

LETTERS

The importance of niches for the maintenance of species diversity

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Ecological communities characteristically contain a wide diversity of species with important functional, economic and aesthetic value. Ecologists have long questioned how this diversity is maintained^{1–3}. Classic theory shows that stable coexistence requires competitors to differ in their niches^{4–6}; this has motivated numerous investigations of ecological differences presumed to maintain diversity^{3,6–8}. That niche differences are key to coexistence, however, has recently been challenged by the neutral theory of biodiversity, which explains coexistence with the equivalence of competitors⁹. The ensuing controversy has motivated calls for a better understanding of the collective importance of niche differences for the diversity observed in ecological communities^{10,11}. Here we integrate theory and experimentation to show that niche differences collectively stabilize the dynamics of experimental communities of serpentine annual plants. We used field-parameterized population models to develop a null expectation for community dynamics without the stabilizing effects of niche differences. The population growth rates predicted by this null model varied by several orders of magnitude between species, which is sufficient for rapid competitive exclusion. Moreover, after two generations of community change in the field, Shannon diversity was over 50 per cent greater in communities stabilized by niche differences relative to those exhibiting dynamics predicted by the null model. Finally, in an experiment manipulating species' relative abundances, population growth rates increased when species became rare—the demographic signature of niche differences. Our work thus provides strong evidence that species differences have a critical role in stabilizing species diversity.

For over a century, ecologists have explored the wide diversity of niche differences thought to stabilize coexistence⁸, exemplified by species' differences in rooting depth¹², the resources most limiting growth⁷ and interactions with specialist consumers^{13,14}. What unifies these differences is that they all cause species to limit themselves more than they limit their competitors¹⁵ (Fig. 1). Niche differences thus stabilize competitor dynamics by giving species higher per capita population growth rates when rare than when common (Fig. 1), and coexistence occurs when these stabilizing effects of niche differences overcome species differences in overall competitive ability. Although numerous studies have examined morphological, physiological and demographic differences between co-occurring species^{6–8,12}, the collective importance of those differences for the diversity observed in ecological communities is poorly understood¹¹. Ecologists have yet to determine whether species diversity is maintained by strong niche differences stabilizing the interactions of highly unequal competitors or, as suggested by the neutral theory⁹, whether niche differences are largely unimportant, only stabilizing the interactions of nearly equivalent competitors. More formally, these alternatives bracket a continuum of hypotheses concerning the importance of niches for diversity maintenance^{10,11}, one of the longest-standing problems in

ecology². Locating communities along this continuum is critical for understanding the fundamental stability of the diversity we observe in natural systems.

We evaluated the collective importance of niche differences by quantifying how rapidly species diversity decreases when the stabilizing effects of niche differences (advantages when rare and disadvantages when common) are eliminated from communities¹¹. The more important niche differences are for coexistence, the more rapidly inferior competitors are excluded when these differences are eliminated. Specifically, we used field-parameterized population models to predict the dynamics of an experimental community of annual plants under the condition that species lack niche differences^{15,16}. We

