

- particles at Cape Grim. *Geophys. Res. Lett.* **24**, 3197–3200 (1997).
25. Gäbler, H. E. & Heumann, K.-G. Determination of particulate iodine in aerosols from different regions by size fractioning impactor sampling and IDMS. *Int. J. Anal. Chem.* **50**, 129–146 (1993).
26. Wimschneider, A. & Heumann, G. Iodine: speciation in size fractionated atmospheric particles by isotope dilution mass spectrometry. *Fresenius J. Anal. Chem.* **353**, 191–196 (1995).
27. Baker, A. R., Thompson, D., Campos, M. L. A. M., Parry, S. J. & Jickells, T. D. Iodine concentration and availability in atmospheric aerosol. *Atmos. Environ.* **34**, 4331–4336 (2000).
28. Huang, S., Arimoto, R. & Rahn, K. A. Sources and source variations for aerosol at Mace Head, Ireland. *Atmos. Environ.* **35**, 1421–1437 (2001).
29. Jayne, J. T. *et al.* Development of an aerosol mass spectrometer for size and composition analysis of submicron particles. *Aerosol Sci. Technol.* **33**, 49–70 (2000).
30. Bloss, W. J., Rowley, D. M., Cox, R. A. & Jones, R. L. Kinetics and products of the IO self-reaction. *J. Phys. Chem. A* **105**, 7840–7854 (2001).

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Biodiversity as a barrier to ecological invasion

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Biological invasions are a pervasive and costly environmental problem^{1,2} that has been the focus of intense management and research activities over the past half century. Yet accurate predictions of community susceptibility to invasion remain elusive. The diversity resistance hypothesis, which argues that diverse communities are highly competitive and readily resist invasion^{3–5}, is supported by both theory⁶ and experimental studies^{7–14} conducted at small spatial scales. However, there is also convincing evidence that the relationship between the diversity of native and invading species is positive when measured at regional scales^{3,11,15,16}. Although this latter relationship may arise from extrinsic factors, such as resource heterogeneity, that covary with diversity of native and invading species at large scales, the mechanisms conferring greater invasion resistance to diverse communities at local scales remain unknown. Using neighbourhood analyses, a technique from plant competition studies^{17–19}, we show here that species diversity in small experimental grassland plots enhances invasion resistance by increasing crowding and species richness in localized plant neighbourhoods. Both the establishment (number of invaders) and success (proportion of invaders that are large) of invading plants are reduced. These results suggest that local biodiversity represents an important line of defence against the spread of invaders.

The relative contribution of extrinsic factors and resident diversity to invasion resistance varies across spatial scales^{11,12}. For example, the initial arrival of propagules of invading plants into a

formerly isolated region or field is regulated by extrinsic factors, such as human transport that breaches isolation. Similarly, if an invading plant lands on a bare patch within a field, extrinsic factors such as the frequency and intensity of disturbance, soil fertility and climate are likely to be more important than resident diversity in regulating the success of invaders. Within a field, however, in a vegetated patch, an invading plant will find itself surrounded by neighbouring plants, and it is here that biotic factors such as species composition and plant density will regulate the competitive environment the invader faces.

To test for the impacts of biodiversity on invasion resistance independent of extrinsic factors, we examined how variation in plant species richness among 147 experimental grassland plots at Cedar Creek, Minnesota, affected plant neighbourhood properties, and how these properties, in turn, affected the establishment and success of the 13 species of exotic non-native plants (primarily Eurasian, see Methods for species list) that invaded these plots. We focused on three properties of plant neighbourhoods that are widely used in studies of intra- and interspecific competition and have been shown to affect the performance of plants^{17–19}. These properties are (1) the number of species within the neighbourhood (S_N), (2) the number of plants in the neighbourhood (N) and (3) θ_{sum} (ref. 12), an index of crowding that takes into account both the distance and size of all the plants within the neighbourhood.

Studies in which invading plants are established in neighbourhoods of a fixed size and composition^{13,18} cannot test whether neighbourhood properties affect invasions in spatially heterogeneous systems like natural vegetation. We avoided this limitation by examining the neighbourhood properties of all naturally invading exotic plants, as well as the neighbourhood properties of 100 randomly placed ‘null’ positions, in each plot. The former neighbourhoods reflect the biotic environment where invaders successfully established, whereas the latter null neighbourhoods reflect the typical biotic environments found within the plot, independent of invader establishment.

