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# The Contrasting Roles of Growth Traits and Architectural Traits in Diversity Maintenance in Clonal Plant Communities

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**ABSTRACT:** Plant communities often exhibit high diversity, even though pairwise experiments usually result in competitive hierarchies that should result in competitive exclusion. Such experiments, however, do not typically allow expression of spatial traits, despite theoretical studies showing the potential importance of spatial mechanisms of diversity maintenance. Here we ask whether, in a clonal plant model system, spatial trait variation is more likely than growth trait variation to maintain diversity. We used a field-calibrated, spatially explicit model to simulate communities comprising sets of four simulated species differing in only one of a suite of architectural or growth traits at a time, examining their dynamics and long-term diversity. To compare trait manipulation effects across traits measured in different units, we scaled traits to have identical effects on initial productivity. We found that in communities of species differing only in an architectural trait, all species usually persist, whereas communities of species differing only in a growth trait experienced rapid competitive exclusion. To examine the roles of equalizing and stabilizing mechanisms in maintaining diversity, we conducted reciprocal invasion experiments for species pairs differing only in single traits. The results suggest that stabilizing mechanisms cannot account for the observed long-term co-occurrence. Strong positive correlations between diversity and similarity both in monoculture carrying capacity and reciprocal invasion ability suggesting equalizing mechanisms may instead be responsible.

**Keywords:** individual-based model, coexistence, competitive exclusion, species diversity, plant architecture, equalizing mechanisms, stabilizing mechanisms, clonal growth, spatial traits.

## Introduction

Plants have few potentially limiting resources and therefore have few opportunities for resource partitioning that could result in long-term maintenance of diversity within communities. This implies that competitive interactions in plants will often result in consistent hierarchies, with par-

titular traits leading to superior competitive ability under given conditions and consequent competitive exclusion. Consistent with this expectation, pairwise pot, common garden, and field experiments often result in consistent competitive hierarchies (Goldberg 1996; Keddy 2001; Suding and Goldberg 2001; Dybzinski and Tilman 2007). Further, particular sets of traits appear to influence different components of competitive ability, with initial size and maximum potential growth rate especially important for competitive effect or competitive response in even-aged stands (Keddy 2001). These observations suggest that competitive exclusion should be widespread and diversity generally low in plant communities. Nevertheless, we commonly see high diversity in many plant communities, with multiple species occurring together even at small spatial scales.

How can we reconcile these two sets of observations? Persistent diversity, whether representing coexistence, *sensu stricto*, by satisfying the criterion of mutual invasibility or merely consisting of prolonged “co-occurrence” (Siepielski and McPeck 2010), implicates the operation of mechanism(s) acting against the force of competitive exclusion. We suggest that most experiments on competitive hierarchies prevent the expression of a key set of diversity maintenance mechanisms for plants, namely, those that have a spatial basis. Research over the last 2 decades has greatly expanded our understanding of the potential importance of mechanisms of diversity maintenance that require consideration of spatial use of resources, especially for plants (Tilman and Kareiva 1997; Bolker et al. 2003). Such mechanisms include temporal or spatial heterogeneity in the abiotic environment that lead to mass effects (Shmida and Ellner 1984), the creation of spatial refuges through aggregation of superior competitors (Pacala and Silander 1985; Silvertown et al. 1992; Rees et al. 1996; Pacala and Levin 1997; Bolker and Pacala 1997), trade-offs between competitive ability and colonization ability (Levins and Culver 1971; Hastings 1980; Tilman 1994),

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and dispersal limitation and competitive equivalence (Hubbell 2001). However, effects of spatial structure on long-term co-occurrence are not necessarily straightforward and depend on the mechanism involved. In theory, spatial structure can increase diversity (such as in competition-colonization trade-offs) or decrease it (due, e.g., to small neighborhoods and the discrete nature of individuals; see Bolker et al. 2003). It remains to be seen how particular mechanisms combine in field systems and whether they lead to extended co-occurrence of species that would otherwise rapidly exclude each other.

Understanding persistent diversity in plant communities must take into account the processes by which plants spread in space and occupy it. Although plants possess various dispersal traits, we focus in this study on clonal plants, where the short-range dispersal traits that could influence the local co-occurrence of species are easily quantified in terms of the processes that control the formation and spatial distribution of new ramets (Silvertown et al. 1992; Cain et al. 1995; Winkler et al. 1999). In this article, we first compare the degree to which prolonged co-occurrence is facilitated by variation in two different sets of traits: growth-related traits that directly control resource use, such as maximum potential growth rate, resource requirement, and maximum potential plant size, and architectural traits that control the spatial distribution of resource use, such as inter-ramet distance, branching angle, branching frequency, and allocation to new horizontal growth.

Second, we investigate the extent to which our observed patterns of co-occurrence for sets of species differing in different traits can be attributed to stabilizing mechanisms (Chesson 2000). Stabilizing mechanisms include all forms of niche partitioning that result in negative frequency dependence, that is, where each species in a mixture can increase when at low frequency but declines at high frequency. In contrast, equalizing mechanisms are those that reduce fitness or competitive ability differences between species and thus essentially slow the rate of exclusion and prolong co-occurrence (Chesson 2000). Because the degree of stable coexistence is determined by the combination of equalizing and stabilizing mechanisms, understanding patterns and mechanisms of diversity maintenance requires understanding the magnitudes of both. Further, while equalizing mechanisms alone cannot result in coexistence at equilibrium, they can extend the long-term co-occurrence of species well beyond the timescales of secular trends in the environment and thus can contribute substantially to observed patterns of diversity (Hubbell 2001).

Finally, of the possible spatial coexistence mechanisms described above, the most widely discussed is the creation of spatial refuges through aggregation of superior competitors (Pacala and Silander 1985; Silvertown et al. 1992;

Rees et al. 1996; Pacala and Levin 1997). We assess the importance of this mechanism in our system by testing whether more diverse mixtures are those with greater intraspecific aggregation and/or interspecific segregation in space.