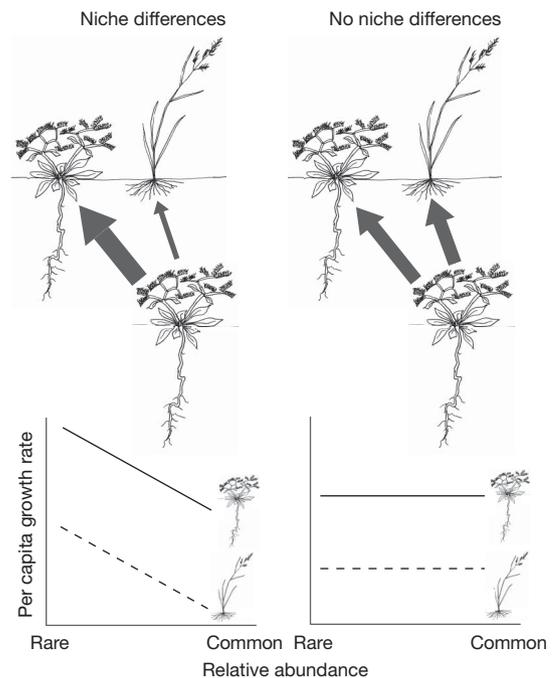


Figure 1 | How niche differences maintain diversity. Niche differences, including variation in rooting depth, cause species to limit individuals of their own species more than they limit competitors. This gives species greater per capita growth rates when they are rare and their competitors are common than when they are common and their competitors are rare. Such relationships stabilize coexistence by hindering competitors that reach high density and threaten other species with exclusion. With no niche differences, species limit themselves and their competitors equally, per capita growth rates do not change with species' relative abundances and variation between species reflects differences in fitness or competitive ability¹⁵. Arrow width represents the degree to which individuals limit one another.

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then compared this null expectation to observed community dynamics in the field to quantify the impact of niche differences on coexistence. Finally, we tested for the demographic signature of these differences, namely greater per capita population growth rates when species are rare than when they are common (Fig. 1).

Our approach focused on experimentally assembled communities of annual plants on serpentine soils in California, USA. In the Mediterranean climate of our field site, annuals germinate in late autumn or early winter, and set seed in spring and summer. The system is well suited to our research aims because individuals are small, average 2,500 plants per square metre and reach high richness at small spatial scales¹⁷. The frequent co-occurrence of ten or more plant species per 0.0625 m² challenges niche-based theories of diversity maintenance. Most importantly, these annuals have relatively short and simple life cycles that can be reasonably described using the population models that form the basis of our approach.

We exploit the fact that niche differences influence coexistence by causing species to limit themselves more than they limit competitors (Fig. 1). We therefore predicted community dynamics without the stabilizing effects of niche differences as follows. We sowed ten replicate communities in the field, each with equal abundances of ten focal species that co-occur widely^{17,18} (Supplementary Table 1). We then parameterized commonly used annual-plant population models^{19–21} (Methods) with demographic rates measured in each community. Finally, we solved for each focal species' growth rate under the condition that communities are saturated with individuals and that species limit themselves and their competitors equally, as occurs without niche differences. Species differences in these growth rates reflect average competitive ability or fitness differences^{11,15} (Fig. 1).

Our theoretical approach predicts that without niche differences, species differ by several orders of magnitude in their per capita growth rates (Fig. 2a), which is sufficient for rapid competitive exclusion (Fig. 2b). For example, with 2007 demographic rates, the population size of *Navarretia atractyloides* was predicted to more than double per year, whereas that of the most inferior competitor species, *Micropus californicus*, was projected to decrease by 98% (Fig. 2a). We found similarly large variation among competitors with 2008 demographic rates, although in this wetter year the highest performing species was *Chorizanthe palmeri* (Fig. 2a). When these growth rates were averaged across years, *Salvia columbariae* had the highest predicted growth rate, 100 times greater than that of the most inferior species (Fig. 2a). Our theoretical approach is validated by our finding that after two generations of interaction in experimental communities, a species' relative abundance was correlated with its average growth rate predicted by the model (Spearman's rank correlation coefficient, 0.71; $P = 0.03$). The model can also approximate the rate of competitive exclusion without niche differences: communities would become 99.9% *Salvia* in less than 20 yr (Fig. 2b). This prediction emerged from simulations beginning with an equal abundance of all competitors. Each year, we randomly assigned 2007 or 2008 demographic rates, calculated the population growth rates (using equation (2) in Methods), and then updated species' relative abundances.

