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Testing Spatial Theories of Plant Coexistence: No Consistent Differences in Intra- and Interspecific Interaction Distances

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ABSTRACT: Plants stand still and interact with their immediate neighbors. Theory has shown that the distances over which these interactions occur may have important consequences for population and community dynamics. In particular, if intraspecific competition occurs over longer distances than interspecific competition (heteromyopia), coexistence can be promoted. We examined how intraspecific and interspecific competition scales with neighbor distance in a target-neighbor greenhouse competition experiment. Individuals from co-occurring forbs from calcareous grasslands were grown in isolation and with single conspecific or heterospecific neighbors at distances of 5, 10, or 15 cm (*Plantago lanceolata* vs. *Plantago media* and *Hieracium pilosella* vs. *Prunella grandiflora*). Neighbor effects were strong and declined with distance. Interaction distances varied greatly within and between species, but we found no evidence for heteromyopia. Instead, neighbor identity effects were mostly explained by relative size differences between target and neighbor. We found a complex interaction between final neighbor size and identity such that neighbor identity may become important only as the neighbor becomes very large compared with the target individual. Our results suggest that species-specific size differences between neighboring individuals determine both the strength of competitive interactions and the distance over which these interactions occur.

Keywords: competition experiment, heteromyopia, individual-based models, log-response ratio, neighborhood.

Introduction

The role of spatial structure in maintaining plant species diversity is a fundamental and controversial issue in ecology (Pacala and Levin 1997; Barot 2004). Plants stand still, and interactions between individuals usually occur within their immediate neighborhood (Mack and Harper 1977;

Antonovics and Levin 1980; Pacala and Silander 1987, 1990; Stoll and Weiner 2000). Spatially limited dispersal, together with local interactions, can lead to individual neighborhood densities that are much different from mean population densities (Murrell and Law 2003). Local dispersal leads to aggregations of conspecifics (Pacala 1997), and because competition is also expected to occur over small spatial scales, the frequency of intraspecific to interspecific interactions is expected to be greater than what is suggested by the landscape or patch-scale densities. As a major consequence, the exclusion of inferior competitors is slowed because only those individuals on the edges of conspecific clusters compete with heterospecifics; this has been shown both theoretically (Weiner and Conte 1981; Pacala and Levin 1997; Murrell et al. 2002) and experimentally (Schmidt 1981; Stoll and Prati 2001; Monzeglio and Stoll 2005, 2008).

A number of theoretical studies have investigated how spatial structure may affect equilibrium densities for both populations and communities (e.g., Anderson and Neuhauser 2002; Bolker et al. 2003; Law et al. 2003; Snyder 2008), yet empirical information lags behind, and most of the spatial mechanisms for coexistence have yet to be rigorously tested (Tilman and Kareiva 1997; Amarasekare 2003; Barot 2004). During the past three decades, focus has been shifted from the mean-field or population-level approach, which assumes random mixing of species and individuals in the landscape, toward the level of the individual plant (for an overview, see Berger et al. 2008). Individual-based models examine population dynamics by modeling survival and growth for each individual separately (Grimm and Railsback 2005), so assumptions have to be made about the distances over which individuals interact (e.g., Bolker and Pacala 1999; Murrell and Law 2003; Snyder and Chesson 2004). So-called competition or interaction kernels are functions that describe the growth, survival, and reproduction of an individual by means of its own size and the size of and distance to its neighbors (Law et al. 2001). However,

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despite their theoretical importance, very little is known about the actual shape of such competition kernels, and a wide variety of mathematical functions and assumptions have been used to incorporate them into models (see Purves and Law 2002).

Much of the knowledge of the spatial scales of competition is derived from neighborhood analyses of forest systems, but so far no general picture has emerged as to the extent that neighbor identity (i.e., conspecifics vs. heterospecifics) influences the competitive effect and size of the neighborhood. While some studies have concluded that neighborhood sizes do not differ for conspecific and heterospecific neighbors (Hubbell et al. 2001; Uriarte et al. 2004), other studies have shown that conspecific neighbors are of greater importance than and differ in interaction radii from heterospecific neighbors (Peters 2003; Stoll and Newbery 2005; Queenborough et al. 2007).

Despite a large body of competition studies in herbaceous systems (e.g., see Goldberg and Barton 1992; Gurevitch et al. 1992), the spatial scales of interactions in these communities have rarely been investigated. In grassland communities it has been shown that above- and below-ground interactions do not necessarily occur over the same spatial scales (Milbau et al. 2007); this inevitably means that neighborhood size depends on the processes taken into account, because they will ultimately influence the functional shape of interaction kernels. Experimental studies on *Arabidopsis thaliana* have assessed the effect of size and distance of conspecific neighbors in target-neighbor pairs of plants of different ages and plants separated by different distances (Purves and Law 2002), and they fitted a dynamic-competition kernel that was a simple function proportional to the logarithm of neighbor size and decreasing with distance. This approach has been carried forward in even-aged multi-individual stands of *A. thaliana*, where competition was found to increase with plant size and attenuate rapidly at distances of only a few centimeters (Schneider et al. 2006). These two studies experimentally tested basic assumptions of complex theoretical models in a simple and straightforward way. However, they focused on monospecific stands, and there are only a few experiments that have measured heterospecific competition kernels. In a rare multispecies example, the zones of influence for two competing weed species were found to differ both within and between species (Pacala and Silander 1990); however, in this case the authors concluded that, because of weak aggregation and enormous plasticity, a nonspatial model summarized the community dynamics sufficiently well.

Theory has shown that it is important to address the question of whether neighborhood sizes differ for conspecific versus heterospecific neighbors. Most theory has so far assumed symmetric neighborhoods within and be-

tween species, that is, equal interaction distances. However, relaxing this assumption—that is, allowing the spatial scales of within- and between-species interactions to differ, while assuming equal interaction strength, integrated over all distances—can have profound consequences for community dynamics (Murrell et al. 2002; Murrell and Law 2003). Murrell and Law (2003) proposed the term “heteromyopia” for plant individuals that are “short-sighted” in sensing neighbors of other species relative to their own, and they showed how this concept may be sufficient to allow an otherwise weaker competitor to invade a population of a superior species.