Addressing questions about the role of particular traits in diversity maintenance requires comparisons of competitive outcomes in which species differ in values of particular traits while other traits are held constant. One set of approaches manipulates the consequences of an organismal trait rather than directly manipulating the traits themselves, for example, manipulating spatial distribution in lieu of manipulating dispersal-related traits directly (e.g., Stoll and Prati 2001); this does not allow a direct translation from organismal traits to dynamics of communities made up of species with different traits. The ideal approach would be experimental manipulation of the trait of interest, but this is rarely possible without introducing unwanted artifacts. Alternatively, many researchers compare closely related species or genotypes that differ in a trait of interest; such approaches involving phylogenetically independent contrasts are useful but cannot completely eliminate variation in correlated traits (Stocklin and Favre 1994; Bond and Midgley 2003). A different approach is to test linkages between organismal traits and the outcomes of species interactions *in silico*, based on trait manipulation in a calibrated simulation model parameterized by measurements done on real plants (e.g., Winkler and Stocklin 2002; Turnbull et al. 2007; Wildová et al. 2007). This approach uses models as “tamed field systems” (Cain et al. 1995; Bolker et al. 2003) to examine specific questions about the ecological effects of organismal traits. In a model, it is possible to manipulate any single trait independently of all other traits, without the artifacts inevitably introduced when manipulating real plants. At the same time, because the models are parameterized from real plants, tests of effects of any single trait are done in the context of realistic values of the other traits that are not manipulated. Another advantage of using a calibrated model is that effects of particular traits on outcomes of interactions can be examined for entire populations over extended periods of time, whereas real-plant experiments are generally limited to examining consequences for components of individual fitness over relatively short periods (e.g., Cheplick 1997; Skalova et al. 1997). We used such a calibrated model to investigate empirically the plausibility of various mechanisms of diversity maintenance given realistic variation in plant traits.

In this study, we focused on the effects of growth and architectural traits on competitive ability and dynamics in clonal plants. Spatial mechanisms of diversity maintenance are likely to be particularly important in clonal plants, which dominate persistent herbaceous communities

around the globe, including grasslands, tundra, and wetlands. Further, clonal plants provide an excellent opportunity to examine how different kinds of plant traits influence persistence of diversity because spatial distribution and therefore the operation of spatial mechanisms of diversity maintenance are controlled by the plants themselves through architectural traits such as rhizome length, allocation to new horizontal growth, and branching pattern.

In a previous study, Wildová et al. (2007) used data from short-term garden experiments and field observations of several species of wetland sedges and rushes to parameterize and validate Herben and Suzuki's (2001) clonal growth and architecture model. In this study, we used this calibrated model to conduct *in silico* experiments on the effects of differences in traits on diversity maintenance. Using the field-parameterized values for a particular species as the baseline, we generated sets of simulated species that differ only in a single trait and then used the model to investigate competitive dynamics and diversity maintenance among them. Because each simulation comprised only interactions among simulated species derived from a single actual species and that differed in only a single trait at a time, we were able to isolate the effects of variation in single traits on long-term co-occurrence. Because Wildová et al. (2007) found that the population dynamic consequences of variation in architectural traits, although not growth traits, often depended on the values of other traits of the plant, we used the field parameterizations of two different actual species to generate different sets of simulated species and conducted all analyses for each of the actual species separately. Specifically, we used two actual species of *Carex* that showed good fits between simulated and real populations in Wildová et al. (2007) but that differed in growth form (clumper vs. runner), enabling a broader range of inference.

We first identified 12 growth and architectural traits that, when manipulated in the calibrated models for each of two *Carex* species, resulted in ranges of productivity. Then, separately for each of the two actual *Carex* species, we used the following approach to generate the sets of simulated species differing in a single trait and to test the interactions within these sets. We took the baseline parameterization values for these traits from Wildová et al. (2007) and for each trait defined four simulated species such that they differed from the baseline values only in that trait and displayed the following differences among them in monoculture productivity: the highest-productivity simulated species produced 30% more population biomass in the first 3 years than the lowest-productivity simulated species, with the intermediate species producing, respectively, 10% and 20% more biomass than the lowest-productivity species. This standardization through effects

of traits on maximum potential population growth rate enabled us to compare directly the effect of variation of different traits measured in very different units. We then simulated the dynamics of each of these simulated species in monocultures and in mixtures of all four simulated species for each trait. To assess whether competition affects the diversity and co-occurrence of simulated species that differ in various architectural and growth traits, we compared mixture diversity to the expected diversity based on the summed monocultures. We also used spatial correlation analysis to test whether mixtures of simulated species that differed in architectural traits had greater spatial segregation between species and aggregation within species and whether these spatial patterns were associated with higher mixture diversity.

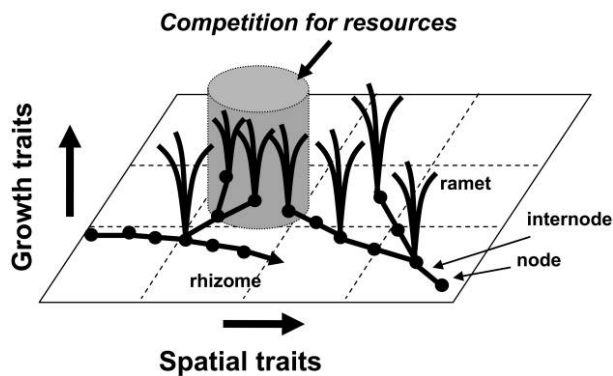
To investigate the extent to which the mechanisms of long-term co-occurrence in high-diversity mixtures of simulated species were due to stabilizing versus equalizing processes, we used a modification of the approach pioneered by Adler et al. (2007). We conducted a separate set of simulations for each trait, where for each actual species, all combinations of the four simulated species (including invasion into the same simulated species) were tested for mutual invasibility. If both reciprocal invasions (e.g.,  $i$  into  $j$ ,  $j$  into  $i$ ) were more successful than both intraspecific invasions (e.g.,  $i$  into  $i$ ,  $j$  into  $j$ , respectively), stable coexistence rather than prolonged co-occurrence would be indicated, suggesting an important role for stabilizing processes in diversity maintenance.

## Methods

### *Model and Calibration*

The model simulates vegetative growth of clonal plants, with the nodes and internodes that form the horizontally growing rhizomes that produce aboveground shoots (ramets) as the basic units in the model (fig. 1; Herben and Suzuki 2001). The model runs on a continuous simulation plane with toroidal boundaries. The simulation plane is initially homogeneous; any heterogeneity is generated by the ramets themselves. Model parameters include both ramet growth traits and architectural traits such as allocation to new ramets, spacers between ramets, and rhizome architecture (see tables A1 and A2 in the appendix, available online). The model incorporates competitive processes between ramets through density-dependent resource uptake and accumulation. The resource is not specified but could be any resource limiting to population growth. Reproduction is assumed to occur only clonally.

