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LETTER

Coexistence of perennial plants: an embarrassment of niches

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Abstract

Despite decades of research documenting niche differences between species, we lack a quantitative understanding of their effect on coexistence in natural communities. We perturbed an empirical sagebrush steppe community model to remove the demographic effect of niche differences and quantify their impact on coexistence. With stabilizing mechanisms operating, all species showed positive growth rates when rare, generating stable coexistence. Fluctuation-independent mechanisms contributed more than temporal variability to coexistence and operated more strongly on recruitment than growth or survival. As expected, removal of stabilizing niche differences led to extinction of all inferior competitors. However, complete exclusion required 300–400 years, indicating small fitness differences among species. Our results show an 'excess' of niche differences: stabilizing mechanisms were not only strong enough to maintain diversity but were much stronger than necessary given the small fitness differences. The diversity of this community cannot be understood without consideration of niche differences.

Keywords

Community ecology, competition, demography, extinction, individual-based model, integral projection model, niche, population dynamics.

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INTRODUCTION

Ecologists have been studying how species coexist in competitive communities for almost a century. Motivated by classical theory (Lotka 1925; Volterra 1926), many field studies have identified niche differences based on resource partitioning (Tilman 1982; Silvertown *et al.* 1999; McKane *et al.* 2002), frequency-dependent predation (Janzen 1970; Connell 1971; Harms *et al.* 2000) and species-specific responses to spatial (Whittaker *et al.* 1973; Sears & Chesson 2007) and temporal (Warner & Chesson 1985; Adler *et al.* 2006; Angert *et al.* 2009; Clark 2010) heterogeneity in the environment. These differences stabilize coexistence by causing species to limit themselves more than they limit their competitors (Chesson 2000).

Since the 1960s, however, ecologists have repeatedly questioned the potential for niche theory to explain how hundreds of species can coexist on a handful of limiting resources (Hutchinson 1959, 1961; Hubbell & Foster 1986; Silvertown & Law 1987; Huston 1994). Recently, the neutral theory of biodiversity (Bell 2001; Hubbell 2001) restated these questions in the form of an alternative hypothesis: Similarity in species' competitive abilities, rather than niche differences, might explain the diversity of natural communities. The debate over neutral theory has shown that current empirical examples of niche differences do not prove that niches are essential for high diversity. Such proof requires quantifying the stabilizing effect of niche differences in relation to the competitive disadvantages that lead to exclusion (Adler *et al.* 2007).

An ideal way to quantify the effect of niches on diversity would be to remove stabilizing mechanisms from a system and then observe changes in composition and richness. Of course, removing stabilizing mechanisms poses an empirical challenge. In controlled settings, homogenizing environmental conditions or forcing species to use the same resources may be possible (e.g. Dornbush & Wilsey 2010). For uncontrolled systems, the closest analogue is fitting population models to field data and then removing the demographic effect of stabilizing niche differences (Adler *et al.* 2006; Levine & HilleRisLambers 2009). This demographic effect appears as negative frequency dependence in per capita growth rates: Stabilizing mechanisms cause species to limit themselves more than they limit others, so each species grows faster when it is rare than when it is common. We can remove this effect by altering model parameters so that each species has the same effect on its competitors that it has on itself.

Once stabilizing mechanisms are removed, the next challenge is quantifying the consequences for coexistence. The classic approach focuses on invasion growth rates, defined as the average per capita growth rate of a species at extremely low abundance in the presence of competitors at their equilibrium abundances (Chesson & Ellner 1989; Ellner 1989). A species with a high invasion growth rate recovers quickly from low abundance and is buffered against competitive exclusion. Thus, one measure of the strength of stabilizing niche mechanisms is how much they contribute to invasion growth rates. Removal of stabilizing mechanisms necessarily decreases invasion growth rates, but the magnitude of the decline depends on the strength of the mechanism. If all stabilizing niche differences are removed, every species except one, which we define as the dominant competitor, must have a negative invasion growth rate. The magnitude of these negative invasion growth rates provides an approximation of the competitive disadvantages that stabilizing mechanisms must overcome to allow coexistence (Chesson 2000). Following Chesson (2000), we refer to these disadvantages as 'fitness differences'.

Analyses of invasion growth rates can also address unresolved questions about the sources of stabilization. First, what is the relative importance of fluctuation-dependent and fluctuation-independent mechanisms for maintaining diversity (Chesson 2000, 2008)? Although evidence has begun to accumulate for mechanisms dependent on environmental fluctuations (Caceres 1997; Descamps-Julien & Gonzalez 2005; Adler *et al.* 2006; Angert *et al.* 2009), no empirical studies have compared the relative contributions of fluctuation-dependent and -independent mechanisms (see Snyder *et al.* 2005 for a theoretical treatment). Second, which vital rates contribute most to stabilization? In theory, distinct stabilizing mechanisms may operate within each life stage (Moll & Brown 2008), but this possibility has not been investigated empirically.

An alternative way to quantify the importance of niches is by measuring time to extinction. Without stabilizing mechanisms, competitive exclusion will occur slowly if fitness differences among species are small, but rapidly if fitness differences are large. The extinction time approach is especially relevant for finite populations influenced by demographic stochasticity, which is ignored by analyses of invasion growth rates (Adler & Drake 2008).