Spatially explicit individual-based models use so-called competition kernels to describe how the strength of competitive interactions declines with distance (fig. 1). Theory typically uses competition kernels that sum to 1, with the overall intensity scaled by a separate parameter, the competition coefficient. The competition coefficient allows one to separate out shape effects of the competition kernel from the per capita effect of a competitor. Modeling competition kernels this way means that if individuals are arranged randomly across the landscape, then the outcome of competition depends only on the magnitude of the scaling coefficients (in other words, the mean-field model is recovered; Murrell and Law 2003). One can therefore think of a competition kernel as a probability density function covering an area of 100% competition (the ecological neighborhood, sensu Antonovics and Levin 1980). Multiplying the competition kernel by the competition coefficient raises or lowers the entire surface of the kernel and results in the actual function describing the strength of competition. In order to get larger within- rather than

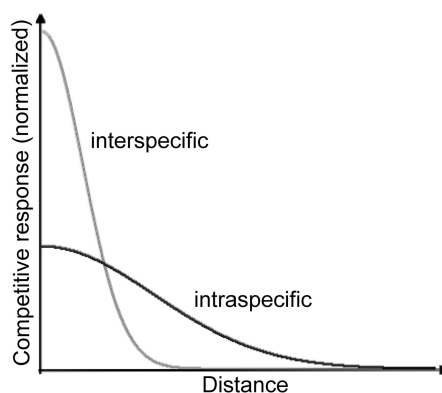


Figure 1: Competition kernels for intraspecific and interspecific competition that lead to heteromyopia. A leptokurtic kernel results in a short interaction distance (interspecific competition), while a platikurtic kernel results in a large interaction distance (intraspecific competition). Since the kernels are normalized to sum to 1 (i.e., the areas below the two curves are the same), the functions must cross.

between-species interaction distances, the intraspecific competition kernel should be of a platikurtic shape and the interspecific competition kernel should be of a leptokurtic shape; this forces the two kernel functions to cross (fig. 1). The key feature of heteromyopia is that interspecific interactions must be more intense than intraspecific interactions at short distances, whereas at longer distances, this relationship should be reversed. This pattern promotes coexistence by allowing conspecific clusters to build up, leaving gaps in the landscape for other species to exploit; the species remain segregated because of the rapid removal of nearby heterospecific neighbors (Murrell and Law 2003; Snyder and Chesson 2004). Other outcomes are possible, and there is now a growing body of theory that shows how different scales for conspecific and heterospecific interactions may influence the outcome of competition (Murrell et al. 2002; Murrell and Law 2003; Snyder and Chesson 2004; Snyder 2008); however, the relevance of this theory to real communities remains an open question, and to our knowledge, heteromyopia has not been tested.

Our experiment aimed to help close the gap between theory and data and to evaluate potential differences in within- and between-species interaction distances. Competition in nature results from a complex interplay of components such as neighbor number, size, identity, and distance. To advance our understanding of local competition, one has to reduce this complexity to its components and vary these components experimentally (Purves and Law 2002; Ramseier and Weiner 2006). Greenhouse experiments allow one to control for environmental heterogeneity and isolate the actual effects of the components in focus from natural complexity. We examined the most basic elements of individual-based models by studying pairwise interactions addressing resource competition. In a target-neighbor competition experiment, we combined target individuals of four herbaceous grassland species with either a conspecific or a heterospecific neighbor at several distances and compared their performances with those of control plants grown in isolation. We expected neighbor individuals to have a negative effect on target individuals and the strength of this effect to decline with distance. We hypothesized that, if species are not equal (as opposed to neutral; e.g., Bell 2000; Hubbell 2001), then the competitive responses to conspecific and heterospecific neighbors and the distances over which conspecific and heterospecific neighbors compete should differ from each other. If heteromyopia contributes to coexistence, then conspecific neighbors should compete over longer distances than heterospecific neighbors and interspecific competition should be more intense at close distances but decline more rapidly with distance compared with intraspecific competition. Finally, we examined the importance of neighbor identity in relation to neighbor size.

Material and Methods

Plant Species

Heteromyopia has been hypothesized to be a coexistence mechanism for similar competitors. We therefore decided to work with morphologically and ecologically similar species from diverse calcareous grasslands: *Hieracium pilosella* L. (mouse-ear hawkweed; Asteraceae), *Plantago lanceolata* L. (ribwort plantain; Plantaginaceae), *Plantago media* L. (hoary plantain; Plantaginaceae), and *Prunella grandiflora* (L.) Schaller et Jacq. (big self-heal; Lamiaceae). These species are perennial forbs that are native to Europe, with dry and semidry grasslands on alkaline soils being among their main habitats. They are common, often growing together on calcareous grasslands.

Experimental Design

The four experimental species were combined in two pairs (*P. lanceolata* and *P. media*, *H. pilosella* and *P. grandiflora*), which represented different aspects of similarity. *Plantago lanceolata* and *P. media* are congeners and keep a rosette growth form, while *H. pilosella* and *P. grandiflora*, although taxonomically distant, share the capability of vegetative reproduction (tillers and reptant shoots, respectively). Target individuals of each plant species were grown with either a conspecific neighbor or a heterospecific neighbor from the other species within the pair. As a control treatment, individuals of each species were grown without a neighbor. Target and control individuals were always placed at the same position within containers, and neighbors were placed at distances of 5, 10, or 15 cm. This resulted in seven treatments per target species: one control treatment, three conspecific neighbor treatments, and three heterospecific neighbor treatments. Each combination was replicated four times, but for *P. media* the replicate number was reduced to three in two cases (heterospecific neighbor at a distance of 10 cm and conspecific neighbor at a distance of 15 cm) as a result of death of the target individuals after 2 months.

Growth Conditions

The aim of our experiment was to compare intra- and interspecific competition on a local scale. Plants were therefore grown in relatively small containers (22 cm × 11.5 cm × 9 cm) to ensure competition and root contact. A total of 112 plastic containers were filled with 1.47 L of substrate mixture consisting of 650 mL quartz sand (Si-helco 30; Sihelco, Rheinfelden, Switzerland), 170 mL of sieved (2-mm) soil from a calcareous grassland, and 650 mL of sieved loess. Seeds were obtained from commercial Swiss ecotypes (fenaco, Winterthur, Switzerland) and di-

rectly sown into the containers (five seeds per individual position). We used small plastic tubes to prevent relocation until primary leaves had emerged. After 24 days, all but the largest seedling at each individual's position were removed. A few individuals died during the first 3 weeks (nine *P. grandiflora* and three *P. media* individuals), and these were replaced by transplanting separately raised seedlings. The experiment was set up in a greenhouse at the University of Basel on June 6, 2006, and it ran for 260 days until plant growth stopped. Replicates of all treatment combinations were equally distributed between two parallel greenhouse chambers. Within these chambers, containers were randomly placed on benches and rerandomized every 3–4 weeks. Plants were watered with distilled water as needed, several times a week, and from November 9 until the end of the experiment, additional lighting was supplied (16L : 8D regime).

