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Competitive size asymmetry, not intensity, is linked to species loss and gain in a native grassland community

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Abstract

Competition is often highlighted as a major force influencing plant species diversity. However, there are multiple facets of competition (e.g., strength, intransitivity, and size asymmetry) that may have independent and differential impacts on diversity, making understanding the degree to which competition structures communities difficult. Unfortunately, field-based experiments that decouple multiple facets of competition are lacking, limiting our ability to test theoretical frameworks and reducing understanding of the actual linkages among competition and coexistence. Here, we experimentally manipulate the size structure of local grassland communities to examine the relative impacts of competitive size asymmetry (i.e., competitive advantage based on relative size) and intensity (i.e., mean effect of neighbors on plant growth) on species loss and gain. Increased competitive size asymmetry was associated with increased species loss and decreased species gain, while no relationship was found between competitive intensity and species loss and gain. Furthermore, the probability of loss was not dependent on a species initial size, suggesting that small species may not always be the losers of size-asymmetric interactions. Instead, loss was dependent on species rarity, where loss was higher for rare species. Overall, these results suggest that competitive size asymmetry may be more important for species loss than intensity in some plant communities and demonstrates the importance of decoupling different aspects of competition to better understand their drivers and ecological consequences.

KEYWORDS
coexistence, competitive intensity, determinants of plant community diversity and structure, plant–plant interactions, rare species, size structure, size-asymmetric competition, species gain, species loss, species turnover

INTRODUCTION

Competition is often cited as a process that limits species coexistence and diversity. Consequently, mechanisms suggested to promote and maintain diversity tend to focus on limiting competitive interactions either through niche partitioning in space and time (HilleRisLambers et al., 2012; Levine & HilleRisLambers, 2009; Macarthur & Levins, 1967), intransitivity (Laird & Schamp, 2006), or the presence of density-independent forces than limit competitive dominance (Chesson, 2000; Connell, 1978). All of these processes act to neutralize the competitive exclusion principle that assumes intense interspecific competition leads to species loss (Hardin, 1960; Huston, 1979) in the absence of

counterbalancing forces (Chesson, 2000). However, the few empirical studies that have tested links between competitive strength and species diversity have inconsistent results (e.g., Bagousse-Pinguet et al., 2014; Hautier et al., 2009; Lamb et al., 2009; Lamb & Cahill Jr., 2008; Martorell & Freckleton, 2014; Michalet et al., 2015; Mitchell et al., 2009), suggesting either that competition is not important for community structure or that we do not have a clear understanding of how competition may limit species diversity.

Within plants, one of the major mechanisms by which plants compete is through resource competition, where plants limit each other's growth and performance through the capture of finite resources within a shared resource pool (Aschehoug et al., 2016). Thus, a large part of resource competition is a plant's ability to find, reach, and uptake (i.e., preempt) a limiting resource before its neighbors (Novoplansky, 2009; Craine et al., 2005). Size is often related to a plant's ability to preempt resources. For example, it is well understood that a plant's size is directly related to its ability to preempt sunlight, such that larger individuals are able to overtop and shade-out their neighbors (Schwinning & Weiner, 1998). This ability of larger plants to preempt a disproportionate amount of resources relative to their size is described by the size asymmetry of competitive interactions (Hara, 1986; Weiner, 1990), which can have direct impacts on species diversity through the species loss (DeMalach et al., 2017; Goldberg & Miller, 1990; Hautier et al., 2009). Due to the

link between competitive size asymmetry and the mechanisms by which plants compete, competitive size asymmetries may be more linked to community dynamics than competitive intensity.

If competitive size asymmetry is particularly important for the maintenance of species diversity, one may expect species loss and gain to depend on the size structure of communities (Figure 1). For example, if size impacts an individual's or species' fitness or ability to acquire a larger amount of resources (Goldberg, 1996; Goldberg et al., 2017; Grime, 1977; Keddy, 2001), then manipulations to size structure should alter levels of competition within a community either through altering resource availability or fitness differences between individuals or species within the community. It may be expected then that when conditions favoring competitive size asymmetry are heightened (i.e., large individuals are present), community dynamics and turnover in a community will be dominated by the loss of species particularly vulnerable to competitive size asymmetries. However, with size sensitivity being a species-level trait (Brown et al., 2019), it is unclear whether loss will necessarily target small species (DeMalach et al., 2016), species that cannot tolerate resource inequalities (Newman, 1973), or is random and thus first targets rare species (Goldberg & Miller, 1990; Oksanen, 1996).

Size-asymmetric competition may be more common than once thought, making understanding its role in community assembly critical. There is increasing evidence that size-asymmetric competition is not restricted to
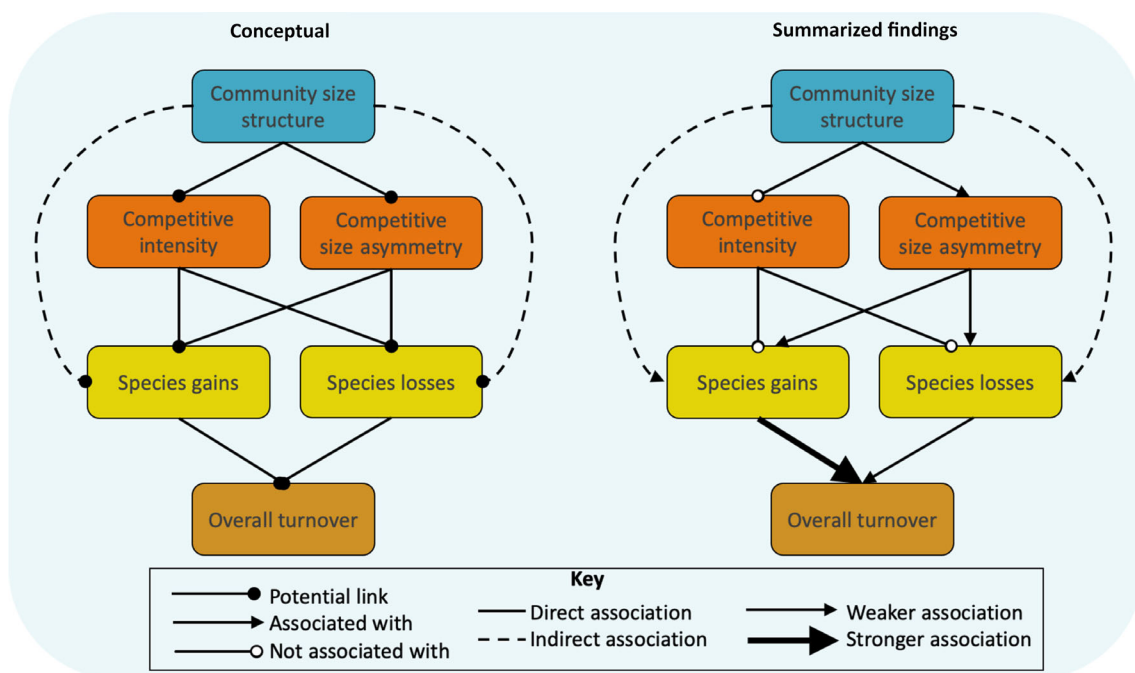