To quantify the influence of niche differences on coexistence in the field, we compared the dynamics of experimental communities stabilized by niche differences with that of communities experiencing the unstabilized population growth rates predicted by our null model. We established 20 replicate communities initially sown with an equal fraction of the ten competitors (by seed mass). Half of these communities were assigned the 'niche-removal treatment'. In each of these ten communities, we quantified model parameters and predicted population growth rates without niche differences (Methods). We then multiplied species' predicted growth rates by their seed numbers at the beginning of the growing season to determine the following year's seed composition (Supplementary Fig. 1). This process was repeated, each year incorporating year-specific demographic rates. By imposing population growth rates that were independent of species' commonness and rarity, this manipulation

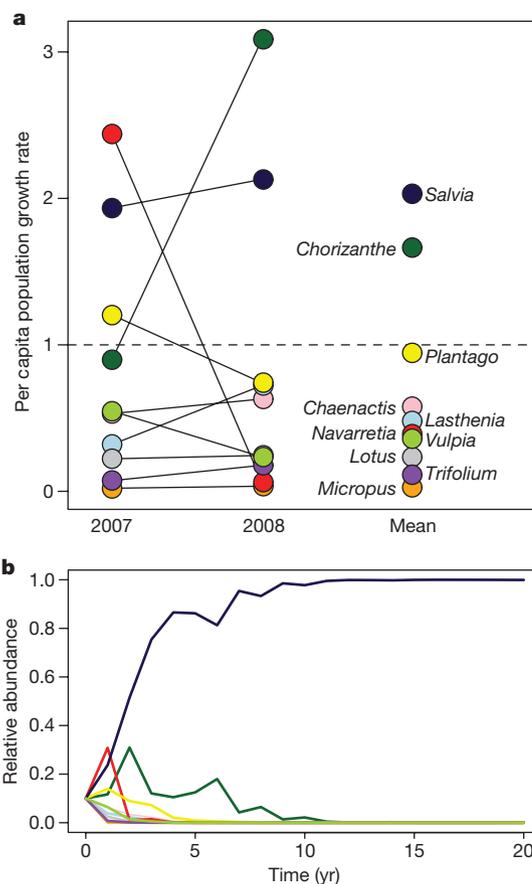


Figure 2 | Lack of competitive equivalence. **a**, Ten species' population growth rates (the number of individuals produced per individual, with species indicated by their genus) without the demographic influence of niche differences, for 2007 and 2008; the two-year geometric mean is also shown ($n = 10$). **b**, Theoretical projection of community dynamics without niche differences (the mean and median times to 99.9% dominance by *Salvia columbariae* are respectively 15.7 and 12 yr, based on 10,000 simulations). Colours correspond to species as in **a**.

removed the stabilizing effects of niche differences but retained species' differences in average competitive ability¹¹. We compared the dynamics with those in the remaining ten communities, used as controls, in which we replicated the seed-handling artefacts of the niche-removal treatment but retained the influence of niche differences (advantages when rare and disadvantages when common). In these communities, each year's seed composition was determined by species' measured seed production and the estimated seed bank carry-over (Supplementary Fig. 1).

After two generations of community change, Shannon diversity was 50% greater in communities stabilized by niche differences than in systems from which niche differences had been removed (treatment: $F_{1,36} = 51.2$, $P < 0.001$; year: $F_{1,36} = 48.6$, $P < 0.001$; treatment \times year: $F_{1,36} = 16.5$, $P < 0.001$ (from analysis of variance); Fig. 3). In both treatments, species composition shifted from an even abundance of all ten species to communities in which *Salvia columbariae* and *Plantago erecta* were more common. However, in the absence of niche differences the most common species, *Salvia columbariae*, became considerably more common, constituting almost 60% of 2008 community seed mass. Conversely, the seven rarest species constituted 35% of the community in the presence of niche differences, but only 8% in their absence. Given that niche differences influence coexistence by favouring species when they drop to low relative abundance^{11,15} (Fig. 1), our results qualitatively match the predictions of ecological theory: in the absence of niche differences, the common species become more common and the rare species