Data Collection

On days 27, 53, 85, 113, 182, 212, 247, and 260 after sowing, the number of leaves of all individuals and the length and width of the three largest leaves were measured. Linear regressions between these measurements and aboveground biomass at harvest were used to estimate aboveground biomass during growth for control individuals. The resultant growth curves served as descriptions of intrinsic growth performance of the four target species (see app. A in the online edition of the *American Naturalist*). After 260 days, all plants were harvested. Aboveground and belowground biomass was separated, and dry mass (48 h at 60°C) was determined for each individual. We refer to aboveground biomass as a measure of plant performance.

Statistical Analyses

We analyzed our data with a focus on three main aspects. First, we estimated intra- and interspecific interaction distances, on the basis of our three experimental distances, for each species separately. Second, we analyzed whether the average competitive response to neighbors differed between target species and neighbor identity and how the competitive response declined over distance. Third, we tested whether neighbor identity effects were related to final neighbor size.

All statistical analyses were performed with the statistical program R, version 2.6.1 (R Development Core Team 2007). Data were transformed as necessary to meet the requirements of a normal distribution. Aboveground biomass data for *P. lanceolata*, *P. media*, and *P. grandiflora* were square root transformed for determination of interaction distances; log-response ratio (lnRR) data (described

below) were square root transformed after an addition of 0.25, since some values were negative.

Interaction Distances. We defined interaction distance for species *x* on species *y* as the maximum distance at which the performance of an average target individual of species *y* growing with a neighbor of species *x* was significantly worse compared with an average isolated (control) individual of species *y*. This maximum distance is essentially measuring the zone of influence of one species on another, although in our experiment we measure how the influence attenuates within the zone. Since aboveground biomass differed between species, we estimated intra- and interspecific interaction distances using separate ANOVAs for each target species. These ANOVAs included neighbor treatment as a factor with seven levels: one control treatment and six neighbor identity-distance treatments. We then defined the contrast matrices so that each neighbor treatment was tested against the control treatment within the separate ANOVAs. The aim of these analyses was to test whether intraspecific competition could be detected over distances larger than those for interspecific competition (heteromyopia).

Competitive Response and Neighbor Distances. In order to analyze the general performance of target individuals (i.e., all species taken together), we calculated the log-response ratio of each target individual on the basis of aboveground biomass:

$$\ln RR_{ijd} = \ln(\overline{BM}_i / BM_{ijd}^t),$$

where \overline{BM}_i is the mean aboveground biomass of four control individuals of target species *i* and BM_{ijd}^t is the aboveground biomass of a target individual of species *i* grown with a neighbor of species *j* (con- or heterospecific) at distance *d*. The log-response ratio is a measure of the competitive response, that is, how much a target individual suffered because of its neighbor (Goldberg et al. 1999; Weigelt and Jolliffe 2003). Because lnRR is standardized between all species, it can be used to test for differences in average competitive response of target species to neighbor identity. We analyzed the competitive response of target individuals to their neighbors using an ANOVA that tested for effects of target species, neighbor distance, neighbor identity, and all second-order interactions. Greenhouse chambers differed in mean temperature and were therefore included in the model as a random block factor. Because *P. lanceolata* showed no competitive response to its heterospecific neighbor (*P. media*), the analysis was performed with two data sets, either including all four target species or with *P. lanceolata* excluded.

In these analyses, a significant interaction between dis-

tance and target species would indicate that $\ln RR$ declines differently with distance for the target species and, accordingly, for a significant interaction between distance and neighbor identity. In other words, testing for distance effects means testing for differences in the slope of the respective regressions of $\ln RR$ against distance (fig. 2A, 2B, 2D). Equal slopes would indicate that identical competition kernels could be used for our species pairs. Even if the slopes were equal, different interaction distances within and between species could result as long as the average response (or total competitive response, as in fig. 2) to conspecific and heterospecific neighbors differs (analogous to the competition coefficients that scale the competition kernels; fig. 2C). This would require significant main effects of target species or a significant interaction between target species and neighbor identity. A steeper slope for heterospecific than for conspecific neighbors, together with equal total competitive responses, would result in heteromyopia (fig. 2D). Different slopes and different total competitive responses to conspecific and heterospecific neighbors may or may not result in different interaction distances (fig. 2A, 2B). Both the slopes and the total competitive response to conspecific and heterospecific neighbors may differ between target species and may further depend on relative size differences between neighboring plants.

Size Effects. Conspecific and heterospecific neighbors of three target species differed significantly in total biomass (two sample t -tests: *P. lanceolata*: $t_{22} = 6.5$, $P < .001$; *P. media*: $t_{20} = 3.9$, $P < .001$; *H. pilosella*: $t_{22} = 2.3$, $P < .05$). To test whether target species-specific responses to neighbor identity, as revealed by the ANOVA, were mainly due to such size differences, we performed the same analyses with an ANCOVA model that included final neighbor size as a covariate. We used information criteria to select the best measure for neighbor size from a set of six ANCOVA models and found the log-transformed relative total neighbor size (total neighbor biomass divided by total target biomass) to be the best. Detailed descriptions of statistical models and the model selection process are given in appendix B in the online edition of the *American Naturalist*.

Results

Effects of Neighbor Presence

Most target individuals grown with a neighbor were substantially smaller than control individuals grown alone, and the effects of neighbors decreased with distance (fig. 3). An exception was *Plantago lanceolata* when it was grown with its heterospecific neighbor *Plantago media*: aboveground biomass was not significantly reduced at any

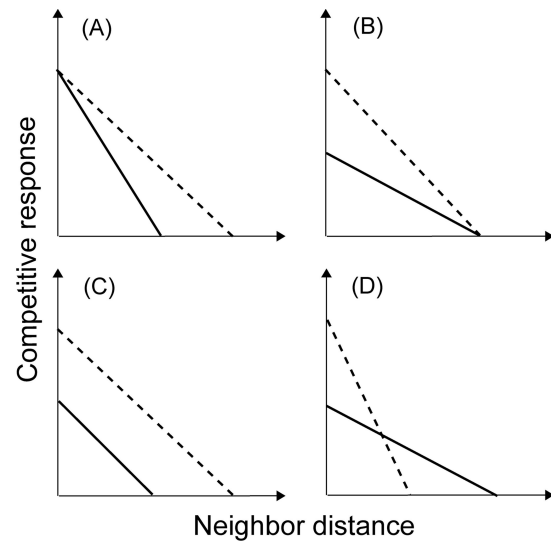


Figure 2: Hypothetical relationships between the slopes describing how the competitive response to a neighbor declines with distance and total competitive response to a neighbor. Differences in slopes and total competitive response may or may not result in different interaction distances. The total competitive response to a neighbor, integrated over all distances, corresponds to the area below the lines (formed as right triangles). The different lines (solid and dashed) may represent different target species, conspecific and heterospecific neighbors, or neighbors of different relative sizes. Assumptions are different slopes and different total competitive responses, resulting in different interaction distances (A); different slopes and different total competitive responses, resulting in equal interaction distances (B); equal slopes and different total competitive responses, resulting in different interaction distances (C); and different slopes and equal total competitive responses, resulting in different interaction distances (D).