FIGURE 1 Conceptual and realized relationship between community size structure, the degree of competitive intensity and size asymmetry, and species turnover. Summarized findings represent inferred relationships based on tested links within the manuscript

environments with intense competition, high productivity, and low light availability, as previously thought (reviewed in Schwinning & Weiner, 1998). Competitive size asymmetry has been shown to be independent of competitive intensity (Brown et al., 2019) as competition can be intense but equal among species (i.e., size symmetric) or weak and focused on small individuals (i.e., size asymmetric; Schwinning & Weiner, 1998), ultimately having differential impacts on community assembly and species coexistence. Further, these effects of size-asymmetric competition are expected to apply in both resource-rich and resource-poor environments for aboveground and belowground resources (Brown et al., 2019; DeMalach et al., 2016; Rasmussen et al., 2019). Thus, there is a need to determine the relative importance of competitive intensity and size asymmetry on species diversity and what environments they are both strongest.

Here, we experimentally manipulated the size structure within 57 native grassland communities while monitoring the growth of eight focal species over three growing seasons to test: (1) how the removal of large individuals alters the relative importance of species gain and loss for turnover within communities, (2) whether species gain and loss is driven by competitive intensity or size asymmetry, and (3) what environments promote increased competitive intensity and size asymmetry.

MATERIALS AND METHODS

Study site

The study site is located in a 50-ha field at the Roy Berg Kinsella Research Ranch in Kinsella, AB, Canada (53°5′ N, 111°33′ W). It is a savannah-like habitat with stands of trembling aspen (*Populus tremuloides* Michx.) within a matrix of rough fescue prairie. The rough fescue prairie is primarily dominated *Hesperostipa curtiseta* (Hitchc.) Barkworth, *Festuca hallii* (Vasey) Piper and *Poa pratensis* L.; however, much of the diversity is among forbs (Brown & Cahill, 2019). The study site ranges in plant size structures (Brown & Cahill, 2019), is primarily limited by water and nitrogen (Lamb et al., 2007) and typically has strong root competition (Lamb & Cahill, 2008). Historically, the site has been grazed by cattle, the last grazing event occurring the fall before the study began.

Focal species

Two hundred and fifty-five in situ focal ramets (hereafter referred to as individuals) were selected semi-randomly (needed to appear healthy) prior to experimental thinning and represent the most dominant species at the study site (Brown & Cahill, 2019; Lamb & Cahill Jr., 2008). Focal individuals were one of eight species from four families: Asteraceae (*Artemisia frigida* Willd. and *Artemisia ludoviciana* Nutt.), Poaceae (*F. hallii* (Vasey) Piper, *H. curtiseta* (Hitchc.), and *P. pratensis* L.), Rubiaceae (*Galium boreale* L.), and Rosaceae (*Geum triflorum* Pursh and *Rosa arkansana* Porter.). Due to the system being dominated by long-living perennials, we utilized in situ focal individuals rather than transplants since transplants typically do not fully reflect established vegetation responses in these systems (Lamb & Cahill, 2006). Consequently, we chose to focus on competitive interactions between established individuals rather than the impacts of competition on other life stages (e.g., seedlings).

Experimental design

Fifteen experimental blocks (160 × 320 cm) were set up within one of the largest contiguous grassland patches (~250 × 350 m) at the study site. Each block contained three to four in situ focal individuals grown in one of five neighbor removal treatments that varied in neighbor abundance and size structure: total neighbor removal, no neighbor removal, and three partial neighbor removals, where 30% of the plot biomass was removed by size class (i.e., small, medium, and large ramets; Figure 2a). No and partial neighbor removal treatments were used to obtain variation in the relative initial size of focal individuals needed to measure competitive size asymmetries (Figure 2b; Brown et al., 2019; Weiner, 1990.) The total neighbor removal treatment was used to obtain a measure of focal individual performance in the absence of neighbors needed to measure competitive intensity.

Partial neighbor removal treatments were applied to ensure equal total biomass reduction regardless of the neighbor size class removed due to the recognition that overall intensity of competition can be driven by productivity differences and per-gram effects. Consequently, removal led to a variation in ramet density between treatments. On average, 85 ± 12 (mean $\pm$ SE), 262 ± 19, and 791 ± 19 ramets/m^2 were removed from the large, medium, and small neighbor removal treatments, respectively. Changes in ramet density can be important for competitive size asymmetry as they may indicate that it is acting (Weiner, 1986), so we measured community-level ramet density throughout the experiment to determine if it altered our observed levels of competition.