Parameterization and validation of the model for the two actual species used in this study, *Carex lasiocarpa* Ehrh. and *Carex sterilis* Willd., were described in detail in Wil-



**Figure 1:** Schematic picture of the spatially explicit, individual-based clonal plant growth simulation model developed by Herben and Suzuki (2001). In the model, plants are represented by two sets of traits: (1) growth traits that describe ramet growth dynamics (maximum ramet size, ramet growth rate, and density-dependent growth) and (2) architectural traits that describe spatial organization of ramets as determined by rhizome architectural traits and spatially specific resource allocation dynamics (internode length\*, distance between ramets\*, minimum distance between branchings, branching angle\*, probability of branching from a dormant bud, internode cost\*, resource fraction put into new daughter, node developmental period; an asterisk indicates that traits were not used in monoculture vs. mixture simulations; for details see tables A1 and A2, available online). Plant growth is affected by a feedback through intra- and interspecific competition between ramets, where competitive effect on a ramet is given by the density and size of ramets in a neighborhood of a specific size.

dová et al. (2007; see also tables A1 and A2). *Carex sterilis* has a phalanx or clumper growth form with very short inter-ramet distances, while *C. lasiocarpa* has somewhat longer rhizomes with higher biomass allocation to rhizomes (table A2). Wildová et al. (2007) parameterized the model mostly by direct estimation from measurements of plants collected in fens in southeastern Michigan or of plants grown in a short-term garden experiment (90 days). For two parameters, they indirectly estimated parameters by testing a broad range of trait value combinations and then finding the best fit with data from a separate 300-day experiment (done over two growing seasons). Comparison of model simulations with other data from the 300-day experiment suggest that, despite the necessary structural simplifications made in the model, the model seems to capture the major processes accounting for growth of a clonal plant.

#### *Trait Manipulations and Simulated Species Definition*

In this study, we identified 12 traits parameterized by Wildová et al. (2007) that could clearly be categorized as growth or architectural traits (table A1). To compare the consequences of differences in growth traits vs. architec-

tural traits for coexistence, we standardized across these traits by using ranges of trait values that produced similar increments of total population productivity in monocultures. Specifically, for each trait and each of the two actual *Carex* species, we defined four simulated species that differed only in the values of the focal trait, with all other traits kept at the original values of the actual species from which they were derived. The lowest-yielding simulated species (species A) and the highest-yielding simulated species (species D) differed by 30% in productivity, with intermediate species B and C having 10% and 20%, respectively, greater biomass than the lowest-yielding simulated species. To define these simulated species, for each trait, in each of the two actual *Carex* species, we first constructed a response curve of performance as a function of values of that trait, by manipulating trait values above and below the original (parameterized) value and simulating stand biomass after 500 time steps (= 3.3 years). We performed 10 replicate simulations for each trait value. We attempted to fit linear functions to each set of stand biomass-trait data, but because they did not visually show satisfactory fit, we then tried fitting quadratic and, if necessary, cubic functions and used the satisfactorily fitting functions for subsequent analysis (see table A1). From these stand biomass-trait response curves, we then identified a range of trait values centered around the observed value in the given *Carex* species and resulting in a 30% difference in simulated short-term productivity (table A1). Traits whose variation did not lead to this much difference in productivity, that is, traits whose value had only a small effect on yield, were eliminated from further analysis (see table A1). For most of the traits examined, the ranges over which the trait values have been changed within each species falls within the range of natural variation within that species at the field sites (data not shown).

#### *Simulation Experiments: Monocultures versus Mixtures*

For each trait for each of the two actual *Carex* species, we assessed short-term (500 time steps or 3.3 years) and long-term outcomes (15,000 time steps or 100 years) for monocultures of each of the four simulated species and for the mixtures of all four simulated species derived from each actual species, with 20 replicate runs of each simulation. Simulation of a subset of mixtures to 200 years showed no qualitative change in results (not shown). The monoculture and mixture simulations started with the same total number of randomly placed individuals (200 individuals for monocultures and 50 individuals of each simulated species in the four-species mixtures). The whole simulation area corresponded to 43.2 cm × 43.2 cm (corresponding to the scale of the validation data), and the final data were collected from the inner square plot (21.6



cm × 21.6 cm). This area typically contained 350–500 ramets (simulations based on *C. lasiocarpa*) or 800–1,000 ramets (based on *C. sterilis*) at steady state, so it is much larger than the scale of interactions among individual plants. In all simulations, one step corresponded to one day during the growing season; we used 150 days of growing season per year to convert results to years. A previous test of the realism of the parameterized model using this conversion showed good fit with a 2-year garden pot experiment (Wildová et al. 2007).

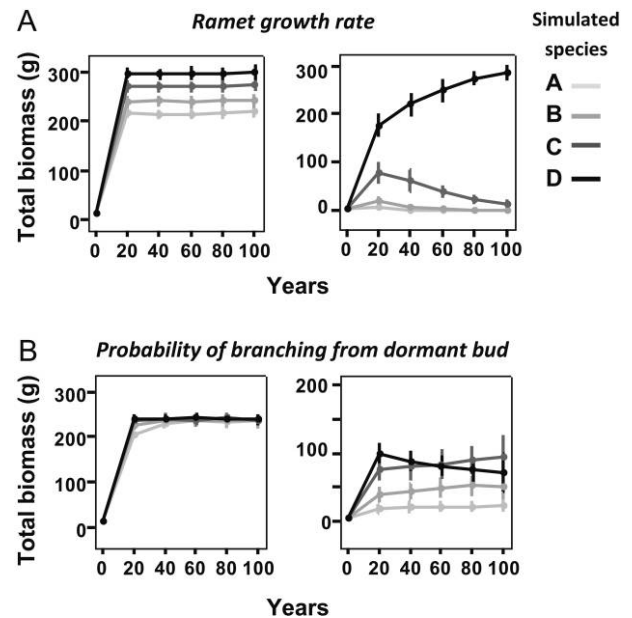
We compared stand biomass over time across simulated species in monoculture with that of the same simulated species in mixtures to determine how differences in each trait influenced the outcome of competitive interactions. To compare the consequences for coexistence between architectural and growth traits, we calculated the expected species diversity for each trait from the summed monocultures of individual simulated species and actual diversity of the simulated species mixtures for short-term (3.3 years) and long-term (100 years) simulations. Simulated species diversity was assessed using Simpson's index of diversity (SI). The mean diversity consequences of variation in each trait were averaged from 20 replicate runs and calculated as

$$SI = 1 - \sum \left( \frac{n_i}{N} \right)^2,$$

where  $n_i$  was the biomass produced in a run by simulated species  $i$  in monoculture or mixture;  $N$  was the total biomass of all simulated species in a mixture or the summed biomass of simulated species produced in monocultures. The “diversity” calculated from summing measurements from the monocultures as if they were all in a single stand is used to represent the expected diversity of the mixture if interspecific competition had no effect on relative performance of the simulated species (Goldberg 1994).

#### Identifying Mechanisms of Diversity Maintenance

To investigate the processes that account for the observed patterns of diversity persistence, we examined the role of equalizing and stabilizing mechanisms for individual traits, using a modified version of the approach pioneered by Adler et al. (2007). The existence of net negative frequency dependence, which requires the presence of stabilizing mechanisms, was assessed by a series of pairwise invasion experiments. We first simulated monocultures initialized with 200 individuals of simulated species  $j$  (resident) for 2,990 steps (~20 years) to get the stable state (see fig. 2). Then we introduced 20 individuals of the same or another one of the simulated species ( $i$ , invader) based on the same actual species, ran the simulation for further 310 time steps



**Figure 2:** Long-term simulations of monocultures and mixtures of four simulated species based on *Carex lasiocarpa*. Each pair of graphs is based on manipulation of one trait: A, ramet growth rate as an example of a growth trait, and B, probability of branching from a dormant bud as an example of an architectural trait. The error bars represent mean  $\pm$  standard deviation. For full results on all traits, see figures A1 and A2, available online.