distance (fig. 3A). In the case of *Hieracium pilosella*, control individuals produced tillers, resulting in substantially more aboveground biomass compared with target individuals, and all stayed within the rosette stage (fig. 3C).

Interaction Distances

We found no common pattern such as generally larger intraspecific than interspecific interaction distances or vice versa. Instead, interaction distances seemed to be target-neighbor species specific (fig. 3). Significant competition was still occurring at a distance of 15 cm in the cases of *P. lanceolata* (conspecifics; fig. 3A) and *H. pilosella* (con- and heterospecifics; fig. 3C). For *P. media*, interspecific competition occurred over a longer distance than did intraspecific competition (10 and 5 cm, respectively; fig. 3B), while the opposite was found for *Prunella grandiflora* (fig. 3D).

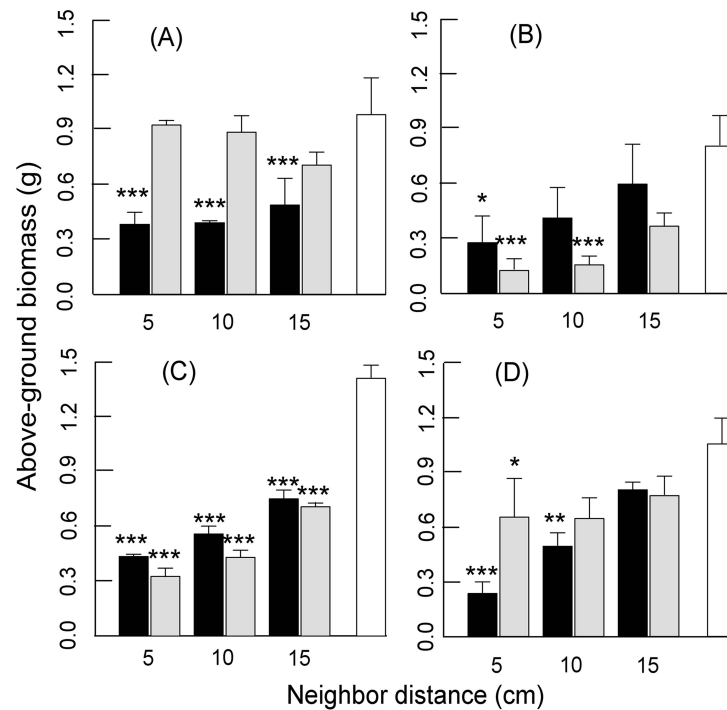


Figure 3: Mean aboveground biomass and estimated intraspecific and interspecific interaction distances of *Plantago lanceolata* (A), *Plantago media* (B), *Hieracium pilosella* (C), and *Prunella grandiflora* (D). Target individuals were grown with a conspecific neighbor (black bars) or with a heterospecific neighbor (gray bars) at different distances or without a neighbor (control; white bars). Heterospecific neighbor species were *P. lanceolata* for *P. media*, and vice versa, and *H. pilosella* for *P. grandiflora*, and vice versa. Error bars show 1 standard error ($n = 4$, except for *P. media*, with a heterospecific neighbor at 10 cm and a conspecific neighbor at 15 cm, where $n = 3$). Asterisks above black and gray bars indicate significant differences between control and neighbor treatments on the basis of per species ANOVAs with treatment contrasts. P values are as follows: * indicates $P < .05$, ** indicates $P < .01$, and *** indicates $P < .001$.

Average Competitive Response

In both ANOVAs and ANCOVAs, $\ln RR$ differed significantly among target species while main effects of neighbor identity were not significant (table 1). This shows that target species differed in their average competitive responses to a neighbor: *P. media* was the species most affected by its neighbors (average $\ln RR \pm$ standard error, 1.31 ± 0.21), followed by *H. pilosella* (1.02 ± 0.07), *P. grandiflora* (0.71 ± 0.13), and *P. lanceolata* (0.55 ± 0.10). However, there was no difference in the average competitive response to conspecific and heterospecific neighbors, that is, all target species and neighbor distances taken together. The ANOVAs further indicated a strong interaction between target and neighbor species (table 1). However, this interaction became nonsignificant when neighbor size was taken into account (ANCOVAs). Thus, target-neighbor species-specific differences in competitive response were due to (species-specific) size differences between target and neighbor individuals.

Competitive Response and Neighbor Distance

The competitive response clearly declined with neighbor distance (fig. 4). This effect was weaker when neighbor size was taken into account, indicating some correlation of neighbor size with distance (cf. F values of ANOVA with those of ANCOVA in table 1). Regardless, a neighbor, growing to a given size, became significantly less important the farther away it was. The ANOVA revealed a significant interaction between target species and distance when data from all four species were used; this vanished when *P. lanceolata* was excluded (table 1). The cause of this, therefore, was that the competitive response of *P. lanceolata* did not decline with distance when it was grown with a conspecific neighbor, and it even increased with distance when *P. lanceolata* was grown with a heterospecific neighbor (fig. 4). We found no significant interaction between neighbor identity and distance. Thus, with all species taken together, $\ln RR$ decreased equally over distance for conspecific and heterospecific neighbors, although we note that the variability of $\ln RR$ was substantially larger with heterospecific

Table 1: Results of ANOVA versus ANCOVA testing for effects of neighbor size (CoV), target species (TG), neighbor distance (D), neighbor identity (NB), and pairwise interactions on the log-response ratio of target individuals of perennial forbs from calcareous grasslands

Source	ANOVA + PI		ANCOVA + PI		ANOVA – PI		ANCOVA – PI	
	df	F	df	F	df	F	df	F
Chamber ^a	1	1.9	1	4.6*	1	.4	1	1.1
CoV ^b	1	308.8***	1	214.6***
TG	3	9.5***	3	6.1***	2	5.4**	2	6.6**
D	1	23.2***	1	5.3*	1	28.5***	1	5.6*
NB	1	1.4	1	.1	1	1.4	1	.2
CoV × TG	3	3.6*	2	4.6*
CoV × D	1	.2	1	2.8
CoV × NB	1	5.3*	1	4.4*
TG × D	3	4.2**	3	2.3	2	.8	2	.5
TG × NB	3	12.1***	3	2.1	2	6.7**	2	.7
D × NB	1	2.3	1	.7	1	.8	1	.1
Residuals	80	...	74	...	59	...	54	...