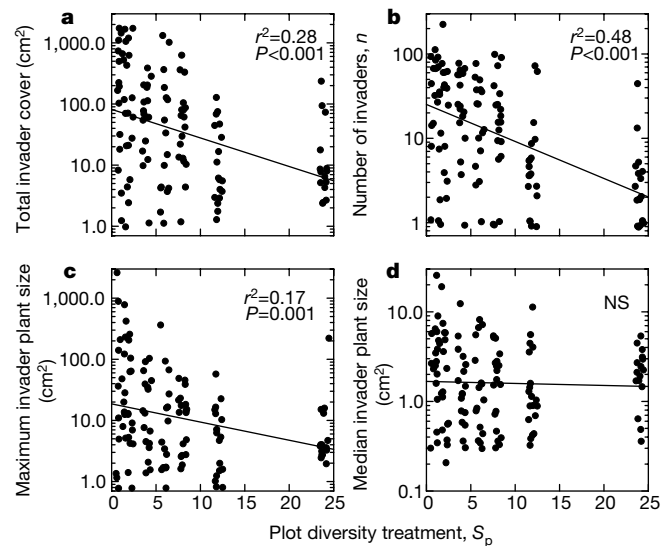


Figure 1 Plot diversity and invader performance. Effects of plot diversity treatment on total invader cover per subplot (a), the number of invading plants per subplot (b), the largest individual invader per subplot (c), and the median size of individual invaders in a subplot (d). Plot level patterns (a) are the result of a decrease in the number of invaders (b), and a reduction in the size of the largest invading plants in a subplot (c), but not a change in the median size of individual invaders (d), in more diverse plots. The least-squares regression lines are shown. Data are from 1998. Note the log scale on all y axes; NS, not significant.

Our experimental system consisted of 147 different 3 × 3 m plots in which plot diversity (S_p) initially varied from 1, 2, 4, 6, 8, 12 and 24 grassland species drawn at random from a pool of 24 species²⁰. We recorded the spatial coordinates and size of approximately 53,000 individual plants, 40,000 residents and 13,000 invaders, in 40 × 125 cm subplots within each plot during 1997 and 1998. Three years of weeding before the invasions study, and an initial disking and removal of the topmost layer of soil when the plots were established, eliminated most of the seed bank. Weeding ceased within the subplot for the two years that we conducted our experiment. Established invaders were therefore primarily derived from newly arriving seeds from large stretches of adjacent weedy fields. Random assignment of treatments to plots within the experimental site normalized seed rain distances from adjacent fields. We analysed these invasions using high-resolution digitized maps that recorded plants as small in area as 0.1 cm². We used the amount of bare ground within the subplot as a covariate in order to account for a known negative relationship between S_p and bare ground in these experimental plots²⁰, and thus test specifically for the effects of diversity on invasions. Average neighbourhood crowding and density of resident plants increased slightly across all treatment levels from 1997 to 1998, indicating that our results are not due to invader effects, such as a reduction in resident cover, as a result of not weeding during the two years of this experiment.

Plot species richness (S_p) had significant negative effects on the total area covered by invading plants, even after correcting for differences in the amount of total area covered by bare ground (analysis of covariance, ANCOVA, $F = 3.164$, $P = 0.006$; Fig. 1a). There were 91% and 96% reductions in invader cover in plots where $S_p = 24$ compared to the monocultures (that is, $S_p = 1$) in 1997 and 1998, respectively. This strong negative effect of diversity on total area covered by invaders was due to reductions in both the number of invaders (Fig. 1b) and the maximum size of individual invading plants in diverse plots (Fig. 1c), but not due to changes in the median size of individual invaders (Fig. 1d). Thus, S_p had a strong negative effect on both invader establishment (fewer invaders) and success (smaller maximum size) that was independent of bare ground. S_p also had a significant and positive effect on neighbourhood characteristics associated with crowding (Fig. 2a and b). Increasing S_p was positively associated with plant neighbourhoods that had greater S_N , greater N and increased θ_{sum} . These effects were also independent of covariance owing to bare ground (Table 1).