Neighbor ramets were removed by clipping their stem at the soil surface and then painting the cut stems with glyphosate herbicide to ensure complete plant death
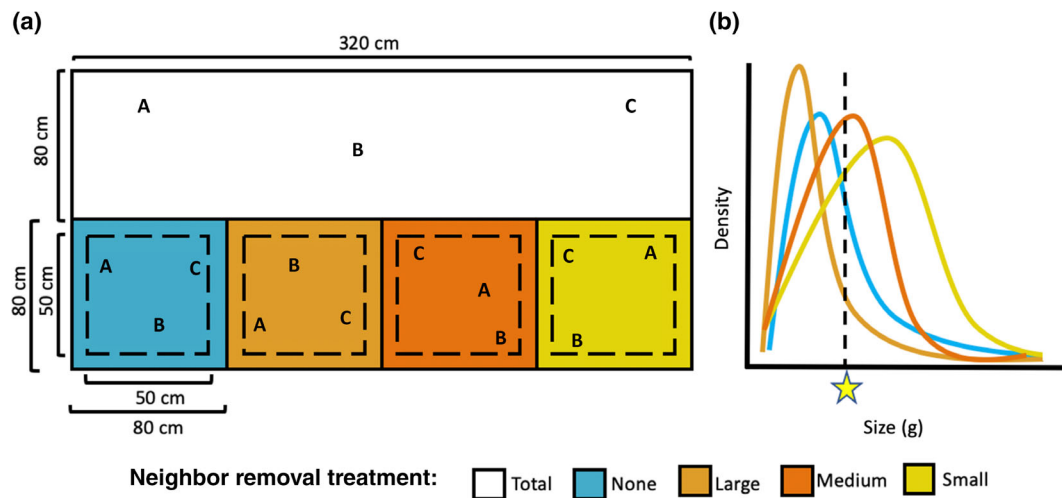
FIGURE 2 (a) Schematic representation of the experimental thinning treatments. A, B, and C represent different focal species within each plot. The five treatments were "total" (all neighbors removed), "none" (no neighbors removed), "large" (30% of the biomass removed using large individuals), "medium" (30% of the biomass removed using medium individuals), and "small" (30% of the biomass removed using small individuals). These five treatments were replicated 15 times. The total removal treatment was used as a reference to calculate competition metrics. (b) Conceptual representation of how neighbor removal treatments alter the relative initial size of focal individuals. Each line represents the size distribution of all individuals within a local community in each removal treatment. The star represents the initial size of a focal individual and the dotted line shows where that focal individual falls in the community's size distribution

aboveground and belowground. In the partial removal treatments, removal by size was based on visual inspection and was not proportional between species; however, partial removals did not alter species richness within plots (Appendix S1: Figure S1). Glyphosate application was applied once at the start of the experiment (i.e., May 2016) in all treatments except the total neighbor removal treatment, where glyphosate was applied every month during the growing season to ensure focal individuals had continued growth without neighbors. At the beginning of the experiment, root and rhizome connections were severed to a depth of 15 cm around each experimental plot to reduce belowground interactions between treatments (Lamb & Cahill Jr., 2008). All plots were 80 by 80 cm except for the total neighbor removal plots, which were 80 by 320 cm to reduce interactions between focal individuals in the plot.

The initial size of focal individuals was estimated using species-specific biomass regressions based on height, width, and flowering traits that were calibrated on additional plants collected at the field site (see Appendix S1: Table S1). R^2 values were between 0.945 and 0.989 for all species. The final performance of focal individuals was measured using aboveground biomass at the end of the experiment. In August 2018, after three growing seasons, focal plants were clipped at the soil surface, dried, and weighed. Due to mortality during the experiment, 209 focal plants were used in the analysis (see Appendix S1: Tables S2 and S3 for the exact number of each species that remained per treatment).

Competition metrics

The intensity and size asymmetry of competition within local communities were estimated using the average performance of the focal individuals within each plot (see Appendix S1: Figure S2). Here, we make the assumption that individual plant responses will correlate to community-level processes. We were unable to calculate a community-level measure for three plots due to focal plant mortality resulting in only one focal plant being left at the end of the experiment. These plots were excluded from analyses requiring focal plant data.

The intensity of competition was measured as competitive response, which is the natural log of the proportion of aboveground biomass of a plant growing with and without neighbors (Cahill, 1999; Weigelt & Jolliffe, 2003). To better incorporate variation in alone plant performance, for each individual, a log-response ratio was calculated for every possible pairing of that individual's performance and the performance of individuals of the same species in each replicate of the total neighbor removal treatment (Lamb & Cahill, 2006). More formally,

$$\mathrm{CR_{ind}} = \frac{\sum\limits_{i=1}^{N} \ln\left(\frac{\mathrm{AB_{Neighbor}}}{\mathrm{AB_{TNR},i}}\right)}{N}$$

where $\mathrm{AB_{Neighbor}}$ is the aboveground biomass of an individual within a plot grown with neighbors and $\mathrm{AB_{TNR}}$ is the aboveground biomass of an individual of the same

species in each replicate (N) of the total neighbor removal treatment (i.e., grown without neighbors).

The community-level intensity of competition used in the analysis was estimated by averaging the competitive response of all focal species found within a plot. More formally,

$$\mathrm{CR}_{\mathrm{plot}} = -1 \times \frac{\sum_{i=1}^{S} \mathrm{CR}_{\mathrm{ind},i}}{S}$$

where $\mathrm{CR}_{\mathrm{ind},i}$ is the competitive response of species i within a plot and S is the number of unique focal species found within that plot. Increasingly positive values of $\mathrm{CR}_{\mathrm{plot}}$ indicate that local community is experiencing stronger competition, while increasingly negative values indicate stronger facilitation within the local community.

The degree of size-asymmetric competition experienced by a species can be measured as the slope of a logarithmic regression between an individual's competitive response and its initial size relative to its neighbors (Brown et al., 2019). The degree of size-asymmetric competition experienced by an individual ($\mathrm{CSA}_{\mathrm{ind}}$) was calculated as the derivative of the species-level logarithmic regression, or

$$\mathrm{CSA}_{\mathrm{ind}} = \mathrm{CSA}_{\mathrm{spp}} \times \frac{1}{\mathrm{RIS}_{\mathrm{ind}}},$$

where $\mathrm{CSA}_{\mathrm{spp}}$ is the species-level degree of competitive size asymmetry (values reported in Appendix S1: Figure S3) and $\mathrm{RIS}_{\mathrm{ind}}$ is the initial size of a focal individual relative to its neighbors. $\mathrm{RIS}_{\mathrm{ind}}$ was calculated as the estimated initial biomass of a focal individual (Appendix S1: Table S1) relative to the average initial biomass of neighbor plants (estimated by dividing the plots total biomass by its ramet density (Appendix S1: Figure S4). Results were not sensitive to how relative initial size was defined (Appendix S1: Table S4).