(~2 years), and calculated the invasion rate of simulated species  $i$  into simulated species  $j$  as

$$R_{ij} = \frac{\log(B_{i \text{ final}}) - \log(B_{i \text{ invasion}})}{\Delta t}, \quad (1)$$

where  $B_{i \text{ final}}$  is the biomass of the invading simulated species at the end of the simulation,  $B_{i \text{ invasion}}$  is the biomass of the invading simulated species at the time step when it was introduced, and  $\Delta t$  is the duration of the invasion (310 time steps). We performed 100 replicate runs for each simulated species combination. This was done for all possible simulated species combinations for all traits, yielding for each trait a  $4 \times 4$  matrix of invasion coefficients (table 1). The diagonals of these matrices represent intraspecific invasions, that is, population growth rate at high frequency, whereas interspecific invasions in the same row represent the low-frequency case. Although, in theory, invasion rate into an equilibrium stand of the same simulated species should be zero (diagonal elements), this is not necessarily the case in a complex model when new individuals are introduced to an established stand of clonal plants with a developed bud bank and internal resource levels that need not be equal to those of the invaders. We therefore subtracted the intraspecific invasion rates (di-

**Table 1:** Example of the invasion matrix for one trait (density-dependent growth) for simulated species based on *Carex sterilis*

Invading simulated species	Invasion matrix				Adjusted invasion matrix			
	Resident simulated species				Resident simulated species			
	A	B	C	D	A	B	C	D
A	<b>.0532</b>	.0323	.0161	.0075	<b>0</b>	.0208	.0370	.0457
B	.0707	<b>.0571</b>	.0351	.0199	-.0136	<b>0</b>	.0220	.0373
C	.0889	.0762	<b>.0578</b>	.0385	-.0311	-.0184	<b>0</b>	.0193
D	.0990	.0867	.0750	<b>.0635</b>	-.0355	-.0232	-.0119	<b>0</b>

Note: The left matrix contains relative population growth rates (invasion rates) of the row simulated species into the column simulated species (see equation in "Methods"); the right matrix contains inter-(simulated)-species invasion rates adjusted by subtracting the intra-(simulated)-species invasion rate (bold) from each of the rates in the same row and then reversing sign. The upper triangular matrix represents lower-yielding simulated species invading higher-yielding simulated species, while the lower triangular matrix represents the reverse invasion. Stabilizing effects would be indicated by consistently negative adjusted invasion rates in both the upper and lower triangular parts of the right matrix.

agonal elements) from the whole matrix to get an effective invasion rate that by definition was fixed to zero for self-invasion. We reversed the signs of the resulting rates so that they clearly expressed the strength of the competitive effect of the resident (column) against the invader (row), with positive numbers indicating invasion would be prevented and negative numbers meaning it would be allowed (see table 1). We then plotted the adjusted invasion rate of simulated species  $i$  into simulated species  $j$  against the adjusted invasion rate of simulated species  $j$  into simulated species  $i$ . Negative values of both adjusted invasion rates indicate reciprocal frequency dependence and hence net stabilization; association of one negative and one positive value indicates a competitive hierarchy with no or insufficient frequency-dependent stabilizing mechanisms to result in stable coexistence. We also used these pairwise simulations to estimate degree of competitive inequality, by calculating the total difference in competitive ability for each pair as the sum of absolute values of adjusted reciprocal invasion rates. Competitive inequality increases as this difference increases. For simplicity, we averaged values of competitive inequality over all simulated species pairs for a given trait.

Because we defined the simulated species to have equal increments in maximum productivity of monocultures across traits (initial growth rates), we could not also use this metric to calculate fitness inequality. Instead, we focused on competitive equivalence as an indicator of equalizing mechanisms; less similar competitive ability should result in faster competitive exclusion and hence lower diversity. We used two independently derived indicators of difference in competitive ability for shared resources and related each one to diversity of the mixtures: first, we used competitive inequality as defined above from the reciprocal invasion experiments. Second, we used the difference in carrying capacity (efficiency in resource use) between the

two most extreme simulated species for a trait (typically D and A). Carrying capacity was estimated as biomass in monocultures, calculated after 3,000 steps (20 years) when biomass had largely stabilized in all monocultures and no simulated species had yet started to decline in mixtures (see fig. 2 and figs. A1 and A2, available online).

Spatial segregation between simulated species as one particular stabilizing mechanism of diversity maintenance was tested in simulated mixtures at 20 years (3,000 time steps), just before poorer competitors started to decline (see fig. 2). We divided the simulation plot into  $100 \times 100$  cells (each  $0.19 \text{ cm}^2$ ). This scale was fine enough that most cells contained only a single ramet, with a maximum of 2 per cell. We then used Moran's I (Upton and Fingleton 1985) with varying spatial lags to assess the cross-correlations of pairs of simulated species in these mixtures. As cross-correlations over lags of 0, 1, and 2 cells were tightly correlated, we present results only for the spatial lag of 1. Mean Moran's I over all pairs of simulated species in the mixture was then used as a measure of overall spatial segregation of ramets of different simulated species. We also calculated Moran's I for the most productive species, D, with a spatial lag of 1 cell, to assess the spatial distribution of its ramets in mixtures, because clustering of the superior competitor has been shown to be important for maintaining diversity (Pacala and Silander 1985; Rees et al. 1996; Pacala and Levin 1997).

## Results

### *Monocultures and Mixtures*

The trait values for all the simulated species for each trait are shown in table A1, as defined by the short-term simulations in monoculture. Not surprisingly, increasing maximum ramet size, maximum ramet growth rate, and degree

of density-dependent growth response all increased low-density productivity, although the quantitative relationship between simulated species trait value and stand biomass differed according to the actual *Carex* species from which the simulated species were derived. The architectural traits also had largely intuitive but more indirect changes on initial productivity in monoculture: increasing resource fraction put into new daughter ramets, increasing distance between ramets (lower intraspecific competition at early stages of stand development), and increasing probability of forming branches from a dormant bud all increased short-term productivity as did shorter node developmental period and shorter distance between branches regardless of the actual *Carex* species from which the simulated species were derived. However, two architectural traits (resource fraction put into new daughter ramets and distance between ramets) had unimodal relationships with productivity (data not shown). In this study we explored only the monotonically increasing part of the response curve around the original observed value for these traits.

