for conservation. – Conserv. Biol. 6: 324–337.

Hobbs, R. J. and Humphries, S. E. 1994. An integrated approach to the ecology and management of plant invasions. – Conserv. Biol. 9: 761–770.

Hooper, D. U. 1998. The role of complementarity and competition in ecosystem responses to variation in plant diversity. – Ecology 79: 704–719.

Hooper, D. U. and Vitousek, P. M. 1997. The effects of plant composition and diversity on ecosystem processes. – Science 277: 1302–1305.

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

Knops, J. M. H., Griffin, J. R. and Royalty, A. R. 1994. Introduced and native plants of the Hastings Reservation, central coastal California: a comparison. – Biol. Conserv. 71: 115–123.

Knops, J. M. H., Tilman, D., Haddad, N. M. et al. 1999. Effects of plant species richness on invasion dynamics, disease outbreaks, insects abundances and diversity. – Ecol. Lett. 2: 286–293.

Law, R. and Morton, D. 1996. Permanence and the assembly of ecological communities. – Ecology 77: 762–775.

Leach, M. K. and Givnish, T. J. 1996. Ecological determinant of species loss in remnant prairies. – Science 273: 1555–1558.

Levine, J. M. and D'Antonio, C. M. in press. Elton revisited: a review of evidence linking diversity and invasibility. – Q. Rev. Biol.

Lindsay, D. R. 1953. Climate as a factor influencing the mass ranges of weeds. – Ecology 34: 308–321.

Lockwood, J. L., Powell, R. D., Nott, M. P. and Pimm, S. L. 1997. Assembling ecological communities in time and space. – Oikos 80: 549–553.

Lodge, D. M. 1993. Species invasions and deletions: community effects and responses to climate and habitat change. – In: Kareiva, P. M., Kingsolver, J. G. and Huey, R. B. (eds) Biotic interactions and global change. Sinauer, pp. 367–387.

Loreau, M. 1998a. Separating sampling and other effects in biodiversity experiments. – Oikos 82: 600–602.

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

Luh, H.-K. and Pimm, S. L. 1993. The assembly of ecological communities: a minimalist approach. – J. Anim. Ecol. 62: 749–765.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.

Macdonald, I. A. W., Thébaud, C., Strahm, W. A. and Strasberg, D. 1991. Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean). – Environ. Conserv. 18: 51–61.

Mack, R. N. 1989. Temperate grasslands vulnerable to plant invasions: characteristics and consequences. – In: Drake, J. A., Mooney, H. A., Castri, F. D. et al. (eds) Biological invasions: a global perspective. Wiley and Sons, pp. 155–180.

Mack, R. N. and Harper, J. L. 1977. Interference in dune annuals: spatial pattern and neighborhood effects. – J. Ecol. 65: 345–364.

Manly, B. F. J. 1992. The design and analysis of research studies. – Cambridge Univ. Press.

McGrady-Steed, J., Harris, P. M. and Morin, P. J. 1997. Biodiversity regulates ecosystem predictability. – Nature 390: 162–165.

McIntyre, S. and Lavorel, S. 1994a. How environmental and disturbance factors influence species competition in temperate Australian grasslands. – J. Veg. Sci. 5: 373–384.

McIntyre, S. and Lavorel, S. 1994b. Predicting richness of native, rare, and exotic plants in response to habitat and disturbance variables across a variegated landscape. – Conserv. Biol. 8: 521–531.

Milchunas, D. G. and Lauenroth, W. K. 1995. Inertia in plant community structure state changes after cessation of nutrient-enrichment stress. – Ecol. Appl. 5: 452–458.

Mooney, H. A. and Drake, J. A. 1986. Ecology of biological invasions of North America and Hawaii. – Springer-Verlag.

Naeem, S., Thompson, L. J., Lawler, S. P. et al. 1994. Declining biodiversity can alter the performance of ecosystems. – Nature 368: 734–737.

Palmer, M. and Maurer, T. A. 1997. Does diversity beget diversity: a case study of crops and weeds. – J. Veg. Sci. 8: 235–240.

Planty-Tabacchi, A., Tabacchi, E., Naiman, R. J. et al. 1996. Invasibility of species-rich communities in riparian zones. – Conserv. Biol. 10: 598–607.

Post, W. M. and Pimm, S. L. 1983. Community assembly and food web stability. – Math. Biosci. 64: 169–192.

Ramakrishnan, P. S. 1991. Ecology of biological invasion in the tropics. – International Scientific Publ.

Ramakrishnan, P. S. and Vitousek, P. M. 1989. Ecosystem-level processes and the consequences of biological invasions. – In: Drake, J. A., Mooney, H. A., Castri, F. D. et al. (eds) Biological invasions: a global perspective. Wiley and Sons, pp. 281–300.

Rejmánek, M. 1989. Invasibility of plant communities. – In: Drake, J. A., Mooney, H. A., Castri, F. D. et al. (eds) Biological invasions: a global perspective. Wiley and Sons, pp. 369–388.

Robinson, G. R., Quinn, J. F. and Stanton, M. L. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. – Ecology 76: 786–794.

Robinson, J. V. and Dickerson, J. J. E. 1984. Testing the invulnerability of laboratory island communities to invasion. – Oecologia 61: 169–174.

Robinson, J. V. and Edgemon, M. A. 1988. An experimental evaluation of the effect of invasion history on community structure. – Ecology 69: 1410–1417.

Silander, J. A., Jr. and Pacala, S. W. 1985. Neighborhood predictors of plant performance. – Oecologia 66: 256–263.

Stohlgren, T. J., Binkley, D., Chong, G. W. et al. 1999. Exotic plant species invade hot spots of native plant diversity. – Ecol. Monogr. 69: 47–68.

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

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

Tilman, D., Wedin, D. and Knops, J. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystems. – Nature 379: 718–720.

Tilman, D., Knops, J., Wedin, D. et al. 1997a. The influence of functional diversity and composition on ecosystem processes. – Science 277: 1300–1302.

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

Timmins, S. M. and Williams, P. A. 1991. Weed numbers in New Zealand's forest and scrub reserves. – N. Z. J. Ecol. 15: 153–162.

Turelli, M. 1981. Niche overlap and invasion of competitors in random environments. – Theor. Popul. Biol. 20: 1–56.

Turnbull, L. A., Crawley, M. J. and Rees, M. 2000. Are plant populations seed-limited? A review of seed sowing experiments. – Oikos 88: 225–238.

Ullmann, I., Bannister, P. and Wilson, J. B. 1995. The vegetation of roadside verges with respect to environmental gradients in southern New Zealand. – J. Veg. Sci. 6: 131–142.

Underwood, A. J. 1997. Experiments in ecology. – Cambridge Univ. Press.

Waller, D. M. 1981. Neighborhood competition in several violet populations. – Oecologia 51: 116–122.

Wilkinson, L. 1992. SYSTAT. – SYSTAT.

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