The plot-level measure of the degree of size-asymmetric competition that was used in the analysis was calculated by averaging the degree of size-asymmetric competition experienced by all focal species in each plot. More formally,

$$\mathrm{CSA}_{\mathrm{plot}} = \frac{\sum_{i=1}^{S} \mathrm{CSA}_{\mathrm{ind},i}}{S},$$

where $\mathrm{CSA}_{\mathrm{ind},i}$ is the degree of size asymmetry experienced by species i within a plot and S is the number of unique focal species found within that plot. Increasingly positive values of $\mathrm{CSA}_{\mathrm{plot}}$ indicate that a local

community is experiencing size-asymmetric competition, while increasingly negative values indicate partially symmetric competition and values of zero indicate that competition is size symmetric within the local community (as defined by Schwinning & Weiner, 1998 and Brown et al., 2019).

Community composition and temporal beta-diversity

Species presence and absence was measured within a 50 by 50 cm region of each experimental plot at the start (i.e., June 2016) and end (i.e., August 2018) of the experiment. For each plot, we measured temporal beta-diversity, which provides the dissimilarity in species composition between the two timepoints (Legendre, 2019). The dissimilarity was computed using the Jaccard index and range from 0 to 1, where 0 represents exact similarity in species present between the two timepoints and 1 represents no similarity in the species present between the two timepoints. The total dissimilarity is the sum of the scaled number of gains and loss, so we can partition species compositional change between the two timepoints into relative gains (number of species gained over time relative to the number of species shared, gained, and lost over time) and losses (number of species lost over time relative to the number of species shared, gained, and lost over time; Legendre, 2019). Partitioning temporal beta-diversity into species gain and loss allows us to test (1) whether species turnover is mostly driven by species gain or loss over time and (2) whether species gain and loss are differentially related to the same ecological processes (i.e., competitive intensity and size asymmetry).

Environmental measures

To determine what environmental factors are associated with competitive intensity and size asymmetry, environmental variables were measured in each plot during peak biomass from mid-July to mid-August 2018. Before harvest, we measured stem density, light availability, and soil moisture. Stem density was measured as the number of ramets that touched one of three 50-cm transects placed 10, 25, and 40 cm from and parallel to one of the edges of the plot (Brown & Cahill, 2019). Vegetative height of ramets that touched these transects was also taken at the beginning of the study (June 2016) to estimate a species initial height. These height measures were used to determine if probability of loss was a consequence of a species initial height. Light availability was measured as the ratio of photosynthetically active

radiation (PAR) found below versus above the vegetation using an Accu-Par light meter (Decagon). Soil moisture (%) was measured using an ML3 ThetaProbe Soil Moisture Sensor (Delta-T Devices). During harvest, plots were raked to measure litter biomass, and the remaining standing biomass was clipped at the soil surface to measure shoot biomass. Root biomass was measured from a 5 by 20 cm soil core taken in the middle of each plot. Roots were washed over a 2 mm sieve. All biomass samples were dried at 65°C for 48 h before being weighed. To determine soil pH and inorganic nitrogen content, soil from the root cores was saved for pH determination and nutrient extraction using the methods outlined in Chagnon et al. (2018).

Statistical analysis

To determine whether the degree of species turnover differed among thinning treatments, we used a linear mixed model with the temporal beta-diversity index as a response variable, the thinning treatment (no and partial removal treatments) as a fixed effect, and block as a random effect. For each thinning treatment, we then used a paired t test of the difference between the relative contribution of gain and loss using the TBI function in R (Dray et al., 2012) to test whether temporal beta-diversity was primarily driven by gain or loss in each treatment.

To determine the relative importance of competitive intensity versus the degree of competitive size asymmetry for species gain and loss, we ran two linear mixed models with either the relative contributions of gains or losses as response variables. For each model, community-level competitive intensity and the degree of size-asymmetric competition were fixed factors and block was a random factor. Since the scale of size asymmetry ranges from partially symmetric (slope < 0) to size symmetric (slope = 0) to size asymmetric (slope > 0), the degree of size-asymmetric competition was initially included as both a linear and quadratic term to determine if these relationships were dependent on only larger individuals having the competitive advantage (linear) or any individual, small or large, having the competitive advantage (quadratic). To determine whether species loss was a consequence of a species initial size or abundance, two binomial generalized linear models were fit with either initial height or abundance as fixed factors and whether or not that species was lost as the response variable. For both models, block and species identity were fit as random factors.

To determine which environmental factors were associated with competitive intensity and size-asymmetric competition, two linear mixed models were fit with either community-level competitive intensity or size asymmetry as response variables. Fixed factors included (1) focal species identity, measured as two axes of a nonmetric multidimensional scaling with focal species presence or absence, (2) productivity, measured as shoot, litter, and root biomass separately, (3) stem density, (4) light availability, (5) soil properties, measured separately as pH, inorganic nitrogen, and moisture. Variables were standardized to have a mean of 0 and a standard deviation of 1 prior to analysis to permit comparisons between environmental factors (Maynard et al., 2017). Block was included as a random effect. All analyses were run using the *lmerTest* (Kuznetsova et al., 2017), *lme4* (Bates et al., 2015), *adespatial* (Dray et al., 2012), and *vegan* (Dixon, 2003) packages in R (v 3.4.3).

RESULTS

Impacts of community size structure on species turnover

The degree of species turnover did not vary as a function of community size structure manipulations ($F_{3,38.6} = 1.913$, $p = 0.144$), with mean turnover being 0.39 ± 0.02 (mean $\pm$ SE) over all plots. However, whether turnover was driven by species gain or loss differed among treatments indicating differences in assembly processes. The removal of medium and large neighbors resulted in species gain contributing more to species turnover than species loss ($t_{14} = 2.75$, $p = 0.016$ and $t_{14} = 3.42$, $p = 0.007$, respectively). There was no significant difference between the contribution of species gain and loss when no neighbors or small neighbors were removed ($t_{14} = 1.05$, $p = 0.311$ and $t_{14} = 1.29$, $p = 0.219$, respectively).