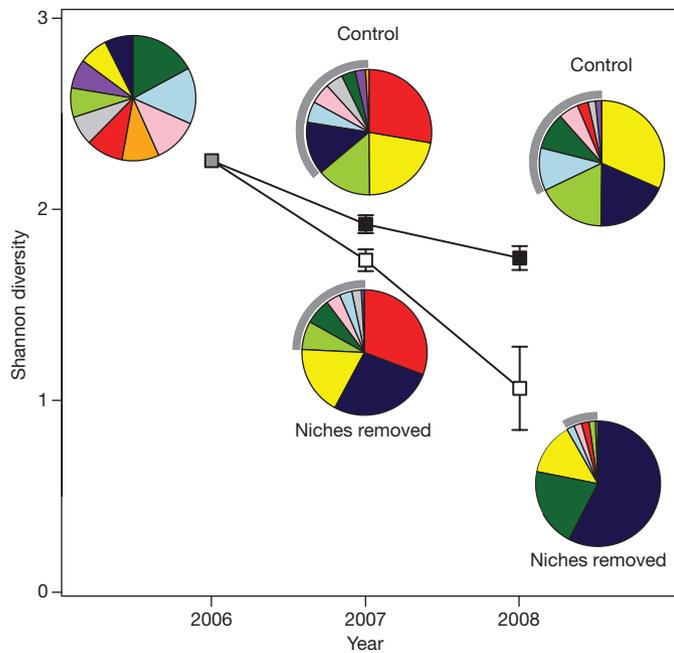


Figure 3 | Niche differences stabilize community dynamics. Two generations (2006–2007, 2007–2008) of change in the diversity and composition of communities stabilized by niche differences, versus those in which the demographic influence of niche differences was removed ($n = 10$). Pie charts show the average proportion of total community seed mass constituted by each focal species in each treatment and year. The grey arcs show the collective abundances of the seven rarest species. Species' relative abundances are not perfectly equal in the initial communities (2006) owing to differences in seed viability. Colours correspond to genus as in Fig. 2a and points show mean \pm s.e.

more rare (Fig. 3). Moreover, the observed changes in diversity in each treatment are too large to be explained by demographic stochasticity alone (Supplementary Fig. 2), as proposed by neutral theory.

Finally, we tested for the demographic signature of niche differences, namely species per capita population growth rates that increase as species become more rare¹¹ (Fig. 1). To accomplish this, we experimentally assembled serpentine annual communities and varied the relative abundance of each focal species from low to high. We then calculated a per capita population growth rate for each species by summing the number of seeds produced at the end of the growing season and the number of those carrying over in the seed bank.

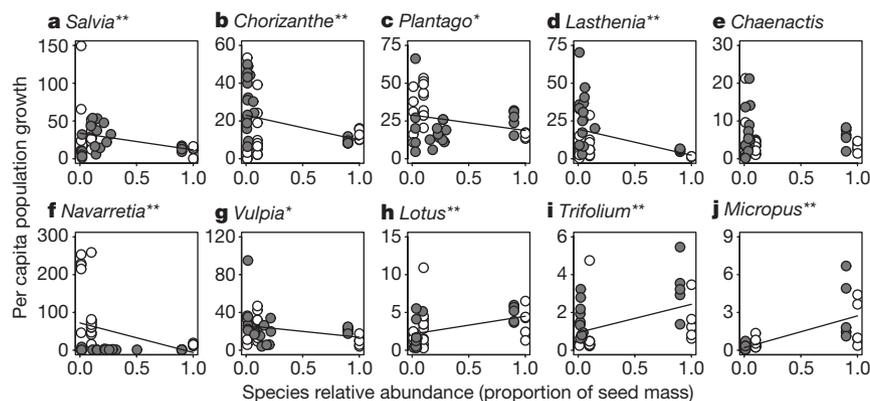


Figure 4 | Demographic effects of niche differences. The influence of a species' relative abundance in a community (commonness and rarity) on its population growth rate (the number of individuals produced per individual) in 2007 (open symbols) and 2008 (filled symbols). Species are ordered (a–j; referred to by their genus) by decreasing relative abundance in

communities in which the influence of niche differences on dynamics has been removed (Fig. 3, 2008 pie chart for niche-removal treatment). The vertical-axis scale differs between plots. * $P < 0.10$, ** $P < 0.05$, from linear regression ($n = 40$).