Our objectives were to (1) quantify the stabilizing effect of niche differences in a sagebrush steppe community, (2) compare the relative strength of stabilizing mechanisms and fitness differences and (3) partition the stabilizing effect into contributions from temporal fluctuations and individual life stages (recruitment, growth and survival). To achieve these objectives, we analysed a spatially explicit individual-based model (IBM) and a spatially implicit, integral projection model (IPM) fit to 22 years of demographic data. After showing that the models reproduce historical abundances, size distributions and spatial patterns, we perturbed model parameters to simulate community dynamics in the absence of stabilizing mechanisms. We used the IBM to study extinction times and the IPM to estimate invasion growth rates and species' equilibrium abundances without the complicating influence of demographic stochasticity.

MATERIALS AND METHODS

Study site and data set description

The U.S. Sheep Experiment Station (USSES) is located 9.6 km north of Dubois, Idaho (44.2°N, 112.1°W), 1500 m above sea level. During the period of data collection (1926–1957), mean annual precipitation was 270 mm and mean temperatures ranged from −8 °C (January) to 21 °C (July). The vegetation is dominated by the shrub, *Artemisia tripartita*, and the C3 perennial bunchgrasses *Pseudoroegneria spicata*, *Hesperostipa comata* and *Poa secunda*. These four species, the focus of our models, accounted for over 70% of basal cover (grasses) and 60% of canopy cover (shrubs and forbs).

Scientists at the USSES established twenty-six 1 m^2 quadrats between 1926 and 1932. Eighteen quadrats were distributed among four ungrazed exclosures, and eight were distributed in two paddocks grazed at medium intensity spring through autumn. All quadrats were located on similar topography and soils. In most years until 1957, all individual plants in each quadrat were mapped using a pantograph (Blaisdell 1958). Digitized versions of the original maps are available online (http://www.knb.ecoinformatics.org). Our models are based on data from 22 year-to-year transitions between 1926 and 1957. For the first two transitions only four quadrats were observed, while at least 16 quadrats were observed for all subsequent transitions.

Model fitting

We used the long-term data to parameterize a spatially explicit IBM and a spatially implicit IPM. Both models describe how recruitment, growth and survival depend on interannual variability and interspecific interactions. Here we describe the basic steps in building these models; a complete description is available in Appendix S1.

The first step was to identify the individuals in each quadrat. Our approach tracks genets, which may be composed of multiple polygons, as they fragment and/or coalesce. Each mapped polygon is classified as a surviving genet or a new recruit based on its spatial location relative to genets present in previous years (Lauenroth & Adler 2008). Our model represents individual genets as circles with two attributes, area (basal cover for grass, canopy cover for the shrub) and a spatial location (Figure S1).

The next step is fitting statistical models for survival, growth and recruitment. We model the survival probability of each genet as a function of genet size, temporal variation among years, permanent spatial variation among groups of quadrats, and local neighbourhood crowding from both conspecific and heterospecific genets. The crowding experienced by the focal genet depends on the size of and distance to all neighbouring genets. We use a Gaussian function to describe how neighbour influence declines with distance. The spatial scale over which individuals influence competitors varies among species, but for each species the same scale is used for growth and survival. Fitted regression coefficients determine how crowding by each species influences the focal individual's survival probability. We can present these regression coefficients as a matrix of interaction coefficients, with each j,k entry giving the effect of crowding by species k on the survival probability of a genet of species j. Our model for growth, the change in size of a genet from one year to the next, depends on the same factors as the survival model, with crowding effects described by the coefficients of a growth interaction matrix.

We fit the survival and growth regressions using generalized linear mixed effects models, treating genet size and neighbourhood crowding as fixed effects, and spatial and temporal (interannual) variation as random effects. The fitted models showed that the survival probability of large plants approached 1, but small individuals had very low survival rates (Figure S2), whereas relative growth was higher for small genets than large genets (Figure S3).

While the survival and growth regressions operate at the level of individual genets, we model recruitment at the quadrat scale. We assume that the number of recruits produced in each year in each quadrat follows a negative binomial distribution with a mean that depends on the cover of the 'parent' species, temporal variation among years, permanent spatial variation among groups of quadrats, and intra- and interspecific interactions dependent on each species' total cover in the quadrat. We fit this model using a hierarchical Bayesian approach, treating spatial and temporal variation as random effects. For all four species, recruitment was low in most years and quadrats, with occasional years of high recruitment (Figure S4). Parameters for all the vital rate regressions are given in Table S1.

Building the dynamic models

Building the IBM is straightforward. We initialize the model by assigning plants spatial coordinates, sizes and species identities. At each time step in the simulation, we use the survival regression to determine whether each genet lives or dies, the growth regression to determine changes in size of surviving genets, and the recruitment regression to calculate the production of new individuals, which are distributed randomly in space.

To model temporal environmental variation, at each time step we randomly select a set of estimated survival, growth and recruitment parameters specific to one of the 22 observed years; these values were estimated year-specific random effects from the fitted mixed model for that vital rate. This approach, an analogue of the 'matrix-selection' technique used in stochastic simulations of structured population models, preserves observed covariances in demographic parameters within and among species. Based on little evidence of temporal structure in the time-varying demographic rates, our simulations ignore temporal autocorrelation. Our simulations also ignore permanent spatial variation among quadrats, and thus represent dynamics on an idealized, 'average' site.