Influence of competitive strength and size asymmetry on species gain and loss

The relative contribution of species gain and loss to species turnover varied with competitive size asymmetry but not intensity (Figure 3). Species loss was more likely to occur when larger individuals had the competitive advantage (i.e., under size-asymmetric competition), whereas species gain was more likely to occur when competition was size symmetric. Surprisingly, the probability of loss was independent of a species' initial height but increased with a species' rarity (Figure 4); the rarity of a species was independent of its initial height (Appendix S1: Figure S5).
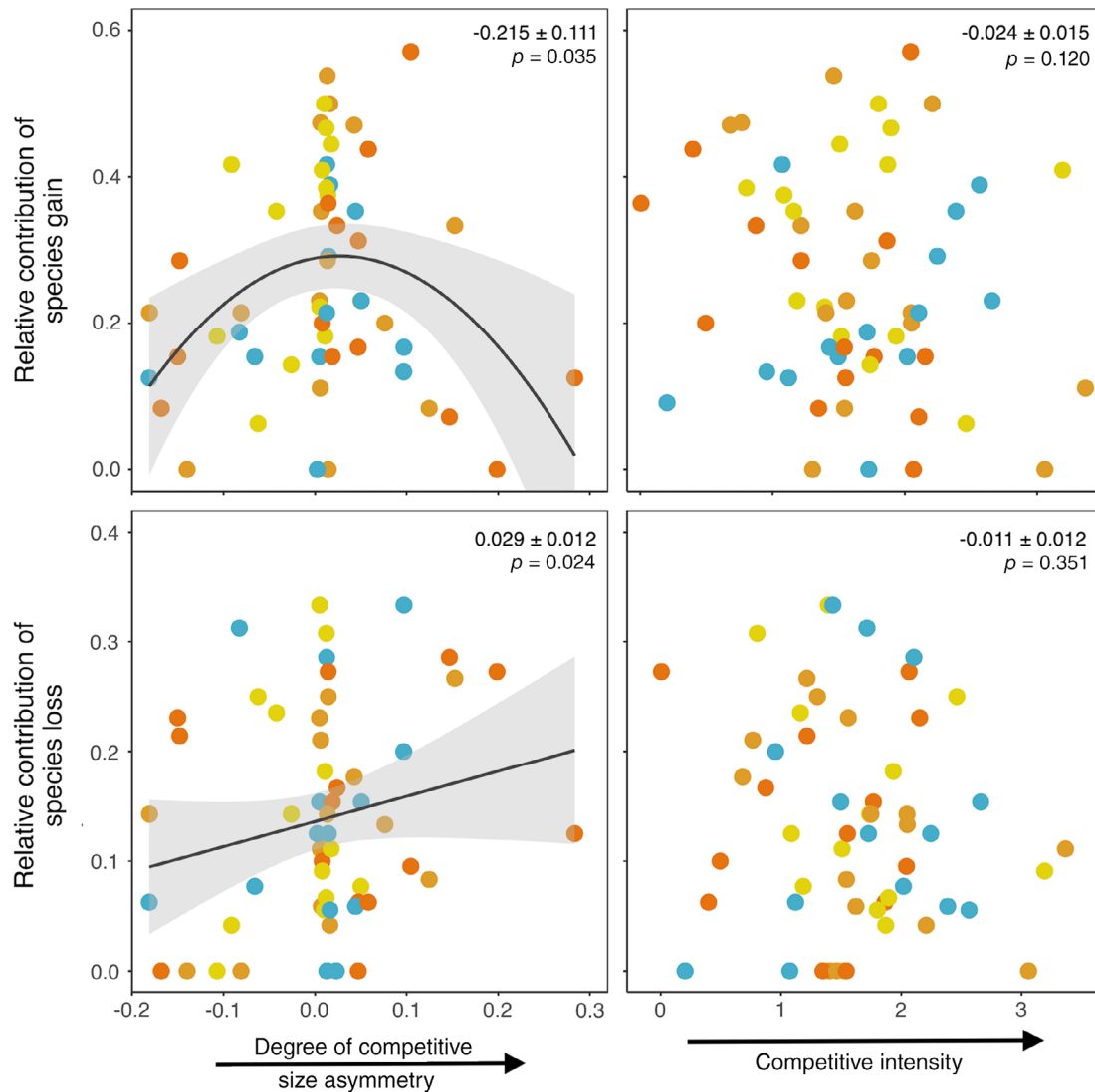
FIGURE 3 The relationship between competitive intensity and size asymmetry and the contribution of species gain and loss to species turnover. Higher contributions for the degree of size-asymmetric competition, values <0 represent partial symmetry, values = 0 represent size-symmetric competition, and values >0 represent size-asymmetric competition. For competitive intensity, values <0 represent facilitation, values = 0 represent no competition, and values >0 represent competition. Regression estimate and corresponding significance value are displayed in the top-right corner. Regression lines are included when there was a significant relationship at the 0.05 significance level. The color of points corresponds to neighbor removal treatments

Environmental conditions associated with competitive intensity and size asymmetry

Competitive intensity and size asymmetry were not correlated within local communities (Appendix S1: Figure S6) and were associated with different environmental factors (Figure 5, Appendix S1: Table S5). On average, local communities typically experienced competition (mean ± SE: 1.626 ± 0.090), but the degree of size asymmetry was variable, ranging from partially symmetric to size asymmetric (0.007 ± 0.011; Appendix S1: Table S6). Both competitive intensity and size asymmetry were associated with litter biomass, where competition was strongest