Consistent with the expected influence of niche differences, the per capita population growth rates of the seven most abundant species decreased as each became increasingly common (although not significantly so for *Chaenactis glabriuscula*, whereas *Plantago erecta* and *Vulpia microstachys* had respective P values of 0.09 and 0.06) (Fig. 4a–g). By contrast, the three rarest species, presumably on their way to exclusion, showed positive relationships (Fig. 4h–j). These probably reflect intraspecific facilitative interactions (*Lotus wrangelianus* and *Trifolium willdenovii* are legumes) or the advantages these species experience when common and surrounded by other conspecific individuals of low competitive ability. More important than the number of species showing greater per capita population growth rates when rare than when common is the identity of those that did. *Salvia columbariae*, which dominated the communities from which niche differences had been removed, had a per capita growth rate that decreased by two-thirds as its relative abundance increased. The growth rate of *Chorizanthe palmeri*, the second most abundant in these communities, declined by one-half. Although the specific niche mechanisms responsible are unknown, *Salvia* can access a deeper resource base than all its competitors (Supplementary Table 1) and *Chorizanthe* grows several months later in the season than all but one of its competitors (Supplementary Table 1). These differences potentially stabilize their dynamics with the remainder of the community and contribute to patterns of relative abundance.

Our results support the hypothesis that niche differences strongly stabilize coexistence. However, our experiments probably miss niche mechanisms operating over larger spatial and longer temporal scales. For example, serpentine annual plants specialize on soil variation that occurs over tens of metres, which is not captured in our square-metre plots¹⁷. Similarly, species performing poorly in our experiment may germinate best under climatic conditions not experienced during the study. Given the spatial and temporal scale of our experiments, the importance of niche differences for coexistence proves unexpectedly strong.

Ecologists studying the maintenance of species diversity have traditionally examined individual coexistence mechanisms, such as resource partitioning^{3,7}, frequency-dependent enemy attack^{13,14} or the storage effect¹⁶. Our approach, by contrast, evaluates the collective importance of multiple niche mechanisms for coexistence. This is a critical distinction, because evidence for the latter uniquely justifies further study of individual niche mechanisms and bears on where natural communities fall along the continuum between classic niche theory and the neutral theory^{10,11}. Most importantly, our findings provide strong empirical support for the critical role niche differences have in stabilizing species diversity, one of the longest unresolved problems in ecology.

METHODS SUMMARY

Field work was conducted in a 500-m² area of serpentine habitat 30 km inland from Santa Barbara, USA. We parameterized the growth rates projected without niche differences (see equation (2) in Methods) in square-metre experimental communities. In autumn 2006, ten plots were sown with 15 g of seed per square metre, evenly divided between species. After recording germination, we thinned the plots to contain ≤10 individuals per species, from which we determined the seed production per germinant in the absence of competition. We measured seed bank survival by estimating seed viability using tetrazolium staining before and after a year of burial in nylon mesh bags. The year-specific growth rates for each species, calculated as described in full Methods, were averaged across plots to produce Fig. 2a.

We used the same plots to project communities forwards in the absence of niche differences (Supplementary Fig. 1). For each replicate, we multiplied each species' seed number at the beginning of the growing season by its theoretically projected growth rate over that season (calculated at season's end for each plot using plot-specific demographic rates). This product determined the seed mass added at the end of the growing season to a new plot adjacent to the previous year's community. Ten control communities experiencing the stabilizing effects of niche differences were of the same size, initial composition and total seed mass as the ten communities receiving treatment. Their reseeded amounts, however, were determined by species' actual seed production and seed bank carry-over. Shannon diversity ($-\sum_i p_i \ln p_i$) was calculated from each species' proportion, p_i , of total seed mass.