Note: D = 5, 10, or 15 cm. NB is either conspecific or heterospecific. Log-response ratio was calculated as $\ln RR_{ijl} = \ln (\overline{BM}_i^c / BM_{ijl}^t)$, where \overline{BM}_i^c is the mean aboveground biomass of four control individuals of target species i , and BM_{ijl}^t is the aboveground biomass of a target individual of species i grown with a neighbor of species j (con- or heterospecific) at distance d . Either data included all four target species (+PI) or *Plantago lanceolata* was excluded (–PI). Degrees of freedom (df) and F values are shown.

^a Greenhouse chamber was included as a random factor.

^b Covariate: log-transformed relative neighbor size (total neighbor biomass divided by total target biomass).

* $P < .05$.

** $P < .01$.

*** $P < .001$.

neighbors than with conspecific neighbors, especially at close distances (fig. 4).

increasing relative neighbor size, conspecific neighbors became more important than heterospecific neighbors.

Size Effects

Relative neighbor size was highly significant as a covariate (table 1; fig. 5), and it accounted for 70% of total variance regardless of whether *P. lanceolata* was included. This was also reflected in the much better fit of all ANCOVA models compared with the ANOVA model when selecting for the best covariate (app. B). We found significant interactions between relative neighbor size and both target species and neighbor identity (fig. 5). Thus, not only did species differ in their average competitive responses to a neighbor (main effect of target species), but they also differed in how the strength of the competitive response scaled with relative neighbor size (fig. 5A). Moreover, the relative strength of the competitive response to conspecific and heterospecific neighbors changed with relative neighbor size (fig. 5B). While target individuals had a stronger response to heterospecific neighbors than to conspecific neighbors when the neighbors were smaller than the target, this relationship was reversed for neighbors that were larger than the target (note that the lines in fig. 5B cross at relative neighbor size around 1 [0 on the log scale]). In other words, with

Discussion

The central goal of this investigation was to close the gap between theory and data in spatial plant ecology by investigating species-specific interactions between neighboring pairs of individuals. Such individual-level processes influence population and community dynamics (Grimm and Railsback 2005), and they depend on the spatial distances and size differences between individuals as well as their species identity. All of these variables have been incorporated into at least some theory for neighborhood competition in plants (e.g., Bolker and Pacala 1999; Law et al. 2001; Murrell and Law 2003; Snyder and Chesson 2004; Murrell 2009), and yet there is very little empirical information on how important each of these neighbor components is in determining the intensity of competition between two neighboring individuals. As we discuss below, our investigation yielded three main results: (1) there was no general pattern of within- and between-species interaction distances, and consequently, there was no evidence for heteromyopia; (2) species-specific relative size differences between neighboring plants are likely to be key factors in determining the intensity and distance of com-

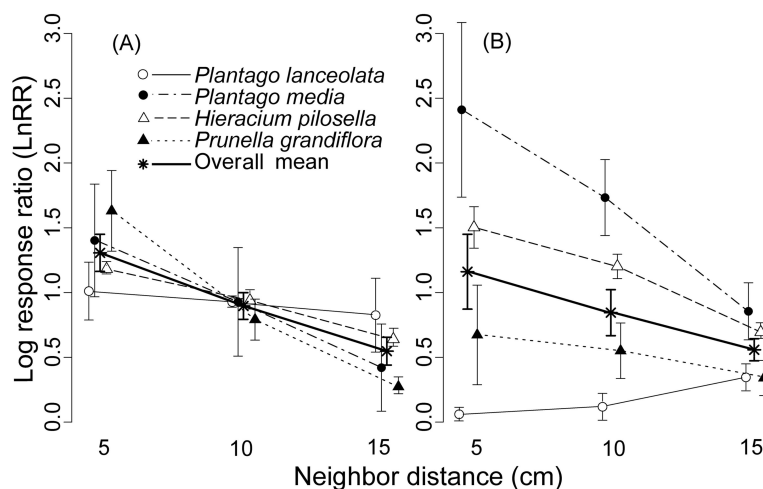


Figure 4: Decrease of mean log-response ratio of target individuals of four perennial forbs from calcareous grasslands with distance of conspecific neighbors (A) or heterospecific neighbors (B). Heterospecific neighbor species were *Plantago lanceolata* for *Plantago media*, and vice versa, and *Hieracium pilosella* for *Prunella grandiflora*, and vice versa. Error bars show ± 1 standard error. Log-response ratio was calculated as $\ln RR_{jd} = \ln (\overline{BM}_i / BM_{jd}^i)$, where \overline{BM}_i is the mean aboveground biomass of four control individuals of target species i , and BM_{jd}^i is the aboveground biomass of a target individual of species i grown with a neighbor of species j (con- or heterospecific) at distance d .

petitive interactions; and (3) a conspecific neighbor may be more important than a heterospecific neighbor, but only as the neighbor becomes very large compared with the target individual.

Interaction Distances

Theory has shown that differences between pairwise intraspecific and interspecific interaction distances can have profound consequences at the population and community levels. The two defining features of the coexistence mechanism known as heteromyopia are (1) that interspecific competition occurs over shorter distances than intraspecific competition (Murrell et al. 2002; Murrell and Law 2003) and (2) that interspecific interactions are more intense than intraspecific interactions at short distances, whereas at longer distances this relationship is reversed (fig. 1). However, our experiment revealed no empirical evidence for heteromyopia. The distances over which intraspecific and interspecific competition could be detected varied substantially, but we found no general pattern (e.g., intraspecific interaction distances being larger than interspecific interaction distances). We found larger intraspecific than interspecific interaction distances for only the stronger competitors within each species pair, that is, the species least affected by their neighbors, and we found no evidence for a reversal of the relative importance of intraspecific and interspecific competition at larger distances.