The vital rate regressions are also the building blocks of the IPM (Easterling *et al.* 2000; Ellner & Rees 2006, 2007). However, because the IPM is spatially implicit, we cannot calculate a neighbourhood crowding index for each individual. Instead, we used a mean-field approximation that captures the essential features of the observed spatial pattern. In the observed data and in IBM simulations, pairs of heterospecific genets are randomly distributed in space, but conspecific pairs show non-random, size-dependent patterns: while very small genets are randomly distributed, large genets are overdispersed and do not overlap in area. Based on these patterns, our approximation for local crowding uses a 'no-overlap' rule for conspecifics, but assumes random distances between heterospecifics. Temporal environmental variation is handled exactly as in the IBM.

Removing stabilizing mechanisms

Our method for removing stabilizing mechanisms follows the coexistence framework of Chesson (2000) in which species' invasion growth rates are decomposed into scaled sums of fitness differences and stabilizing niche differences. Stabilizing niche differences include all processes that cause species to limit conspecific more than heterospecific individuals, creating an advantage when rare. Fitness differences, by contrast, are those differences in intrinsic demographic rates that favour one species over another and lead to competitive exclusion. Once niche differences are removed, as we describe next, fitness differences (and the sensitivity of population growth to these differences) determine the rate of competitive exclusion.

The fitted IBM and IPM, which we refer to as the 'all-niches' models, contain both fluctuation-dependent and fluctuation-independent stabilizing mechanisms. We removed the fluctuation-dependent mechanisms by running simulations in a constant environment, implemented by setting all random year effects to zero. This 'constant' environment model eliminates the effect of fluctuations *per se*, and the effect of nonlinear averaging (Rees *et al.* 2004).

Fluctuation-independent stabilizing mechanisms are produced by differences between the intra- and interspecific coefficients in the recruitment, growth and survival interaction matrices (intraspecific effects are the diagonal entries). When the intraspecific effects limit vital rates more than the interspecific effects do, each species has an advantage when it is rare, because it faces a suite of competitors that have a relatively weak limiting effect on its performance. Thus, to remove stabilizing mechanisms, we removed the difference between intra- and interspecific effects in the fitted interaction matrices by setting each species' effects on all other species equal to its effect on itself, i.e. we set $c_{jk} = c_{kk}$ for all j, where c_{jk} is the effect of species k on species j.

Because intraspecific effects (the c_{kk}s) are unchanged, the performance of each species in isolation is not affected. Our alteration of the interaction coefficients also retains fitness differences between species, because it does not alter demographic rates in the absence of competition. We did not need to alter the spatial scale of competitive effects, because model fitting had shown that each species has a characteristic scale of effect on all other species (see Table S2).

To evaluate the contribution of each vital rate to fluctuation-independent stabilizing mechanisms, we began with the 'constant' environment model. We then removed stabilizing mechanisms from the recruitment function alone, producing a 'no-niche-R' model. We also built 'no-niche-G' and 'no-niche-S' models, in which we removed stabilizing mechanisms from growth or survival respectively. Finally, we removed stabilizing mechanisms from all three vital rates at once, the 'no-niche-RGS' model. We used the invasion growth rates estimated by this last model to approximate fitness differences (Chesson 2000).

Removing niches from the growth and/or survival process altered emergent spatial patterns in IBM simulations, resulting in less overlap between large heterospecific pairs than in the fitted model. To account for these regular spatial patterns in the IPM, we applied the 'no-overlap' local crowding approximation to all species pairs, not just conspecifics, in IPM simulations of the no-niche-G, no-niche-S and no-niche-RGS models. This perturbation of conspecific and heterospecific spatial patterns corresponds to our perturbation of intra- and interspecific interaction coefficients.

Estimating invasion growth rates, equilibrium abundances and extinction time

To simulate species' invasion growth rates with the IPM, which removes the complications of demographic stochasticity, we first initialized the resident species at arbitrarily low abundances and allowed them to equilibrate in the absence of the invader. We then introduced and maintained the invader at such low abundance (10^{-6}) that it would not influence the growth of itself or the residents. At each time step, we calculated the per capita growth rate as $\log(C_{t+1}/C_t)$ where C is the area occupied by the focal species. After performing this calculation, we returned the focal species' cover to 10^{-6} while allowing its size distribution to evolve. After a burn-in period of 500–2000 years (depending on the model), we simulated 1000 subsequent years. The species' mean per capita growth rate when rare over this 1000 year period estimates its long-term invasion growth rate. We repeated these simulations for the all-niches, constant, no-niche-R, no-niche-G and no-niche-RGS versions of the IPM.

We also estimated invasion growth rates using the IBM to check that our results were not sensitive to differences between the models. We initialized the focal species at zero and the residents at 1% cover on a 3 × 3 m landscape. After running the model for 25 years, we introduced the focal species but set all its competitive effects to zero, meaning that it responded to the residents but did not affect them or itself. We allowed an additional 25 years for resident and invader abundances and spatial patterns to equilibrate, and then averaged invader growth rates over the subsequent 50 years. We performed 50 replicate runs for each species.