Invaders became established in neighbourhoods that were sig-

nificantly less crowded than 'null' neighbourhoods. The distribution of θ_{sum} for randomly placed 'null' neighbourhoods differed significantly from those neighbourhoods with invaders (Kolmogorov–Smirnov test, $P = 0.013$). Furthermore, invaders occurred in neighbourhoods with significantly lower θ_{sum} on average than 'null' neighbourhoods (t -test, $t = 2.848$, d.f. = 266, $P < 0.01$).

Increasingly dense, species-rich, and crowded neighbourhoods led to a marked decrease in the number and proportion of invading plants that attain a large size (that is, size >10 cm²; Fig. 3a and b). Logistic regression results indicate that S_N , N and θ_{sum} are significant predictors of whether an invading plant will be large, even when the amount of bare ground in a plot and the diversity treatment of a plot are also included as predictors. (We performed a logistic regression with the categorical response variable of whether the invader is >10 cm². Overall $\chi^2 = 92.68$, d.f. = 4, $P < 0.001$. T -ratio for individual predictors: $S_p = 3.871$, $P < 0.001$, bare ground = 3.147, $P < 0.005$, $S_p \times$ bare ground = -4.200, $P < 0.001$, $N = -6.610$, $P < 0.001$. N , S_N and θ_{sum} are highly correlated, and only N was included in the model to avoid problems with collinearity, but similar results are obtained for each of the neighbourhood level predictors.)

Disentangling the relative contributions of sampling, niche-complementarity, and other potential mechanisms responsible for the observed diversity effects in diversity-gradient experiments requires further experimentation²¹. However, analysis of data from the 24-species plots further supports neighbourhood properties as an important determinant of invasion resistance. In the 24-species plots, neighbourhood properties based on "null" invaders were a significant predictor of total invader cover, just as they were across the entire experimental diversity gradient, even when the plot level variables of bare ground and nitrate in the rooting zone were also included as predictors (linear regression, stepwise backward deletion, $R^2 = 0.35$, $P < 0.03$). In other words, even when plot level diversity is held constant ($S_p = 24$) and covarying extrinsic factors (bare ground and nitrate) are controlled, we still find that neighbourhood characteristics are important and significant determinants of invader success.

Collectively, these results demonstrate that greater local species richness (S_p) increases neighbourhood species richness (S_N), density (N) and crowding (θ_{sum}), and these biotic factors are clearly associated with decreases in invader establishment and success, independently of the amount of bare ground. Because all plots had the same size, history, exposure to extrinsic factors, and an unbiased seed rain from weedy fields, we suggest that the resistance

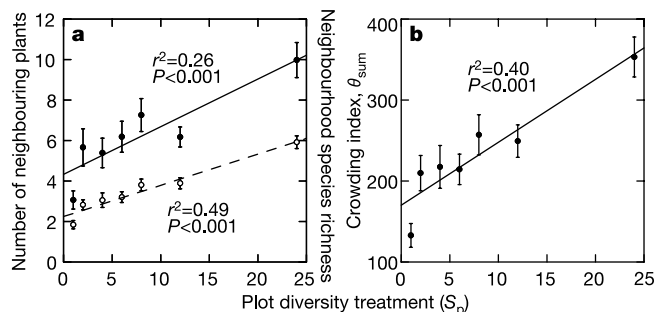


Figure 2 Neighbourhood characteristics and plot diversity treatment. Diverse plots tend to have neighbourhoods with more neighbouring plants (a, solid symbols and line), neighbourhoods that are more species rich (a, open symbols and dashed line), and neighbourhoods that are more crowded (b). Data points are mean values of 100 null points randomly placed into each of the 147 maps from 1998 that were then averaged within diversity treatments, \pm one standard error.

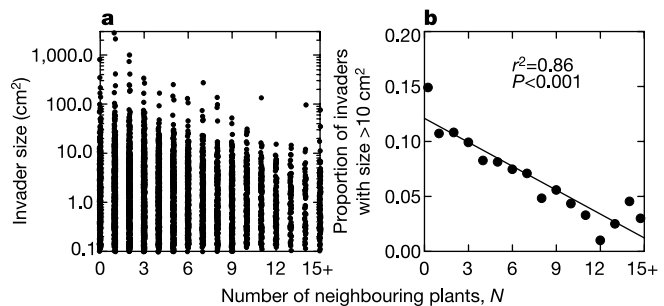


Figure 3 The influence of the number of neighbouring plants on invader performance. The upper bound of individual invader size markedly decreases as the number of neighbouring plants increases (a). Panel b depicts this decrease in upper bound in another way, by plotting the proportion of large invading plants as a function of the number of neighbouring plants (large plants were arbitrarily defined as plants >10 cm², a size cut-off that only 9% of all invaders met. The pattern also holds for other cut-off values and neighbourhood parameters). Data are from both 1997 and 1998.