Within each of our two species pairs, one species turned

out to be a stronger competitor than the other (namely, *Plantago lanceolata* and *Prunella grandiflora*), and when this species was a neighbor, the result was a larger interaction distance than with the other species. These results are in accordance with a previous competition study on weed species, where neighbors of the stronger competitor affected the growth of a focal plant over larger distances than did neighbors of the weaker competitor (Pacala and Silander 1990). The competitive hierarchy between neighboring plants, rather than identity per se, might thus determine interaction distances. According to this, a neighbor that exerts a large competitive effect (see Goldberg and Fleetwood 1987) will result in relatively large interaction distances, irrespective of a target's species identity; this is probably due to the fact that a species' competitive ability is often correlated with average final plant size (Freckleton and Watkinson 2001). At the same time, a competitively tolerant target individual that shows a small competitive response will experience relatively small interaction distances irrespective of a neighbor's species identity. Our study further revealed that the absolute distances over which competition persisted also depended on and differed between target species. Several studies have shown that competitive effect and response are not correlated (Goldberg and Landa 1991; Cahill et al. 2005; Fraser and Miletto 2008), and target-neighbor species-specific interaction distances might therefore result from different combinations of competitive abilities to suppress and tolerate neighbors.

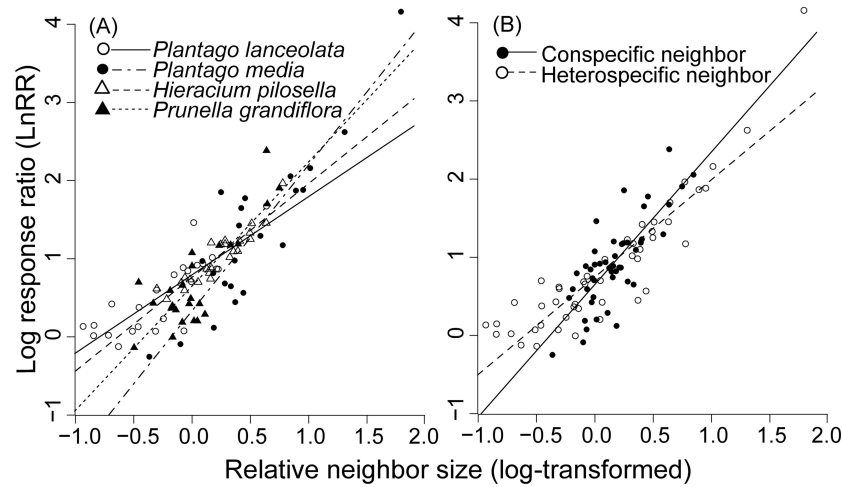


Figure 5: Log-response ratio of target individuals versus relative size of neighbors (pooled over distances) of four perennial forbs from calcareous grasslands by target species (A) and by neighbor identity (B). Linear regression lines are shown. Regressions differed significantly ($P < .05$) between both target species (A) and neighbor identity (B), according to the ANCOVA presented in table 1. Log-response ratio was calculated as $\ln RR_{ijd} = \ln (\overline{BM}_i / BM_{ijd}^i)$, where \overline{BM}_i is the mean aboveground biomass of four control individuals of target species i , and BM_{ijd}^i is the aboveground biomass of a target individual of species i grown with a neighbor of species j (con- or heterospecific) at distance d . Relative neighbor size is calculated as total neighbor biomass divided by total target biomass.

Another spatial process potentially maintaining coexistence is intraspecific aggregation, whereby individuals mainly compete with conspecifics. It has been shown that intraspecific aggregation slows down the competitive exclusion of inferior species in annual (Stoll and Prati 2001; Monzeglio and Stoll 2005, 2008) and perennial (Schmidt 1981) herbaceous species. Besides reducing the frequency of interspecific interactions, intraspecific aggregation can enhance the local abundance of weak competitors and reduce that of strong competitors. This is because intraspecific competition is weaker than interspecific competition for inferior species and vice versa for superior species. Our findings are in accordance with this: the competitively inferior species did better with a conspecific neighbor, while the opposite result was observed for the competitively superior species. However, theory suggests that, individually, within-species aggregation and between-species segregation is insufficient to generate stable coexistence—that is, recovery of all species from a low density—since the stronger species will overrun clusters of the weaker species when the two species meet in space (Neuhauser and Pacala 1999).

If heteromyopia is a general coexistence mechanism, then we should have discovered a strong signal, independent of the biology of the investigated species. It has been hypothesized that heteromyopia might be aided by mechanisms that indirectly shape the competition kernels (Murrell and Law 2003). These might include host-specific vectors, such as specialist pathogens, herbivores, or seed

predators (Janzen 1970; Connell 1971); host-specific mycorrhizal fungi (Stoll and Newbery 2005); or allelopathy. In our experiment, host-specific enemies were excluded, our species associate with arbuscular mycorrhizal fungi (much less host specific than, e.g., ectomycorrhizal fungi), and the frequency and importance of allelopathy in plant-plant interactions is, so far, still widely unknown. Therefore, we assume that direct neighbor interactions—mainly, belowground competition—dominated in our experimental system. From our results, we conclude that if heteromyopia should prove to be a general coexistence mechanism, then it probably does not result from resource competition. Whether this conclusion can be generalized to other sessile communities beyond plants remains an open question. However, Noda (2009) suggested that heteromyopia is unlikely to operate in rocky intertidal sessile assemblages because neither host-specific enemies nor allelopathy have been reported from these assemblages.

Neighbor Identity versus Neighbor Size

Our results clearly showed the performance of target individuals to be inhibited by the presence of a neighbor, and the competitive response to a neighbor declined with distance. Species differed in how strongly they responded to their conspecific and heterospecific neighbors, but these neighbor identity effects were mainly due to species-specific size differences. Including neighbor size substantially increased empirical support of the statistical models

(see app. B). It is interesting to note that the size of the neighbor relative to the target individual, rather than the absolute size of the neighbor, explained most of the variation in the results; this emphasizes the importance of taking on the "plant's eye view" (Turkington and Harper 1979) when examining and modeling plant-plant interactions.

The question of whether competitive strength is determined by neighbor size or neighbor identity has been investigated previously for three dune species in competition experiments using seedlings and adult plants (Weigelt et al. 2002). Competition intensity was analyzed for its relationship with final neighbor size and neighbor identity, and the authors of that study concluded that competition intensity generally depends on species-specific traits such as biomass allocation strategies, while size differences are important only at early life stages such as seedling establishment. This stands in contrast to the results of our experiment, where size differences between neighboring adult plants accounted for 70% of the variability in competitive response. One explanation for this disparity is that, in our study, plants were sown in pairs and grown together for the entire duration of the experiment. It could well be that differences in germination speed and species-specific growth rates have led to differences in size at early life stages. These differences might even have increased during the course of our experiment (app. A).