We demonstrated the link between species' invasion growth rates and their equilibrium cover by simulating species' long-run abundances. For the IPM models, we initialized each species at very low density and uniform size distribution and ran the model until it reached a stochastic equilibrium. For each version of the IBM we ran 50 simulations of 100 years each, initializing the model with *A. tripartita* at 3% cover (to reduce stochastic extinctions in the first simulated time steps) and the three grasses at 1% cover. Estimated mean cover was the average of the final 50 years of each run pooled across the 50 replicate runs.

We used the IBM, which includes the effect of demographic stochasticity, to compare extinction times between the all-niches and no-niche-RGS models. We initialized as for the equilibrium abundance runs, but ran each simulation until all but one species had gone extinct, or a maximum of 1000 years. We averaged the time to the first, second and third extinction event and calculated the proportion of runs that each species was the first, second or third species to go extinct. To aid interpretation of the extinction times, we also calculated a proxy for generation time based on mean lifespans of each species in simulations of the fitted IBM model. When all individuals were included in the calculation, the distribution of lifespans was highly right-skewed and for all four species the mean lifespan was less than 3 years. Considering only individuals that lived longer than 1 year, mean lifespans ranged from 7.5 years for *Poa secunda* to 9 years for *H. comata*.

Increasing fitness differences

After exploring the consequences of removing niche differences, we determined how much fitness differences could be increased before competitive exclusion occurred. We increased fitness differences by adding a constant to the intercepts of the survival and recruitment regressions for the dominant competitor, *H. comata*, and subtracting the same constant from the intercepts of all three inferior species. Perturbing the intercepts in this way increased differences in demographic performance without altering stabilizing mechanisms. To minimize changes in size distributions, we did not perturb the growth regression. After perturbing the intercepts by constants of 0.1, 0.25, 0.5 and 0.75, we estimated invasion growth rates using the IPM all-niches model, and we estimated fitness differences using the IPM no-niches-RGS model.

RESULTS

Model fit

The IBM successfully reproduced historical dynamics of mean cover and density (Fig. 1), as well as realistic, bimodal size distributions (Figure S5). IBM simulations also replicated the essential features of the observed spatial patterns, with regular (overdispersed) spacing among large conspecific genets, but random distributions of small genets and all heterospecific genets (Fig. 2 and Figure S6). This is an important test of the model, because spatial patterns were not used in fitting, meaning that realistic, quadrat-scale spatial patterns emerged from the individual-level processes that operate in the IBM. To incorporate the regular pattern of large conspecifics into the spatially implicit IPM, we used a mean-field approximation that included a conspecific 'no-overlap' rule. Given that the IBM and IPM are based on identical vital rate functions, our treatment of local crowding is the primary difference between the two models. The close agreement in their estimates of invasion growth rates and equilibrium abundances (Fig. 3 and Figure S7) indicates that our mean-field approximation was adequate.

Stabilizing mechanisms and fitness differences

For survival, growth and recruitment, species' per capita intraspecific effects were more negative than their interspecific effects (Table 1). The contrast between intra- vs. interspecific interaction coefficients accounted for more than 50% of the variation in the coefficients for all three vital rates (Figure S8). Consistent with the differences between intra- and interspecific effects, all four species had positive invasion growth rates in the 'all-niches' model (Fig. 3).

Invasion growth rates decreased as we progressively removed stabilizing mechanisms from the IPM, first by excluding temporal fluctuations and then by setting intraspecific effects equal to interspecific effects in recruitment, growth or survival or all three together (Fig. 3). Removal of fluctuation-dependent stabilizing mechanisms led to slight reductions in the invasion growth rates of the three grasses but caused *A. tripartita*'s invasion growth rate to fall below zero. Removal of stabilizing mechanisms from recruitment led to larger reductions in invasion exponents than removal of stabilization from growth or survival. As expected, removal of stabilization from all vital rates led to negative invasion growth rates for all species but one. IPM simulations of pairs of species also implied complete competitive exclusion in the absence of stabilizing mechanisms. A clear competitive hierarchy emerged, with *H. comata* the superior competitor followed by *Poa secunda*, *P. spicata* and finally *A. tripartita*. However, deviations of invasion growth rates from zero were small for the three grasses

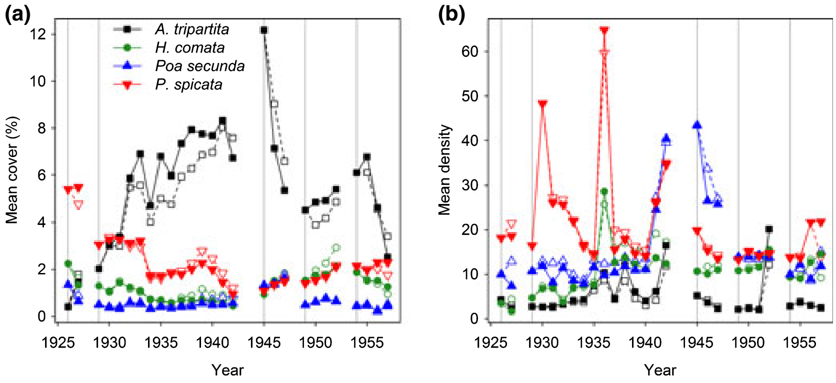

Figure 1 Observed and predicted abundance. Solid symbols show observed means for cover (a) and density (b) and open symbols show simulated means from the individual-based model. For each quadrat, the model was initialized with the observed genet sizes and spatial coordinates at dates indicated by the vertical grey lines and then projected forward until the next data gap. Shown are means across 50 simulations runs for each quadrat.