We quantified the relationship between species' per capita growth rate and their rarity and commonness in communities with 0.25-m² plots sown with 15 g of seed per square metre. Focal species frequency ranged from 1 to 100% of total seed mass, with replication concentrated at the extremes. The other nine competitors constituted the remaining seed mass in the communities.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Author Contributions J.M.L. and J.H. jointly conducted the project, analysed the data and prepared the manuscript.

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METHODS

Study system. We conducted our study in serpentine habitat at the University of California Sedgwick Reserve in Santa Barbara County, USA. The climate is Mediterranean with cool, wet winters and hot, dry summers. Annual precipitation at the reserve was 19.8 cm in 2006–2007, and 40.1 cm in 2007–2008 (38 cm is the 50-yr average). The site is dominated by annual plants, which germinate in late autumn or early winter and set seed in spring and summer. Our experimental communities were assembled in areas cleared of all vegetation (mostly exotic annual grasses) and subsequently weeded to ensure our direct control over community composition. Weed matting lay between the experimental communities.

All seed for experimental communities was locally collected, primarily from the rockier portions of the habitat where our focal species still dominate. Locating experimental communities in these rockier habitats was not feasible, owing to their limited extent and the pre-existing seed bank of the focal species. Our experiment focused on ten native annual plants (Supplementary Table 1) covering a range of natural abundances.

Theoretical approach. To project species' population growth rates without the demographic influence of niche differences, we first defined a model that could reasonably describe competitor dynamics in our annual communities. We then empirically obtained the demographic rates necessary for calculating population growth rates in the hypothetical case in which species limit themselves and their competitors equally. We began with the following well-studied two-species annual-plant model^{19–21}. Maximum-likelihood analyses showed that, relative to seven other candidate models, this model best described how seed production changed with density in the experimental communities (Supplementary Table 2). The population growth rate for species i competing with species j is modelled as follows:

$$\frac{N_{i,t+1}}{N_{i,t}} = s_i(1 - g_i) + \frac{\lambda_i g_i}{1 + \alpha_{ii} g_i N_{i,t} + \alpha_{ij} g_j N_{j,t}} \quad (1)$$

Here $N_{i,t}$ is the number of seeds of species i at the beginning of the growing season of year t before germination. The first term of the sum describes the carry-over of seeds in the seed bank, a function of g_i , the fraction of germinating seeds, and s_i , the annual survival of ungerminated seed in the soil. The second term describes population growth due to germination and eventual seed production: λ_i is the number of viable seeds produced per germinated individual in the absence of competition, and α_{ij} is a competition coefficient describing the effect of a germinated individual of species j on the seed produced per germinant of species i (these differ from the relative α coefficients of the Lotka–Volterra equations¹⁵). Importantly, the terms involving the competition coefficients are phenomenological and represent all processes by which individuals limit one another, including resource competition and interactions with shared consumers and pathogens¹³. Interchanging all i and j subscripts gives the model for species j .

To approximate the growth rate of species i without the demographic influence of niche differences, we imposed two conditions. First, we forced species to limit themselves and their competitors equally by setting the per capita effects of each species on their own growth to equal their effects on competitors ($\alpha_{ij} = \alpha_{ji}$ and $\alpha_{ii} = \alpha_{jj}$). Second, we assumed that for any density of species i , the abundance of species j is equilibrated²², which in effect fills the community with individuals. Under these two conditions, we obtained the following growth rate (see Supplementary Methods for details and an alternative approach):

$$\frac{N_{i,t+1}}{N_{i,t}} = s_i(1 - g_i) + \lambda_i g_i \left[\frac{1 - s_j(1 - g_j)}{\lambda_j g_j} \right] \quad (2)$$

This per capita growth rate is independent of species' relative abundances, as expected in a fully saturated community (the second condition) without niche differences (Fig. 1). Moreover, in these high-density competitive systems, species' germination, survival and low-density fecundity, all of which we measure in our experimental communities (Methods Summary), determine dominance.