It has been suggested that coexisting plant species are those that are equivalent in competitive ability for shared resources (Aarssen 1983). Consequently, competitive effects should be equivalent on a per unit size basis, but not necessarily on a per individual basis, since species vary greatly in average size. Goldberg and Werner (1983) have argued that competitive equivalence per unit size could be expected for three reasons: (1) all plant species compete for the same few resources, (2) individuals of any particular species pair have a low encounter probability, and (3) competitive interactions are predominated by size asymmetries between individuals, such that if a neighbor is larger than a target individual, then the identity of the neighbor is of much lesser importance. This argument is supported by the results of an earlier comparison of competitive effects of seven plant species on *Solidago canadensis* (Goldberg 1987), and our results are similar in that strong neighbor effects were primarily due to species-specific differences in size.

Can we therefore conclude that, on a per unit size basis, species are ecologically equivalent? Our results provide evidence both for and against this. We found no difference in the average response to conspecific and heterospecific neighbors when all species and neighbor sizes were taken together. Similarly, when data were averaged over all species, there was no difference in how competitive response

to conspecific and heterospecific neighbors declined with distance. This would imply that equal competition kernels could be used to model intraspecific and interspecific interactions. On the other hand, species differed in how their responses scaled with neighbor size: the competitive response of *Plantago media* increased most rapidly with neighbor size, and that of *P. lanceolata* increased the least rapidly. This nonequivalence of species might be partly due to species-specific biomass allocation strategies. Moreover, when all species were taken together, the competitive response to conspecifics increased more rapidly with neighbor size than did the competitive response to heterospecifics. Relative size differences between neighboring plants should therefore be accounted for by additional scaling parameters allowing for flexible intraspecific and interspecific competition coefficients.

Size-Identity Interaction

A nearby neighbor that is much larger will have a large negative effect on an individual, regardless of its species identity. However, our results suggest that there might be a general interaction between neighbor size and identity. In considering all species together, we found that the competitive response of a target individual was independent of neighbor identity as long as the neighbor was of equal size or only slightly larger; with increasing size differences, however, individuals became more sensitive to conspecific neighbors (fig. 5B). If such a size-identity interaction is found frequently in empirical data, then this could have important implications for community dynamics. For example, it may well affect seedling establishment, making establishment near a heterospecific of a given size more likely than establishment near a conspecific. As has been shown repeatedly for tropical trees (e.g., Harms et al. 2000), seedling establishment near heterospecifics is often more likely than establishment near conspecifics. Moreover, our data suggest that a size-identity interaction could further influence the performance of individuals at later stages. Both processes may promote coexistence and help maintain community diversity. Specific target-neighbor experiments that combine seedlings and adult plants are needed to test this hypothesis.

Conclusions

As with every experiment, there are trade-offs between controlling for environmental variability and experimental artificiality. Plants in our experiment were grown in relatively small containers, in homogenous substrate, and in the greenhouse without natural enemies or climatic stress. Furthermore, our neighborhoods consisted of a single neighbor, a very unlikely situation in calcareous grasslands.

Nevertheless, individual-based models are built on such pairwise neighbor interactions, and the aim of our study was to experimentally test these basic elements of spatial theory. Given these caveats, our study provided empirical evidence that both the intensity of competitive interactions and the distance over which these occur are primarily determined by the relative size differences between neighboring plants, irrespective of their conspecific or heterospecific identity. Species-specific size differences between individuals, which are most likely related to species-specific life-history traits, account for effects of neighbor identity. Discovering the various life-history traits that are associated with large or small neighborhood ranges is an important next step in uncovering the crucial processes that determine plant community structure and dynamics. Future research should also focus on the dynamics of the patterns observed in our experiment. For example, investigating the onset of competition and how this relates to species identity and size differences between neighbors would foster our understanding of the underlying processes of competition. Moreover, the observation that conspecific interactions may become more important than heterospecific interactions if size differences are large reveals the complex nature of size-based competition, and it points to new processes that must be explored by theoretical models.

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Literature Cited

- Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *American Naturalist* 122:707–731.
- Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a synthesis. *Ecology Letters* 6:1109–1122.
- Anderson, K., and C. Neuhauser. 2002. Patterns in spatial simulations: are they real? *Ecological Modelling* 155:19–30.
- Antonovics, J., and D. A. Levin. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics* 11:411–452.
- Barot, S. 2004. Mechanisms promoting plant coexistence: can all the proposed processes be reconciled? *Oikos* 106:185–192.
- Bell, G. 2000. The distribution of abundance in neutral communities. *American Naturalist* 155:606–617.
- Berger, U., C. Piou, K. Schiffrers, and V. Grimm. 2008. Competition among plants: concepts, individual-based modelling approaches, and a proposal for a future research strategy. *Perspectives in Plant Ecology, Evolution and Systematics* 9:121–135.
- Bolker, B. M., and S. W. Pacala. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist* 153:575–602.
- Bolker, B. M., S. W. Pacala, and C. Neuhauser. 2003. Spatial dynamics in model plant communities: what do we really know? *American Naturalist* 162:135–148.
- Cahill, J. E., S. W. Kembel, and D. J. Gustafson. 2005. Differential genetic influences on competitive effect and response in *Arabidopsis thaliana*. *Journal of Ecology* 93:958–967.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–310 in B. J. den Boer and G. R. Gradwell, eds. *Dynamics of populations*. Centre for Agricultural Publishing and Documentation, Wageningen.
- Fraser, L. H., and T. E. Milette. 2008. Effect of minor water depth treatments on competitive effect and response of eight wetland plants. *Plant Ecology* 195:33–43.
- Freckleton, R. P., and A. R. Watkinson. 2001. Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits. *Ecology Letters* 4:348–357.
- Goldberg, D. E. 1987. Neighborhood competition in an old-field plant community. *Ecology* 68:1211–1223.
- Goldberg, D. E., and A. M. Barton. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *American Naturalist* 139:771–801.
- Goldberg, D. E., and L. Fleetwood. 1987. Competitive effect and response in four annual plants. *Journal of Ecology* 75:1131–1143.
- Goldberg, D. E., and K. Landa. 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79:1013–1030.
- Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant-communities: a null hypothesis and a field experimental approach. *American Journal of Botany* 70:1098–1104.
- Goldberg, D. E., T. Rajaniemi, J. Gurevitch, and A. Stewart-Oaten. 1999. Empirical approaches to quantifying interaction intensity: competition and facilitation along productivity gradients. *Ecology* 80:1118–1131.
- Grimm, V., and S. F. Railsback. 2005. Individual-based modeling and ecology. Princeton series in theoretical and computational biology. Princeton University Press, Princeton, NJ.
- Gurevitch, J., L. L. Morrow, A. Wallace, and J. S. Walsh. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140:539–572.
- Harms, K. E., S. J. Wright, O. Calderon, A. Hernandez, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–495.
- Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.
- Hubbell, S. P., J. A. Ahumada, R. Condit, and R. B. Foster. 2001.