(-0.372 ± 0.141, $F_{1,27.63} = 6.972$, $p = 0.013$) and more size asymmetric (-0.030 ± 0.012, $F_{1,39.4} = 6.386$, $p = 0.016$) in low litter environments (Figure 5). However, the degree of competitive size asymmetry was also associated with nitrogen availability and ramet density, being more size asymmetric in high nitrogen environments (0.024 ± 0.011, $F_{1,34.10} = 4.945$, $p = 0.033$) and less size asymmetric under high ramet density (-0.031 ± 0.013, $F_{1,41.58} = 4.945$, $p = 0.025$; Figure 5). Further, the degree of competitive size asymmetry was associated with focal species identity, suggesting that vulnerability to competitive size asymmetry is species specific (Figure 5, Appendix S1: Table S5). Neither light
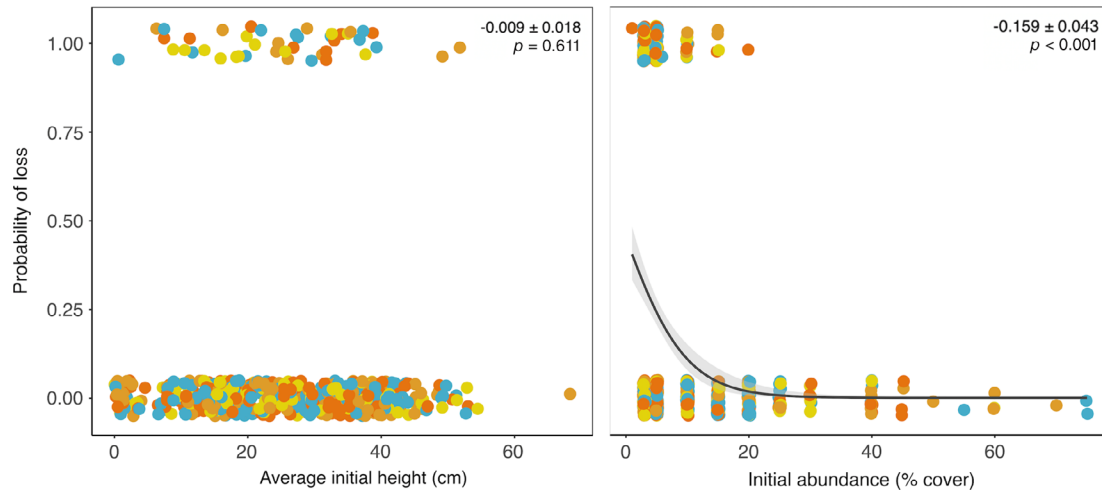
FIGURE 4   The probability of loss as a function of a species' initial size and abundance. Regression estimate and corresponding significance value displayed in the top-right corner. Regression lines are included when there was a significant relationship at the 0.05 significance level. The color of points corresponds to neighbor removal treatments
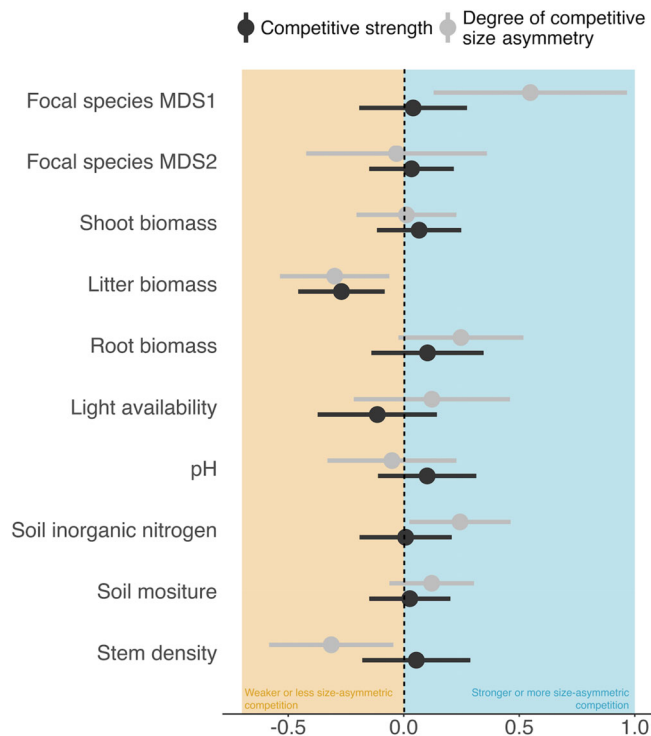

FIGURE 5   Standardized effect sizes linking environmental factors with competitive intensity and degree of size-asymmetric competition. Shown are the effect sizes ±2 SE. Variables were standardized to have a mean of 0 and a standard deviation of 1. Effect sizes represent the coefficients from two separate linear mixed models with either competitive intensity or the degree of size-asymmetric competition as the response variable. A positive effect size means stronger and more size-asymmetric competition. A negative effect size means weaker and less size-asymmetric competition (may include size symmetric or partial symmetry). For significance values associated with each factor, see Appendix S1: Table S5

availability nor standing biomass (shoot or root) was associated with changes in the intensity or size asymmetry of competition (Figure 5, Appendix S1: Table S5).

DISCUSSION

Competitive size asymmetry was independent of and more important for species gain and loss than competitive intensity (Appendix S1: Figure S6, Figure 3), demonstrating that different aspects of competition have independent and differential influence on the components of species turnover. Species loss and gains are likely more strongly associated with the degree of size-asymmetric competition because competitive size asymmetries capture inequalities among species, which has been shown to be important for species loss (Laird & Schamp, 2006; Soliveres et al., 2015). In contrast, competitive intensity captures the overall growth reduction experienced by a community. With only intense competition and no inequality, all plants are disadvantaged, likely reducing the importance of relative fitness differences between species, slowing or stopping exclusion (sensu Chesson, 2000).

Whether small or large individuals have competitive advantage dictates the degree of species gain or loss within a community (Figure 3). Species gains are highest when there is no size advantage between individuals within a community (i.e., under size-symmetric competition) (Figure 3), suggesting that individuals dispersing to a community may be more sensitive to disproportionate resource allocations than individuals already established in the community (Grubb, 1977; Howard &

Goldberg, 2001). Species loss, however, occurs when larger individuals have the competitive advantage (i.e., under size-asymmetric competition; Figure 3), which is further reflected in the reduced influence of species loss on turnover when we removed larger individuals. This could be because large individuals take up more resources relative to small individuals under asymmetric conditions through allometry of resource uptake (Gebauer et al., 1996; Schwinning & Weiner, 1998), potentially leading to a greater reduction in the total amount of resources available.

Our finding that competitive size asymmetry is essential for species loss agrees with prior hypotheses (Goldberg & Miller, 1990; Newman, 1973; Rajaniemi, 2003) and simulation models (DeMalach et al., 2016). However, predictions on which species are lost due to size-asymmetric interactions have varied and include that loss should either target small species (DeMalach et al., 2016), species that cannot tolerate resource inequalities (Newman, 1973), or that loss is random and thus first targets rare species (Goldberg & Miller, 1990; Oksanen, 1996). We found evidence that loss targets rare species but not small species (Figure 4), supporting the assemblage-level thinning or random loss hypothesis (Oksanen, 1996). Loss may not target small species because species differ in their vulnerabilities to size-asymmetric competition (Brown et al., 2019) and ability to tolerate or avoid competition or resource limitations (Craine & Dybzinski, 2013; Novoplansky, 2009). For example, small species may have certain attributes, such as physiological or morphological properties in shade tolerance (Valladares & Niinemets, 2008), that allow them to persist in lower resource environments. These traits may make them less susceptible, or even immune, to size-asymmetric competition. Rare species, on the other hand, could be lost under size-asymmetric competition due to chance (Oksanen, 1996), their sensitivity to changes in resource availability (Suding et al., 2005), or their low abundances, which also makes them vulnerable to environmental perturbations (Fischer & Stöcklin, 1997). Alternatively, since they typically share functional redundancies with more dominant species (Grime, 1998; Jain et al., 2014; Mouillot et al., 2013; Smith & Knapp, 2003), they may have similar vulnerabilities to size-asymmetric competition while also being competitively inferior (Murray et al., 2002). Rarity is sometimes associated with plant size; however, this is not always the case (Murray et al., 2002), and there was no evidence for this relationship within this study (Appendix S1: Figure S5).