Not all traits strongly affected total stand productivity. In particular, variation in several architectural traits (table A1), including branching angle, branching probability, distance between ramets and internode length, had such small effects on short-term productivity in the actual *Carex* species that they did not satisfy the criteria (see "Methods") for use in our simulations. It is possible, of course, that even though these traits do not affect short-term productivity, they (as well as others not examined) might affect competitive ability and coexistence in nature. For other architectural traits, effects on performance were considerably larger in *Carex lasiocarpa* (longer inter-ramet distances) than in *Carex sterilis* (more clumped growth form; table A1).

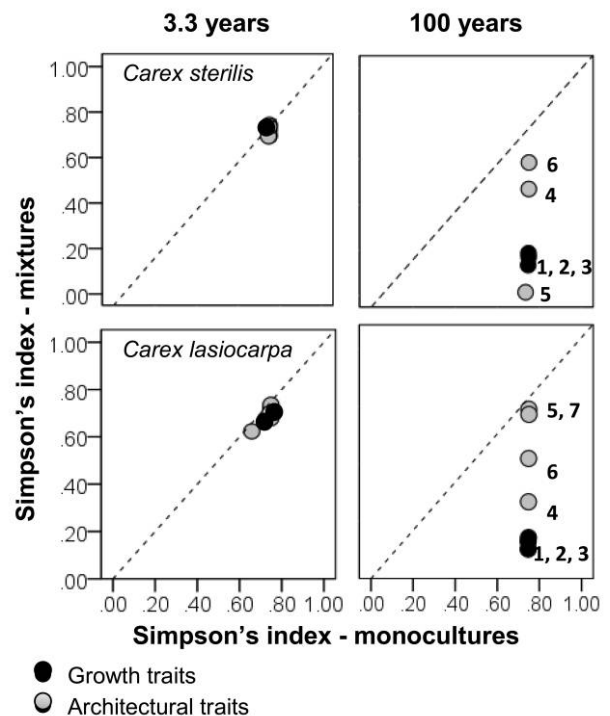
In monocultures, for all growth traits and some architectural traits, the initial differences in productivity used to define the simulated species were sustained over the long-term simulations and resulted in differences in steady-state biomass (figs. 2, A1, and A2). However, the long-term results for some architectural traits diverged considerably from the short-term simulations used to define the simulated species. For example, for the probability of branching from a dormant bud, the initial differences in productivity between simulated species disappeared by the end of the long-term simulations and the four simulated species converged in steady-state biomass (figs. 2, A1, and A2).

In the mixtures of four simulated species, all the growth traits showed the same pattern in the long-term simulations: the simulated species with the highest short-term productivity and steady state biomass in monoculture always strongly outcompeted all three other simulated species in mixture (figs. 2, A1, and A2). However, when sim-

ulated species differed in architectural traits, competitive hierarchies were generally less clear (figs. 2, A1, and A2).

To quantitatively compare competitive dominance when simulated species differed only in growth traits versus only in architectural traits, we calculated the diversity in the mixtures of each simulated species and in the summed monocultures and plotted these against each other (fig. 3). Diversity in the simulated mixtures and the expected diversity from monocultures were identical in the short-term simulations for both growth traits and architectural traits (i.e., values fell on the 1 : 1 lines in fig. 3). However, after 100 years, the diversity of mixtures was consistently higher when simulated species differed in architectural traits than when mixtures differed in growth traits (fig. 3).

The only exception to these trends is an architectural trait, node developmental period in *C. sterilis*. Mixtures of simulated species that differed in this trait had lower diversity than any mixtures of the growth traits (fig. 3). For



**Figure 3:** Simpson's index of diversity calculated for the expected diversity from the summed monocultures and actual diversity of mixtures for short-term (3.3 years) and long-term (100 years) simulations for spatial and growth traits. Each individual point represents one trait, and each row of graphs represents the indices for the simulated species derived from the indicated actual *Carex* species. Traits: 1, density-dependent growth; 2, maximum ramet size; 3, ramet growth rate; 4, resource fraction put into new daughter ramet; 5, node developmental period; 6, probability of branching from a dormant bud; and 7, minimum distance between branchings.

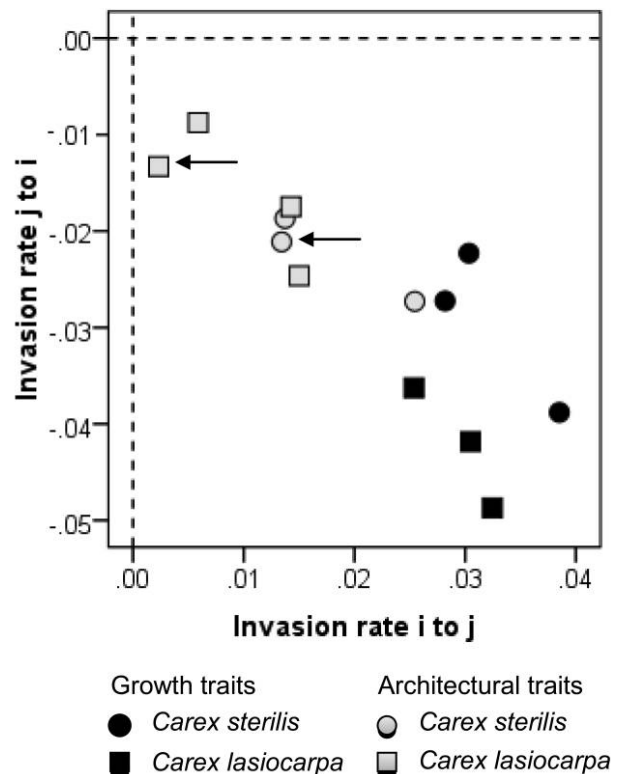


this trait, the rank order of monoculture stand biomass changed over time: simulated species A, which (by definition) had the lowest productivity in the short-term simulations, became the simulated species with the highest steady-state stand biomass in the long-term simulations (fig. A1). A similar reversal was seen in the mixtures. The switch in relative productivity between simulated species A and D in monocultures happened between 10 and 20 years of the simulation runs, thus well after the 3.3 years that we used to define simulated species (see fig. A1).

#### *Equalizing versus Stabilizing Mechanisms*

All the reciprocal pairwise invasion experiments showed clear winners and losers rather than reciprocal negative frequency dependence, regardless of whether simulated species differed only in a growth trait or only in an architectural trait. That is, if one invasion in the pair was successful, the reciprocal invasion was not (fig. 4; note differences in signs of axes). Thus, the reciprocal invasions show no signal of any net stabilization in any of the mixtures of multiple simulated species. The successful invader in the pair was always the higher-productivity simulated species invading the less productive simulated species, that is, below the diagonal in table 1 (T. Herben, unpublished data). Further, the reciprocal invasion rates for a given pair of simulated species were strongly negatively correlated with each other across all traits and both species ( $r^2 = 0.639$ ; fig. 4), indicating some degree of compensation between winners and losers. However, the differences between reciprocal invasion ability tended to be larger for simulated species differing in a growth trait than for simulated species differing in architectural traits, suggesting greater differences in competitive ability for simulated species differing only in a growth trait (fig. 4) and/or weaker stabilizing mechanisms.