Equation (2) separates the demographic rates for species i from those of its competitor, species j , which are in square brackets (see ref. 23 for interpretation of this term). Because our experimental communities are composed of ten rather than two competitors, we averaged the bracketed term for each of the nine

competitors faced by species i and weighted this average by the competitors' relative abundances (relative abundances were initially equal). For our ten-species community, using equation (2) to project growth rates without niche differences meant that we forced species i to equally limit itself and the nine competitors it faces, and these competitors collectively to limit themselves and species i to the same extent. All predicted growth rates were scaled such that total seed mass in a community did not change between years.

Obtaining parameters for species per capita growth rates without niche differences. We measured the demographic parameters in equation (2) for each of the ten competitors in each growing season (2006–2007, 2007–2008). We measured the germination rate in ten circular plots sown with a mixture of the ten focal species (15 g of seed per square metre). Plots were 0.5 m² in 2006–2007 and were enlarged to 1 m² in 2007–2008 owing to greater seed availability. Germination was recorded by placing coloured plastic toothpicks adjacent to each germinant in multiple visits to each plot over the winter. In 2007–2008, we measured the number of seeds produced per germinant in the absence of competition (λ_i) by thinning the ten plots (after germination) down to no more than ten individuals per species. We harvested all seed from those plants to determine the seed production per germinant, and corrected that number for seed viability. In 2006–2007, we measured λ_i by thinning down five 0.0625-m² plots per species and using the same methods as described for 2007–2008.

We measured seed bank survival by estimating seed viability before and after a year of burial in ten nylon mesh bags per species. We measured seed viability by placing seeds on wetted germination paper in a cold room (15 °C) for five days, and then stored them at room temperature (22 °C) until germination ceased. We determined the viability of ungerminated seeds by immersing them in gibberellic acid and, 24 h later, cutting and staining the seeds with tetrazolium²⁴. Those that stained viable were added to the number of germinants to yield total viability.

Measuring the relationship between population growth and species commonness and rarity. In autumn 2006 and autumn 2007, we established 110 circular plots, each 0.25 m² in area. All plots were sown at a density of 15 g of seed per square metre, and were relocated each year to prevent uncontrolled seed bank carry-over. Ten of the plots were 'natural dynamics plots' sown with an equal proportion of the ten competitors in 2006. In autumn 2007, they were sown at a relative abundance matching that found at the end of the 2006–2007 growing season. The remaining 100 plots were equally divided between low-frequency and high-frequency plots for each species. Specifically, we sowed five low-frequency plots per species in which 1% of the total seed mass belonged to the focal species; the remaining 99% of the seed mass consisted of the nine other competitors, with their relative abundances matching those in the natural dynamics plots. Each focal species was also assigned to five high-frequency plots, in which it was sown at 100% of total seed mass in 2006 and 90% of total seed mass in 2007. Owing to limited seed in the first year of the project (2006), the 1% plots and some of the high-frequency plots were 0.0625 m² in size that year.

We estimated species per capita population growth rate, $N_{i,t+1}/N_{i,t}$, in each community using the following equation:

$$\frac{N_{i,t+1}}{N_{i,t}} = s_i(1 - g_i) + F_i g_i$$

Here s_i and g_i are seed survival and germination, measured as described in the previous section, and F_i is the number of viable seeds produced per germinant, implicitly incorporating all intra- and interspecific interactions that occur over the growing season. We measured F_i for each focal species by harvesting all of its seeds as they ripened in a plot and then dividing the total seed number by the number of germinants. Finally, we corrected these values for seed viability, measured as described in the previous section.

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