The recognition that size-asymmetric competition is important for community dynamics has mostly been limited to highly fertile and productive environments where light is limited (Grime, 1973; Hautier et al., 2009; Newman, 1973; Tilman, 1982); however, this view underestimates the ubiquity of size-asymmetric competition and may impede our understanding of how size-asymmetric competition occurs. The degree of size asymmetry was independent of productivity (shoot or litter biomass) and light availability despite up to a 10-fold difference between communities in productivity and light availability (Appendix S1: Table S5). However, competitive size asymmetry increased with soil fertility (Figure 5), suggesting that the role of fertility in promoting size-asymmetric competition may be due to belowground mechanisms rather than aboveground mechanisms or the interaction between the two (Brown et al., 2019). For example, small and large individuals may have differential soil resource preemption or uptake rates (Craine & Dybzinski, 2013; Fransen et al., 2001; Rajaniemi & Reynolds, 2004; Schwinning & Weiner, 1998). Alternatively, there may be an interaction between aboveground and belowground processes such that a size advantage belowground leads to enhanced size asymmetry aboveground (Cahill, 1999). Evidence of partial symmetry (Appendix S1: Table S6), where smaller individuals have a competitive advantage and receive a larger proportion of resources compared to their larger neighbors (Schwinning & Weiner, 1998), further suggests that light alone cannot be the mechanism behind size-asymmetric interactions because a small plant cannot shade out their larger neighbors. Consequently, we need to start thinking of size-asymmetric interactions as a common phenomenon that can be the consequence of both aboveground and belowground processes. Further investigation is needed on how the resource being size asymmetrically competed for (e.g., light vs. nutrients) may alter the consequences of size-asymmetric competition.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Charlotte Brown and James F. Cahill, Jr. designed the study. Charlotte Brown collected and analyzed data and wrote the manuscript. Charlotte Brown and James F. Cahill, Jr. significantly contributed to revisions.

DATA AVAILABILITY STATEMENT

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REFERENCES

Aschehoug, E. T., R. Brooker, D. Z. Atwater, J. L. Maron, and R. M. Callaway. 2016. "The Mechanisms and Consequences of Inter-specific Competition among Plants." *Annual Review of Ecology, Evolution, and Systematics* 47: 263–81.

Bagousse-Pinguet, Y. L., J.-P. Maalouf, B. Touzard, and R. Michalet. 2014. "Importance, but Not Intensity of Plant Interactions Relates to Species Diversity under the Interplay of Stress and Disturbance." *Oikos* 123: 777–85.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48.

Brown, C., and J. F. Cahill. 2019. "Vertical Size Structure Is Associated with Productivity and Species Diversity in a Short-Stature Grassland: Evidence for the Importance of Height Variability within Herbaceous Communities." *Journal of Vegetation Science* 30: 789–98.

Brown, C., and J. F. Cahill Jr. 2022. "Replication Data for: Competitive Size-Asymmetry, Not Intensity, Is Linked to Species Loss and Gain in a Native Grassland." Scholars Portal Dataverse, V1. https://doi.org/10.5683/SP3/XB756A

Brown, C., K. J. Oppon, and J. F. Cahill. 2019. "Species-Specific Size Vulnerabilities in a Competitive Arena: Nutrient Heterogeneity and Soil Fertility Alter Plant Competitive Size Asymmetries." *Functional Ecology* 33: 1491–503.

Cahill, J. F., Jr. 1999. "Fertilization Effects on Interactions between Above- and Belowground Competition in an Old Field." *Ecology* 80: 466–80.

Chagnon, P.-L., C. Brown, G. C. Stotz, and J. F. Cahill, Jr. 2018. "Soil Biotic Quality Lacks Spatial Structure and Is Positively Associated with Fertility in a Northern Grassland." *Journal of Ecology* 106: 195–206.

Chesson, P. 2000. "Mechanisms of Maintenance of Species Diversity." *Annual Review of Ecology and Systematics* 31: 343–66.

Connell, J. H. 1978. "Diversity in Tropical Rain Forests and Coral Reefs." *Science* 199: 1302–10.

Craine, J. M., and R. Dybzinski. 2013. "Mechanisms of Plant Competition for Nutrients, Water and Light." *Functional Ecology* 27: 833–40.

Craine, J. M., J. Fargione, and S. Sugita. 2005. "Supply Pre-emption, Not Concentration Reduction, Is the Mechanism of Competition for Nutrients." *New Phytologist* 166: 933–40.

DeMalach, N., E. Zaady, and R. Kadmon. 2017. "Light Asymmetry Explains the Effect of Nutrient Enrichment on Grassland Diversity." *Ecology Letters* 20: 60–9.

DeMalach, N., E. Zaady, J. Weiner, and R. Kadmon. 2016. "Size Asymmetry of Resource Competition and the Structure of Plant Communities." *Journal of Ecology* 104: 899–910.

Dixon, P. 2003. "VEGAN, a Package of R Functions for Community Ecology." *Journal of Vegetation Science* 14: 927–30.

Dray, S., R. Pélissier, P. Couteron, M.-J. Fortin, P. Legendre, P. R. Peres-Neto, E. Bellier, et al. 2012. "Community Ecology in the Age of Multivariate Multiscale Spatial Analysis." *Ecological Monographs* 82: 257–75.

Fischer, M., and J. Stöcklin. 1997. "Local Extinctions of Plants in Remnants of Extensively Used Calcareous Grasslands 1950–1985." *Conservation Biology* 11: 727–37.

Fransen, B., H. de Kroon, and F. Berendse. 2001. "Soil Nutrient Heterogeneity Alters Competition between Two Perennial Grass Species." *Ecology* 82: 2534–46.