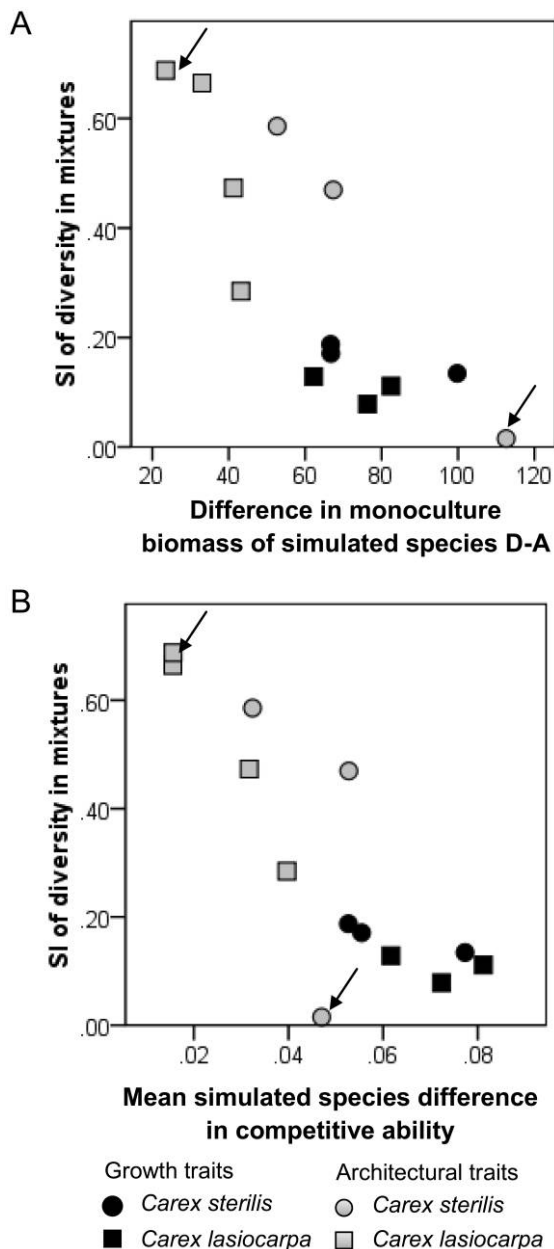
In contrast to the lack of evidence for stabilizing mechanisms strong enough for stable coexistence, both indicators of competitive inequality were correlated with diversity, suggesting that equalizing mechanisms may play a role in diversity maintenance. Traits for which simulated species differed less in monoculture carrying capacity (figs. 2, A1, and A2) tended to have higher simulated species diversity in mixtures at 100 years (fig. 5A;  $r^2 = 0.671$ ). Similarly, traits with more similar competitive ability (less difference in reciprocal invasion ability) between all pairs of simulated species tended to have higher diversity in mixtures both in simple correlations ( $r^2 = 0.695$ ; fig. 5B) and jointly with fitness inequality (multiple  $r^2 = 0.777$ ).



**Figure 4:** Mean adjusted invasion rates between all pairs of simulated species for each trait, labeled to indicate the actual species from which the simulated species were derived. The X-coordinate of each point is the mean of all below-diagonal ( $i > j$ ) elements of the adjusted invasion matrix (see table 1, right), representing invasions of more productive simulated species into monocultures of less productive simulated species. The Y-coordinate of each point is the mean of all above-diagonal ( $j > i$ ) elements of the adjusted invasion matrix, representing invasions of less productive simulated species into monocultures of more productive simulated species. Negative values of adjusted invasion rate indicate negative frequency dependence; that is, invasions at high frequency (intraspecific) are less successful than invasions at low frequency (interspecific). Stabilizing mechanisms would be indicated by negative frequency dependency for both simulated species in a pair. In the points marked with an arrow (node developmental period), the matrix was transposed, as simulated species A was a better invader than simulated species D.

#### *Spatial Structure in Mixtures*

To test whether variation in architectural traits increased diversity through increased aggregation of superior competitors, we examined the relationships between diversity at 100 years and both inter-(simulated)-species segregation and intra-(simulated)-species aggregation in mixtures at 20 years, just before poorer competitors started to decline (figs. 2, A1, and A2). Mixture diversity at 100 years was not significantly correlated with either segregation or aggregation at 20 years (fig. 6A, 6B). Moreover, for a given



**Figure 5:** The relationship between Simpson's index of diversity in mixtures at year 100 and two measures of equalizing mechanisms, labeled to indicate the actual species from which the simulated species were derived. *A*, Fitness inequality measured as difference in total stand biomass of monocultures at year 20 between the most and least productive simulated species for each trait (simulated species D minus simulated species A); ( $R^2 = 0.671$ ), and *B*, competitive inequality measured as sum of absolute values of adjusted invasion rates of simulated species A into D and of simulated species D into A for each trait. ( $R^2 = 0.695$ ). For further details see "Methods." For the points marked with an arrow (node developmental period), total stand biomass was calculated as simulated species A minus simulated species D because simulated species A excluded simulated species D.

level of segregation or intra-(simulated)-aggregation, variation in architectural traits among competing simulated species led to consistently higher diversity than variation in growth traits (fig. 6). These results were true of the simulated species regardless of the actual species from which they were derived, although of course those based on the clumper, *C. sterilis*, showed overall more inter-(simulated)-species segregation than did those based on the spreader, *C. lasiocarpa* (fig. 6).