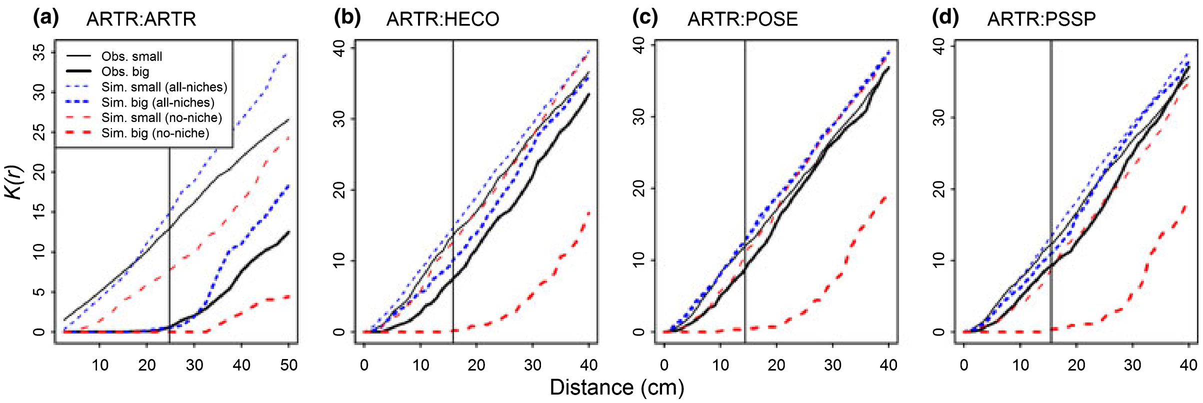

Figure 2 Observed and simulated intra- and interspecific spatial associations for *Artemisia tripartita* (similar results for the other species are shown in Figure S6). *K*(*r*) is the cumulative density of individuals of a neighbouring species as a function of distance to individuals of *A. tripartita*. It is scaled so that the 1 : 1 line represents a random distribution, values below the 1 : 1 line represent regular patterns and values above the 1 : 1 line show aggregated patterns. Solid lines and dashed lines indicate comparisons for large (upper 33% of size distribution) and small genets (lower 33%) respectively. The observed *K*(*r*) values follow the 1 : 1 line for both large and small interspecific associations (b–d), indicating a random spatial pattern. In contrast, for large intraspecific pairs (a), *K*(*r*) does not increase until distances larger than the mean diameter of large genets (the vertical line), indicating that large conspecific genets rarely overlap. Patterns simulated by the 'all-niches' IBM are similar. However, when we removed niche differences in simulations of the 'no-niche' IBM, pairs of large interspecific genets no longer overlapped (b–d). Species codes are given in the footnote to Table 1.

(averaging 0.0068), indicating small fitness differences. Results from IBM simulations were similar (Figure S7).

Changes in equilibrium abundances simulated by the IPM illustrate the consequences of altered invasion growth rates following removal of stabilizing mechanisms (Fig. 3 and Figure S7). Consistent with the analysis of invasion growth rates, removing temporal variability in vital rates had little effect on the abundance of the grasses but reduced *A. tripartita* to zero. When we modelled a constant environment using parameter values for one individual year, rather than long-term average parameters, we found that different years pushed different species to extinction, though in more than half of the years at least three species persisted (Figure S9). Removing fluctuation-independent stabilizing mechanisms from each of the vital rates caused similar reductions in the equilibrium cover of the grass species (Fig. 3). Removing stabilizing mechanisms from survival and or growth also altered spatial patterns, resulting in regular patterns among large, heterospecific genets (Fig. 2 and Figure S6). With stabilizing mechanisms removed from all three vital rates, the abundances of all species except *H. comata* approached zero in the deterministic IPM. The IPM reached equilibria quickly in most cases, but with removal of all niche differences thousands of years were required for *H. comata* to dominate (Figure S10).

In stochastic simulations of extinction times using the fitted IBM on a 3 × 3 m landscape, *A. tripartita* was always the first species to go extinct, at an average time of 243 simulated years (Fig. 4). In 50 simulations, no other species went extinct in 1000 years. In simulations of the no-niche-RGS model, *A. tripartita* was again the first species to go extinct in every case, but the mean extinction time was shorter, averaging 42 simulated years. The second and third extinctions occurred at *c.* 300 and 400 years, and these times only increased slightly in simulations run on a 4 × 4 m landscape. *Hesperostipa comata* was the dominant in every run (Fig. 4).

For a complementary measure of the strength of stabilizing mechanisms relative to fitness differences, we re-estimated the invasion growth rates of the inferior species after perturbing demographic rates to exacerbate their intrinsic disadvantages. Stabilizing mechanisms were strong enough that the disadvantage of *A. tripartita* had to be increased by 50% before it was excluded from the community (i.e. its invasion growth rate became negative) (Fig. 5). Competitive exclusion of *P. spicata* and *Poa secunda* required more than two- and 20-fold increases in their demographic disadvantages respectively.