Table 1 Effects of diversity treatment on neighbourhood properties when controlling for extent of bare ground

Dependent variables	Diversity treatment (S_P)		Bare ground	
d.f.	139		139	
Wilke's λ	0.420		0.361	
(F , d.f., P)	(7.75, 8, 387, < 0.001)		(80.67, 3, 137, < 0.001)	
	CL	UF (d.f., 139)	CL	UF (d.f., 139)
Neighbourhood density (N)	0.536	8.27***	0.001	0.000
Neighbourhood species richness (S_N)	0.890	20.743***	0.126	3.928*
Crowding index (θ_{sum})	0.612	10.402***	0.345	29.326***

Multivariate analysis of covariance results for the effect of plot diversity treatment and bare ground (covariate) on neighbourhood properties. Neighbourhood properties are based on the average of 100 null points placed into each plot. The highly significant effect of diversity treatment on neighbourhood properties, even after inclusion of bare ground within the subplot as a covariate, indicates that the effects of diversity on neighbourhood crowding is not simply the result of the greater plant biomass in diverse plots, but also a product of more evenly and tightly packed plants in diverse plots. Results shown are for 1998, but they are similar for other time periods. CL, canonical loadings; UF, univariate F ; d.f., degrees of freedom; θ_{sum} , crowding index (see Methods). * $P < 0.05$, *** $P < 0.001$

to invasion observed in our diverse plots is due primarily to biotic factors, namely crowded and intensely competitive plant-neighbourhoods. Interestingly, crowding and more complete use of space was also identified as the mechanism for greater invasion resistance of diverse communities of sessile marine invertebrates²².

Our study suggests that losses of biodiversity mean possible degradation of local resistance against invasion once factors that previously insulated habitats from invasion, such as geographical barriers, are breached by the changing patterns of human transport. These results also indicate that restoration and re-vegetation practitioners would benefit from establishing communities with as high a diversity of plants as is ecologically realistic and logistically feasible—diverse communities will probably require minimal maintenance and monitoring because they are generally effective at excluding undesirable invaders. □

Methods

Experimental plots

Invaders were defined as any exotic non-native plants that invaded the 147 experimental grassland plots in central Minnesota that were originally seeded with up to 24 species of perennial grassland plants²⁰. These plots are arranged in a matrix of 7 plots wide by 21 plots long, with total dimensions 24 × 75 m. Plots are a minimum of 6 m, and a maximum of 27 m, from the old fields that probably served as the seed source for invaders. The 24 species that were planted, and more details on these plots, are given elsewhere^{10,20}. Although 41 different species invaded the plots, only the 13 non-native species were included in our analyses. The non-native invaders included *Agropyron repens*, *Berteroa incana*, *Chenopodium album*, *Crepis tectorum*, *Digitaria ischaemum*, *Molluga verticillata*, *Polygonum convolvulus*, *Setaria lutescens*, *Silene antirrhina*, *Taraxacum officinale*, *Trifolium pratense*, *Trifolium repens*, and *Verbascum thapsus*.

Within the 0.5-m² experimental sub-plots where this research was conducted, between 1 and 20 species of resident plants were present. This range of species richness is comparable to the 6–22 species that were recorded in 120 different 1-m² sampling plots in a nearby undisturbed grassland²⁰, indicating that the plot diversity treatment levels roughly match those of natural plant communities. During the three years before this study, from 1994 to 1996, diversity treatments were maintained by weeding all plots at least three times during the growing season. The high frequency of weeding allowed us to remove invaders while they were still quite small and before they had the opportunity to set seed, minimizing the soil disturbance that weeding might otherwise have created. All weeding was conducted from elevated platforms, further minimizing the effects that weeding had on soil disturbance.