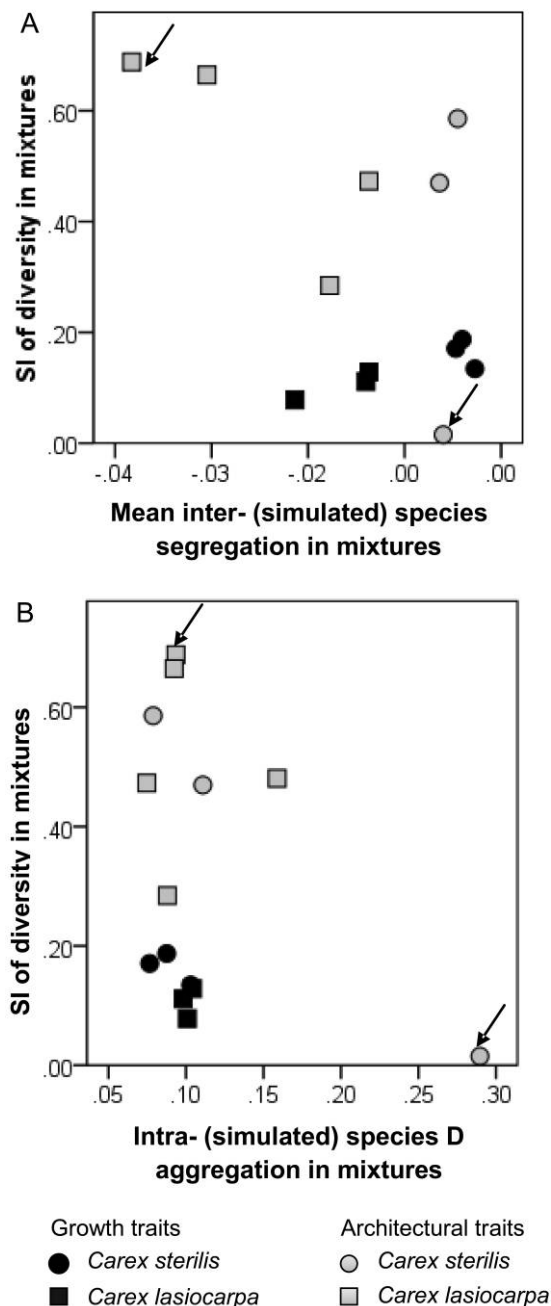
### Discussion

The simulations show clear differences in competitive outcome when simulated species differ in growth traits versus in architectural traits, with much higher diversity typically maintained when competing simulated species differ in an architectural trait than when they differ in a growth trait. This is in spite of the fact that all traits were scaled to have identical effects on initial productivity in monoculture. Below, we explore the possible mechanisms underlying these results and the implications for diversity maintenance and plant community structure.

#### *Growth Traits and Outcome of Competition*

Most experimental, as well as theoretical, studies of competitive interactions in plants focus on the role of traits that have a direct relationship to resource acquisition or resource use efficiency. Which of these traits are correlated with competitive ability depends on the component of competitive ability measured and the timescale. On the short timescales of most experiments, large size or high growth rate lead to strong competitive effects (ability to suppress other plants; Goldberg 1987; Gaudet and Keddy 1988; Goldberg and Landa 1991; Keddy 2001). Fewer studies compare competitive response (ability to avoid suppression), but where plants are initially similar in size, as is the case for ramets of clonal plants where new ramets have maternal subsidies, high growth rate or even small advantages in initial size should also lead to strong competitive response (Goldberg 1990, 1996). The mechanism leading to these relationships is likely to be greater resource acquisition. Even if resources are uniformly distributed and their uptake is the same on a per-unit size basis, larger or faster-growing plants will acquire a larger proportion of shared resources than individuals with less efficient growth traits (Wyszomirski 1986; Miller and Werner 1987; Bonan 1991). The advantage of greater size or faster growth rate becomes even greater in size-asymmetric competition, when even small advantages lead to a disproportionate increase in resource acquisition (Weiner and Thomas 1986).

The role of growth and resource acquisition traits has



**Figure 6:** Relationship between Simpson's index of diversity in mixtures at year 100 and spatial segregation of simulated species in mixtures at year 20 (before poorer competitors started to decline), labeled to indicate the actual species from which the simulated species were derived. *A*, Spatial segregation is measured as Moran's *I* with a spatial lag of 1, averaged over all pairs of simulated species in the mixture; more negative values mean greater segregation; and *B*, spatial aggregation of species *D* in mixtures is measured as Moran's *I* with a spatial lag of 1; more positive values mean greater aggregation. In the points marked with an arrow (node developmental period), we used simulated species *A* instead of *D* because it was the competitive dominant.

rarely been examined directly in multiple species competition studies, but results from sets of pairwise experiments usually reveal strong competitive hierarchies (Goldberg 1996; Keddy 2001). Thus, the single best competitor in a multispecies mixture should suppress all other species, resulting in low diversity.

Our simulation results for growth traits and competitive outcome in mixtures are consistent with these empirical results. When simulated species differ only in maximum ramet size, growth rate, or degree of competitive suppression experienced, the most productive simulated species in monoculture always dominates and excludes or strongly suppresses all the other simulated species (figs. 2, 3, A1, and A2).

#### *Architectural Traits and Outcome of Competition*

Experimental studies relating competitive ability and coexistence to traits related to spatial spread have been sparse, with two groups of exceptions. One set involves several experiments that have directly manipulated degree of spatial aggregation and assessed competitive suppression and diversity in mixtures (Bergelson 1990; Stoll and Prati 2001; Turnbull et al. 2007). While the variation in aggregation is not directly tied to plant traits in these experiments, in nature it presumably could result from differences in seed dispersal. The second set includes experiments with clonal plants that compare the rather coarse integrative categories of runners (long inter-ramet distances) and clumpers (very short inter-ramet distances), rather than the architectural and allocation traits that collectively lead to these types (Schmid 1985, 1990; Schmid and Harper 1985; Cheplick 1997; Humphrey and Pyke 1998; Hershock 2002). Both sets of experiments have largely confirmed the theoretical expectation (Weiner and Conte et al. 1981; Silvertown et al. 1992; Rees et al. 1996; Pacala and Levin 1997) that greater clumping of a superior competitor increases diversity by creating spatial refuges for inferior competitors, resulting in frequency dependence and stable coexistence.

Our simulation results suggest that variation among simulated species in architectural traits does indeed enable persistence of diversity despite large initial differences in low-density productivity of these simulated species in monoculture. However, the mechanism underlying this result is more complex than clumping of a single superior competitor creating refuges for inferior competitors, as we found no trend toward greater inter-(simulated)-species segregation or intra-(simulated)-species aggregation of the best competitor in architectural traits than in growth traits and very different diversities with similar levels of inter-(simulated)-specific spatial segregation. Results were similar for a range of spatial scales of aggregation. Our results

are in agreement with those of other authors (Takenaka et al. 1997; Neuhauser and Pacala 1999; Neuhauser 2001) who challenged the role of spatial aggregation in promoting coexistence because interspecific competition at cluster boundaries may determine the outcome, irrespective of the fact that most contacts are with conspecifics (Chesson and Neuhauser 2002).

#### *Mechanisms of Diversity Maintenance*

Although the initial differences in stand biomass among simulated species in monocultures were proportionally the same across all traits (by definition), the biomass of simulated species that differed only in an architectural trait generally converged over time, while monocultures of simulated species that differed only in a growth trait maintained biomass differences for the entire simulation period. Thus, architecture and growth traits appear to differ in how short-term productivity at relatively low density translates into long-term carrying capacity. Variation in architectural traits can change short-term productivity by changing initial rates of horizontal expansion, but not biomass at steady state, which requires an increase in efficiency of resource use, reflected in this nonmechanistic model by variation in growth-related traits. Growth and architectural traits hence differently affect transient behavior of the stands. For growth traits, the biomass differences early in stand development are predictive of later stand biomass, while transient behavior of stands differing in an architectural trait is much less correlated with their steady state biomass.