DISCUSSION

The importance of stabilizing mechanisms for species diversity

Our first two objectives were to quantify the stabilizing effect of niche differences and to compare this effect to the size of fitness differences. We found an excess of niche differences: Stabilizing mechanisms were not only strong enough to maintain diversity in this system but were much larger than required to overcome the fitness differences.

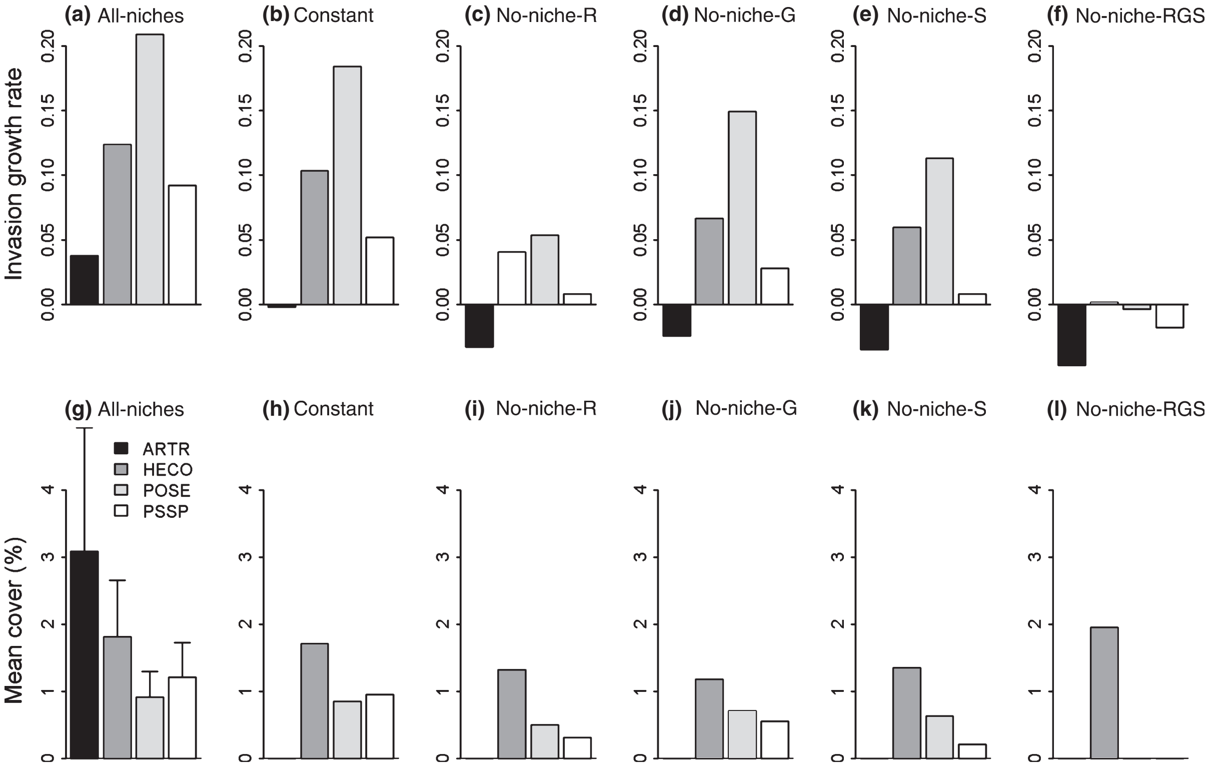

Figure 3 Invasion growth rates and average cover simulated by the IPM models. We simulated the IPM model with observed parameters (all-niches), with a constant environment (constant), a constant environment with stabilizing mechanisms removed from recruitment (no-niche-R), growth (no-niche-G), survival (no-niche-S) or all three vital rates (no-niche-RGS). We ran each simulation until reaching equilibrium. Error bars in panel (g) show 1 standard deviation and reflect temporal variability in demographic rates. Species codes are given in the footnote to Table 1.

Evidence for strong stabilization comes from the positive invasion growth rates of all four species, which approached 0.05 for *A. tripartita* and were near or above 0.10 for the three grasses (Fig. 3). These growth rates correspond to population doubling times for the grasses (when rare) of less than 7 years. The positive invasion growth rates reflect stronger limitation by intraspecific than interspecific competition, the signature of niche differentiation. Even in stochastic simulations of the IBM on a small patch (3 × 3 m), these stabilizing mechanisms were strong enough to produce essentially indefinite coexistence among the three grasses. Although *A. tripartita* did go extinct after *c.* 240 simulated years, the cause was demographic stochasticity amplified by the limited spatial extent of the simulation. We know that competitive pressure did not cause these extinctions because *A. tripartita* had positive invasion growth rates in both the IPM and IBM. Demographic stochasticity had less influence on the grass species because their densities were higher, roughly 125–225 genets per 3 × 3 m patch, compared to an average of only 18 individuals for *A. tripartita.*

Removal of all stabilizing mechanisms caused major qualitative changes in community dynamics. The invasion growth rates of all species except *H. comata* fell from positive to negative values. As a result, extinction times for *A. tripartita* decreased to less than 50 years and the grasses no longer coexisted in stochastic simulations. Instead, *H. comata* excluded all other species within 400 years.