Neighbourhood analyses

We analysed results using a range of neighbourhood sizes (for example, 5–15-cm radius) and all yielded similar results. We present results using neighbourhoods with a 10-cm radius because this size is comparable to published values for neighbourhood analyses of plants that are similar in size to many of the invaders in our experiment¹⁸. θ is the angle subtended at an invader by another plant, and θ_{sum} is the sum of all angles for a given plant¹². To ensure that all invaders had neighbourhoods that were completely mapped, and to minimize any possible edge effects on the distribution of invaders within the subplot, only those invaders that were at least 10 cm from all edges of the subplot were included in neighbourhood analyses. This approach allowed us to monitor the success of a large number of naturally occurring individual invaders and total invader cover within a plot, and collect information on the properties of plant neighbourhoods across a range of species richness. A uniform random distribution was used to determine the placement of 'null' points. The first 100 points selected for each plot were used, regardless of whether they fell near an actual invader or not.

Statistical methods

We used multivariate analyses of variance to test for possible multivariate effects not

detectable with univariate methods. We used logistic regression to determine if neighbourhood characteristics and/or plot level characteristics are significant predictors of the performance of individual invaders. All patterns were comparable for both 1997 and 1998. We present data from only 1998 except for Fig. 3, which includes data from both years.

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- Mooney, H. A. & Drake, J. A. *Ecology of Biological Invasions of North America and Hawaii* (Springer, New York, 1986).
- Vitousek, P. M., D'Antonio, C. M., Loope, L. L. & Westbrooks, R. Biological invasions as global environmental change. *Am. Sci.* **84**, 468–478 (1996).
- Levine, J. & D'Antonio, C. M. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* **87**, 15–26 (1999).
- Crawley, M. J. in *Colonization, Succession and Stability* (eds Crawley, M. J., Edwards, P. J. & Gray, A. J.) Blackwell, Oxford, (1987), 429–453.
- Elton, C. S. *The Ecology of Invasions by Animals and Plants* (Methuen, London, 1958).
- Case, T. J. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proc. Natl Acad. Sci. USA* **87**, 9610–9614 (1990).
- Tilman, D. The ecological consequences of changes in biodiversity: A search for general principles. *Ecology* **80**, 1455–1474 (1999).
- McGrady-Steed, J., Harris, P. & Morin, P. Biodiversity regulates ecosystem reliability. *Nature* **390**, 162–165 (1997).
- Tilman, D. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* **78**, 81–92 (1997).
- Knops, J. M. H. et al. Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecol. Lett.* **2**, 286–293 (1999).
- Levine, J. Plant diversity and biological invasions: Relating local process to community pattern. *Science* **288**, 852–854 (2000).
- Naeem, S. et al. Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos* **91**, 97–108 (2000).
- Symstad, A. J. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* **81**, 99–109 (2000).
- Dukes, J. S. Biodiversity and invasibility in grassland microcosms. *Oecologia* **126**, 563–568 (2001).
- Planty-Tabacchi, A. M., Tabacchi, E., Naiman, R. J., Deferrari, C. & Decamps, H. Invasibility of species-rich communities in riparian zones. *Conserv. Biol.* **10**, 598–607 (1996).
- Stohlgren, T. J. et al. Exotic plant species invade hot spots of native plant diversity. *Ecol. Monogr.* **69**, 25–46 (1999).
- Mack, R. N. & Harper, J. L. Interference in dune annuals: spatial pattern and neighbourhood effects. *J. Ecol.* **65**, 345–364 (1977).
- Pacala, S. W. & Silander, J. A. Jr Neighbourhood interference among velvet leaf, *Abutilon theophrasti*, and pigweed, *Amaranthus retroflexus*. *Oikos* **48**, 217–224 (1987).
- Rejmanek, M. & Messina, J. J. *Multiresource Management of Ponderosa Pine Forests* General Technical Report RM-185 (eds Teale, A., Covington, W. W. & Haure, R. H.) 97–102 (United States Department of Agriculture, Ft. Collins, 1989).
- Tilman, D., Wedin, D. & Knops, J. M. H. Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature* **379**, 718–720 (1996).
- Wardle, D. A. Experimental demonstration that plant diversity reduces invisibility—evidence of a biological mechanism or a consequence of sampling effect? *Oikos* **95**, 161–170 (2001).
- Stachowicz, J. J., Whitlatch, R. B. & Osman, R. W. Species diversity and invasion resistance in a marine ecosystem. *Science* **286**, 1577–1579 (1999).

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