- Local neighborhood effects on long-term survival of individual trees in a Neotropical forest. *Ecological Research* 16:859–875.
- Janzen, D. H. 1970. Herbivores and number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Law, R., D. W. Purves, D. J. Murrell, and U. Dieckmann. 2001. Causes and effects of small-scale spatial structure in plant populations. Pages 21–44 in J. Silvertown and J. Antonovics, eds. *Integrating ecology and evolution in a spatial context*. Blackwell Science, Oxford.
- Law, R., D. J. Murrell, and U. Dieckmann. 2003. Population growth in space and time: spatial logistic equations. *Ecology* 84:252–262.
- Mack, R. N., and J. L. Harper. 1977. Interference in dune annuals: spatial pattern and neighbourhood effects. *Journal of Ecology* 65:345–363.
- Milbau, A., D. Reheul, B. De Cauwer, and I. Nijs. 2007. Factors determining plant-neighbour interactions on different spatial scales in young species-rich grassland communities. *Ecological Research* 22:242–247.
- Monzeglio, U., and P. Stoll. 2005. Spatial patterns and species performances in experimental plant communities. *Oecologia (Berlin)* 145:619–628.
- . 2008. Effects of spatial pattern and relatedness in an experimental plant community. *Evolutionary Ecology* 22:723–741.
- Murrell, D. J. 2009. On the emergent spatial structure of size-structured populations: when does self-thinning lead to a reduction in clustering? *Journal of Ecology* 97:256–266.
- Murrell, D. J., and R. Law. 2003. Heteromyopia and the spatial coexistence of similar competitors. *Ecology Letters* 6:48–59.
- Murrell, D. J., D. W. Purves, and R. Law. 2002. Intraspecific aggregation and species coexistence. *Trends in Ecology & Evolution* 17:211–212.
- Neuhauser, C., and S. W. Pacala. 1999. An explicitly spatial version of the Lotka-Volterra model with interspecific competition. *Annals of Applied Probability* 9:1226–1259.
- Noda, T. 2009. Metacommunity-level coexistence mechanisms in rocky intertidal sessile assemblages based on a new empirical synthesis. *Population Ecology* 51:41–55.
- Pacala, S. W. 1997. Dynamics of plant competition. Pages 532–555 in M. J. Crawley, ed. *Plant ecology*. Blackwell Scientific, Oxford.
- Pacala, S. W., and S. A. Levin. 1997. Biologically generated spatial pattern and the coexistence of competing species. Pages 204–232 in D. Tilman and P. Kareiva, eds. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, NJ.
- Pacala, S. W., and J. A. Silander. 1987. Neighborhood interference among velvet leaf, *Abutilon theophrasti*, and pigweed, *Amaranthus retroflexus*. *Oikos* 48:217–224.
- . 1990. Field-tests of neighborhood population-dynamic models of two annual weed species. *Ecological Monographs* 60:113–134.
- Peters, H. A. 2003. Neighbour-regulated mortality: the influence of positive and negative density dependence on tree populations in species-rich tropical forests. *Ecology Letters* 6:757–765.
- Purves, D. W., and R. Law. 2002. Experimental derivation of functions relating growth of *Arabidopsis thaliana* to neighbour size and distance. *Journal of Ecology* 90:882–894.
- Queenborough, S. A., D. Burslem, N. C. Garwood, and R. Valencia. 2007. Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology* 88:2248–2258.
- Ramseier, D., and J. Weiner. 2006. Competitive effect is a linear function of neighbour biomass in experimental populations of *Kochia scoparia*. *Journal of Ecology* 94:305–309.
- R Development Core Team. 2007. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Schmidt, W. 1981. Über das Konkurrenzverhalten von *Solidago canadensis* und *Urtica dioica*. *Verhandlungen der Gesellschaft für Ökologie* 9:173–188.
- Schneider, M. K., R. Law, and J. B. Illian. 2006. Quantification of neighbourhood-dependent plant growth by Bayesian hierarchical modelling. *Journal of Ecology* 94:310–321.
- Snyder, R. E. 2008. When does environmental variation most influence species coexistence? *Theoretical Ecology* 1:129–139.
- Snyder, R. E., and P. Chesson. 2004. How the spatial scales of dispersal, competition, and environmental heterogeneity interact to affect coexistence. *American Naturalist* 164:633–650.
- Stoll, P., and D. M. Newbery. 2005. Evidence of species-specific neighbourhood effects in the Dipterocarpaceae of a Bornean rain forest. *Ecology* 86:3048–3062.
- Stoll, P., and D. Prati. 2001. Intraspecific aggregation alters competitive interactions in experimental plant communities. *Ecology* 82:319–327.
- Stoll, P., and J. Weiner. 2000. A neighborhood view of interactions among individual plants. Pages 11–27 in U. Dieckmann, R. Law, and J. A. J. Metz, eds. *The geometry of ecological interactions: simplifying spatial complexity*. Cambridge University Press, Cambridge.
- Tilman, D., and P. Kareiva. 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, NJ.
- Turkington, R., and J. L. Harper. 1979. Growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture. I. Ordination, pattern and contact. *Journal of Ecology* 67:201–218.
- Uriarte, M., R. Condit, C. D. Canham, and S. P. Hubbell. 2004. A spatially explicit model of sapling growth in a tropical forest: does the identity of neighbours matter? *Journal of Ecology* 92:348–360.
- Weigelt, A., and P. Jolliffe. 2003. Indices of plant competition. *Journal of Ecology* 91:707–720.
- Weigelt, A., T. Steinlein, and W. Beyschlag. 2002. Does plant competition intensity rather depend on biomass or on species identity? *Basic and Applied Ecology* 3:85–94.
- Weiner, J., and P. T. Conte. 1981. Dispersal and neighborhood effects in an annual plant competition model. *Ecological Modelling* 13:131–147.

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