The shift from indefinite coexistence to competitive exclusion with the removal of stabilizing mechanisms clearly demonstrates that niches are essential for stable coexistence. However, our results also indicate relatively small fitness differences between species. In the absence of stabilizing mechanisms, the grass species all had invasion growth rates close to zero, within 0.02 in the IPM, meaning a population decline rate of under 2% per year. Because of these small fitness differences, competitive exclusion in the IBM occurred on the order of centuries even in the absence of stabilizing mechanisms. These times to extinction are long relative to the generation times of the perennial study species, which were less than 10 years. In contrast, Levine & HilleRisLambers (2009) projected competitive exclusion within 15 years in the absence of niche differences in an experimental system of annual plants. Consistent with our interpretation of strong stabilizing effects acting on small fitness differences, we

Table 1 Matrices of interaction coefficients for the vital rate regressions

	ARTR	HECO	POSE	PSSP
Recruitment				
ARTR	**−0.0731***	−0.2425*	−0.2911	−0.0360
HECO	0.0224	**−0.5471***	−0.2035	−0.0541
POSE	0.0041	−0.1155*	**−1.1114***	−0.0032
PSSP	0.0389*	−0.1330*	−0.1576	**−0.6007***
Growth				
ARTR	**−0.0022**	0.0264†	0.0148	0.0037
HECO	−0.0002†	**−0.0960***	−0.0060	−0.0026
POSE	0.0000	0.0118	**−0.1095***	−0.0052*
PSSP	−0.0002*	−0.0039	−0.0016	**−0.0452***
Survival				
ARTR	**−0.0233***	−0.0180	0.0217	0.0162
HECO	0.0003	**−0.9466***	0.0197	0.0064
POSE	0.0003	−0.0193	**−1.0280***	0.0121*
PSSP	0.0019*	−0.0016	0.0216	**−0.1668***

Species effects vary by column and responses vary by rows (e.g. $c[i,j]$ is the effect of species j on species i). Intraspecific effects are shown in bold. These values correspond to the ωs of eqns 2 and 7 in the Supporting Information. Species codes: ARTR, *Artemisia tripartita*; HECO, *Hesperostipa comata*; POSE, *Poa secunda*; PSSP, *Pseudoroegneria spicata*.

*Coefficients significantly different from zero at the 95% level, based on confidence intervals for recruitment, and *t*-tests for survival and growth.

†Coefficients significantly different from zero at the 90% level, based on confidence intervals for recruitment, and *t*-tests for survival and growth.

had to increase fitness disadvantages by 50–2000% to cause competitive exclusion of the inferior species in the presence of niche differences (Fig. 5).

Identifying the important stabilizing mechanisms

Traditional field studies of coexistence often focus on differences in the way species use resources (e.g. McKane *et al.* 2002) without quantifying the demographic consequences of those species differences. We took the opposite approach, focusing on the demographic effects of species differences as a first step in identifying the most important coexistence mechanisms. Our results provide three important clues to guide future research on specific mechanisms.

First, fluctuation-dependent mechanisms are less important than fluctuation-independent mechanisms in this community. Although our models predict the loss of *A. tripartita* with the removal of temporal variability in demographic rates, the three grasses experienced only small decreases in invasion growth rates, which remained positive even in a constant environment. These results are qualitatively consistent with a previous analysis of this data set that used a more phenomenological modelling approach (Adler *et al.* 2009). The weak effects of interannual variability in precipitation and temperature are surprising; in such a water-limited system it seems natural to expect that temporal partitioning of soil moisture should be important for coexistence.

Second, fluctuation-independent mechanisms, which might include spatial partitioning of soil moisture (Walter 1971), operate throughout the life cycle but appear to be especially powerful at the recruitment stage. Invasion growth rates of all species decreased substantially with the removal of niche differences from survival, growth, or recruitment. Furthermore, *H. comata* did not exclude all competitors in the IPM unless we removed stabilizing mechanisms from all three vital rates. However, removing