Across all traits, greater convergence in long-term monoculture biomass was associated with higher diversity in mixtures. Pairs of simulated species that differed only in architectural traits also had less differentiation in mutual invasion rates and less difference between intra- and inter-(simulated)-species invasion. This suggests greater competitive similarity, as well as more similar monoculture carrying capacities. However, it is important to note that mixtures of simulated species differing only in an architectural trait still exhibited competitive hierarchies, with one successful and one unsuccessful invader in any pair of simulated species.

The positive correlations of both monoculture carrying capacity convergence and similarity in reciprocal invasion ability with high diversity in mixtures suggest that equalizing rather than stabilizing processes are the main mechanisms promoting diversity in these simulated mixtures and the main cause of differences in diversity between mixtures of simulated species that differ in growth versus in architectural traits. This is further supported by the complete absence of reciprocal frequency dependence in

the invasion experiments for either trait type and the lack of any relationship between spatial structure and diversity.

The fact that differences in architectural traits are not associated with specific spatial structures that could lead to stable coexistence, for example, aggregation of superior competitors, seems somewhat surprising. However, it has also been shown that although architectural traits may underlie strong spatial patterns, these patterns often do not persist to the equilibrium state (see e.g., Cain et al. 1995).

#### *Generality of the Findings*

Our analysis simulated results of interactions among simulated species over the course of 100 years and demonstrated stable patterns of simulated species relative abundances for most traits. Extensions of a subset of these simulations for another 200 years showed no diminution of diversity in mixtures of simulated species differing in architectural traits (R. Wildová, unpublished data). While the lack of reciprocal invasibility indicates that the high diversity mixtures are not coexisting *sensu stricto* (Sieliski and McPeck 2010), our results on diversity maintenance and competitive exclusion should be applicable in efforts to explain apparently stable patterns in nature, persisting even over the timescales of long-term ecological studies. However, in communities with nonclonal perennials, similar time periods would require at least periodic reproduction from seed and therefore seedling-adult interactions. For such strongly size-asymmetric interactions, different traits are likely to be important at the individual plant level. Specifically, in strongly size-uneven interactions, tolerance of smaller plants to the low levels of resources due to depletion by adults is likely to be much more important than the ability of individual ramets to preempt resources (Goldberg 1990); traits that confer such tolerance are not included explicitly in our study. In addition, the distribution of adult-offspring distances can be very different between clonal and nonclonal communities (Zobel et al. 2010), so that the spatial pattern of size-specific interactions and therefore population dynamic consequences are also likely to differ. Thus, extrapolation of our results on resource versus spatial traits to coexistence of nonclonal perennial plants would be premature. On the other hand, clonal plants with strong spatial structuring related to architectural traits occur in almost every plant community and dominate many (de Kroon and van Groenendaal 1997; Gough et al. 2001), so that these results may well be broadly applicable.

We also believe that the results are relevant for the real field system from which we parameterized the simulation model. For most of the traits examined, the range over which the trait values have been changed falls within the



natural variation of the trait values. Along with the similarity in results between trait manipulations in the two actual *Carex* species, this gives us confidence in the validity of our most important conclusions comparing diversity and mechanisms of prolonged co-occurrence between growth and architectural traits and the potential importance of equalizing mechanisms in spatially related persistence of diversity. However, direct testing of the mechanisms of co-occurrence for any particular set of species would require taking into account the fact that traits typically do not vary in isolation but as suites of correlated traits and therefore detailed dynamics due to variation in one trait could change as a function of other traits (Goldberg et al. 2008).

Our key conclusion that variation in architectural (short-range dispersal) and growth traits differ in their effects on species diversity has a number of important implications for both theoretical and empirical studies of coexistence in plant communities. First, experimental studies of competition must allow expression of spatial traits if they are to have any relevance to patterns in the field. This is obvious for clonal plants and architectural traits but we suggest that it will also be important for relating competition among individuals to population dynamics even for nonclonal organisms. Second, studies of the trait structure of communities, including those related to community phylogenetics, would greatly benefit by expanding to include traits that determine spatial patterning, such as dispersal mode and mode of clonality. With the exception of seed size, dispersal-related traits have rarely been incorporated into studies of the trait structure of communities (but see, e.g., Sosnová et al. 2010). For example, how does the magnitude of interspecific variation in growth versus spatial traits relate to diversity across a broader range of communities, both in models and the field? Third, differences between architectural and growth traits do not seem to be due to the effects of these traits on spatial structure of the stands but primarily in the degree of variation in competitive ability they confer on the simulated species that bear them. Despite differences in growth rates at low density, simulated species that differ only in an architectural trait eventually converge in biomass so that they have similar carrying capacities and, likely as a consequence of this similar stand biomass, similar abilities for reciprocal invasion. These similarities of competitive ability result in very slow rates of competitive exclusion such that simulated species coexist for extended periods of time. Given the important community consequences of variation in different trait types, further theoretical and empirical exploration of both the generality and the cause of these results are critical.

Our conclusion that differences in diversity for different traits in our field-calibrated models are due to equalizing

rather than stabilizing mechanisms also has important implications. The role of equalizing versus stabilizing mechanisms in maintaining diversity have largely been tested to date in either studies of community-level properties such as species abundance curves (e.g., Volkov et al. 2005) or in experimental studies that seek to detect whether or not a statistically significant signal of some particular niche process exists (e.g., Turnbull 2005). However, both approaches have strong limitations; the latter, in particular, cannot address the broader question of how much of the variation in observed diversity can be accounted for by niche and by neutral processes, since they are not mutually exclusive processes (Chesson 2000; Adler et al. 2007). In a quite different approach, Adler et al. (2007) proposed quantifying overall niche differences by testing for the magnitude of negative frequency dependence and then comparing this to the magnitude of fitness differences (see Levine and HilleRisLambers 2009; Adler et al. 2010 for elegant examples using this approach). We extended their analyses from investigating coexistence mechanisms for single communities in the field to more general questions about what kinds of trait differences lead to diversity maintenance by niche versus by neutral mechanisms. Our finding that degree of difference in competitive equivalence could, by itself, play a very significant role in explaining patterns of diversity maintenance suggests that this could be a valuable tool for understanding patterns of diversity in theoretical and in empirical studies.

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Tree ferns of New Zealand. “Thousands of [ferns] cover the ground with their low and delicate fronds, as in some portions of our own country; others entwine the trunks of trees for support; still others attain the size of forest trees and rear their great crowns of feathery fronds to a height of forty or fifty feet in the air, rivaling in their grace and elegance the date-palm of Arabia.” From “A Sketch of New Zealand with Pen and Pencil” by I. C. Russell (*American Naturalist*, 1879, 13:65–77).