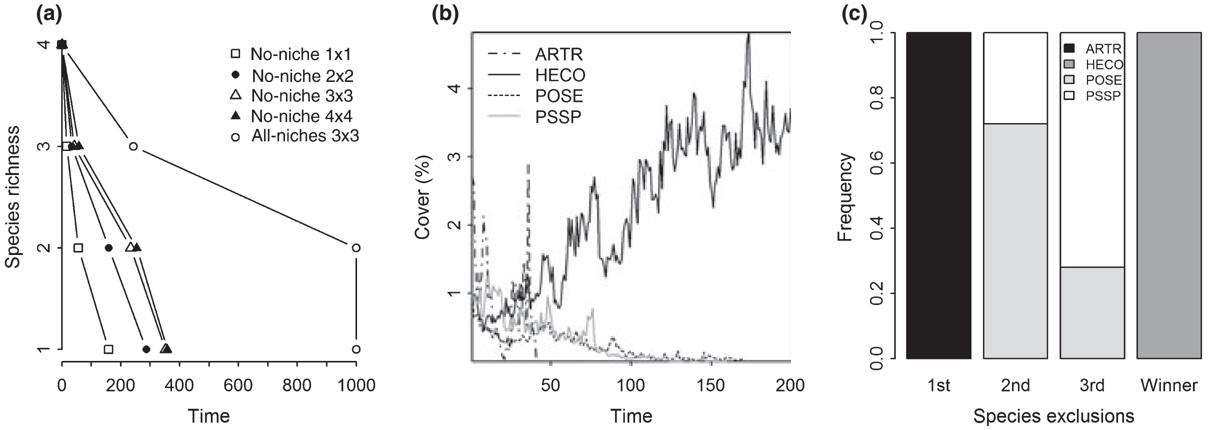

Figure 4 The influence of stabilizing mechanisms on extinction times. (a) Mean time of species losses in IBM simulations of the fitted ('all-niches') and niche removal ('no-niche-RGS') models on virtual landscapes of different sizes (in m). Means are from 50 simulations run for a maximum of 1000 time steps. (b) An example of one simulation of the no-niche-RGS model. (c) The frequency of each species being excluded first, second, third or winning in simulations of the no-niche-RGS model on the 3 × 3 m landscape.

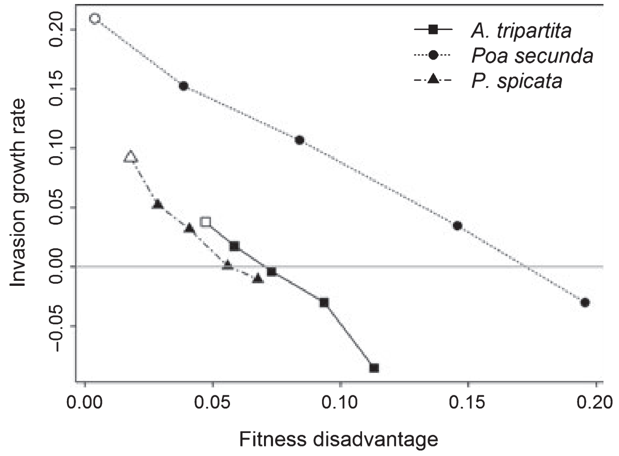

Figure 5 Invasion growth rates after perturbations of fitness differences. We increased fitness differences between the dominant, *Hesperostipa comata,* and the three inferior competitors by perturbing the intercepts of the recruitment and survival regressions. Fitness disadvantage (*x*-axis) was estimated by simulating the IPM no-niches-RGS model (e.g. Fig. 3f). Invasion growth rates (*y*-axis) were estimated by simulating the IPM all-niches model (e.g. Fig. 3a). The open symbols are the values estimated using the fitted parameters; the solid symbols represent values using perturbed parameters.

stabilizing mechanisms from recruitment led to a larger decrease in invasion growth rates than removing stabilizing mechanisms from growth or survival. While analyses of population models for long-lived species emphasize the importance of survival (Pfister 1998; Franco & Silvertown 2004), community-level studies often highlight the role of recruitment. For example, adult effects on recruitment influence species composition in forests (Grubb 1977; Pacala *et al.* 1996) and some fluctuation-independent coexistence mechanisms, such as Janzen–Connell effects (Janzen 1970; Connell 1971), focus on the recruitment stage in particular.

Third, we found strong links between intra- and interspecific competition and the spatial patterning of individuals. In the IBM, strong competition among conspecific individuals at the growth and survival stage led to the emergence of realistic, regular spatial patterns for large genets. When we removed niche differences, the regular pattern extended to heterospecific pairs as well. These emergent spatial patterns had strong effects on community dynamics, as shown by the failure of the IPM to generate realistic abundances unless we incorporated a spatially implicit approximation of the observed spatial pattern.

An important next step is to test the generality of our results in more diverse communities. We plan to ask how stabilizing mechanisms and fitness differences contribute to the coexistence of the many rare species in the sagebrush steppe. The main challenge in answering this question is fitting all the interaction coefficients, the number of which increases as the square of species number. However, the number of parameters could be greatly reduced by fitting just one conspecific and one heterospecific coefficient for each species (e.g. Levine & HilleRisLambers 2009) or by assuming that rare species are limited primarily by competition with dominants, eliminating the need to quantify interactions among the rare species. Another alternative would use functional traits to predict the entire matrix of interaction coefficients (Freckleton & Watkinson 2001).

CONCLUSIONS

Stabilizing mechanisms were much stronger than required to overcome the fitness disadvantages of the inferior competitors, demonstrating that coexistence in this natural system is stable and that its biodiversity cannot be understood without consideration of the niche differences that neutral theory ignores. Determining whether this result is general or unique to our study system will require analyses of additional species and communities. While these demographic studies will complement traditional research on competition for particular resources, ultimately we must link the demographic and functional approaches to coexistence.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Figures S1 An example of mapped and modeled polygons.
Figure S2 Observed and predicted genet survival.
Figure S3 Observed and predicted genet growth.
Figure S4 Observed and predicted recruitment.
Figure S5 Observed and simulated genet size distributions.
Figure S6 Observed and simulated spatial patterns.
Figure S7 Invasion growth rates and species abundances simulated by the individual based model.
Figure S8 Analysis of variance of the recruitment, growth, and survival interaction coefficients.
Figure S9 Species persistence in a constant environment.
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Table S2 The spatial scale of species interactions.
Appendix S1 Detailed methodology.

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