Gebauer, R. L. E., J. F. Reynolds, and B. R. Strain. 1996. "Allometric Relations and Growth in *Pinus taeda*: The Effect of Elevated CO_2, and Changing N Availability." *New Phytologist* 134: 85–93.

Goldberg, D. E. 1996. "Competitive Ability: Definitions, Contingency and Correlated Traits." *Philosophical Transactions: Biological Sciences* 351: 1377–85.

Goldberg, D. E., J. P. Martina, K. J. Elgersma, and W. S. Currie. 2017. "Plant Size and Competitive Dynamics along Nutrient Gradients." *American Naturalist* 190: 229–43.

Goldberg, D. E., and T. E. Miller. 1990. "Effects of Different Resource Additions of Species Diversity in an Annual Plant Community." *Ecology* 71: 213–25.

Grime, J. P. 1973. "Competitive Exclusion in Herbaceous Vegetation." *Nature* 242: 344.

Grime, J. P. 1977. "Evidence for the Existence of Three Primary Strategies in Plants and its Relevance to Ecological and Evolutionary Theory." *American Naturalist* 111: 1169–94.

Grime, J. P. 1998. "Benefits of Plant Diversity to Ecosystems: Immediate, Filter and Founder Effects." *Journal of Ecology* 86: 902–10.

Grubb, P. J. 1977. "The Maintenance of Species-Richness in Plant Communities: The Importance of the Regeneration Niche." *Biological Reviews* 52: 107–45.

Hara, T. 1986. "Growth of Individuals in Plant Populations." *Annals of Botany* 57: 55–68.

Hardin, G. 1960. "The Competitive Exclusion Principle." *Science* 131: 1292–7.

Hautier, Y., P. A. Niklaus, and A. Hector. 2009. "Competition for Light Causes Plant Biodiversity Loss after Eutrophication." *Science* 324: 636–8.

HilleRisLambers, J., P. B. Adler, W. S. Harpole, J. M. Levine, and M. M. Mayfield. 2012. "Rethinking Community Assembly through the Lens of Coexistence Theory." *Annual Review of Ecology, Evolution, and Systematics* 43: 227–48.

Howard, T. G., and D. E. Goldberg. 2001. "Competitive Response Hierarchies for Germination, Growth, and Survival and their Influence on Abundance." *Ecology* 82: 979–90.

Huston, M. 1979. "A General Hypothesis of Species Diversity." *American Naturalist* 113: 81–101.

Jain, M., D. F. B. Flynn, C. M. Prager, G. M. Hart, C. M. DeVan, F. S. Ahrestani, M. I. Palmer, et al. 2014. "The Importance of Rare Species: A Trait-Based Assessment of Rare Species Contributions to Functional Diversity and Possible Ecosystem Function in Tall-Grass Prairies." *Ecology and Evolution* 4: 104–12.

Keddy, P. A. 2001. *Competition*. London, UK: Chapman and Hall.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." *Journal of Statistical Software* 82: 1–26.

Laird, R. A., and B. S. Schamp. 2006. "Competitive Intransitivity Promotes Species Coexistence." *The American Naturalist* 168: 182–93.

Lamb, E. G., and J. F. Cahill. 2006. "Consequences of Differing Competitive Abilities between Juvenile and Adult Plants." *Oikos* 112: 502–12.

Lamb, E. G., and J. F. Cahill, Jr. 2008. "When Competition Does Not Matter: Grassland Diversity and Community Composition." *American Naturalist* 171: 777–87.

Lamb, E. G., S. W. Kembel, and J. F. Cahill, Jr. 2009. "Shoot, but Not Root, Competition Reduces Community Diversity in Experimental Mesocosms." *Journal of Ecology* 97: 155–63.

Lamb, E. G., B. H. Shore, and J. F. Cahill. 2007. "Water and Nitrogen Addition Differentially Impact Plant Competition in a Native Rough Fescue Grassland." *Plant Ecology* 192: 21–33.

Legendre, P. 2019. "A Temporal Beta-Diversity Index to Identify Sites that Have Changed in Exceptional Ways in Space–Time Surveys." *Ecology and Evolution* 9: 3500–14.

Levine, J. M., and J. HilleRisLambers. 2009. "The Importance of Niches for the Maintenance of Species Diversity." *Nature* 461: 254–7.

Macarthur, R., and R. Levins. 1967. "The Limiting Similarity, Convergence, and Divergence of Coexisting Species." *American Naturalist* 101: 377–85.

Martorell, C., and R. P. Freckleton. 2014. "Testing the Roles of Competition, Facilitation and Stochasticity on Community Structure in a Species-Rich Assemblage." *Journal of Ecology* 102: 74–85.

Maynard, D. S., T. W. Crowther, and M. A. Bradford. 2017. "Competitive Network Determines the Direction of the Diversity-Function Relationship." *Proceedings of the National Academy of Sciences of the United States of America* 114: 11464–9.

Michalet, R., J.-P. Maalouf, P. Choler, B. Clément, D. Rosebery, J.-M. Royer, C. Schöb, and C. J. Lortie. 2015. "Competition, Facilitation and Environmental Severity Shape the Relationship between Local and Regional Species Richness in Plant Communities." *Ecography* 38: 335–45.

Mitchell, M. G. E., J. F. Cahill, Jr., and D. S. Hik. 2009. "Plant Interactions Are Unimportant in a Subarctic–Alpine Plant Community." *Ecology* 90: 2360–7.

Mouillot, D., D. R. Bellwood, C. Baraloto, J. Chave, R. Galzin, M. Harmelin-Vivien, M. Kulbicki, et al. 2013. "Rare Species Support Vulnerable Functions in High-Diversity Ecosystems." *PLoS Biology* 11: e1001569.

Murray, B. R., P. H. Thrall, A. M. Gill, and A. B. Nicotra. 2002. "How Plant Life-History and Ecological Traits Relate to Species Rarity and Commonness at Varying Spatial Scales." *Austral Ecology* 27: 291–310.

Newman, E. I. 1973. "Competition and Diversity in Herbaceous Vegetation." *Nature* 244: 310.

Novoplansky, A. 2009. "Picking Battles Wisely: Plant Behaviour under Competition." *Plant, Cell & Environment* 32: 726–41.

Oksanen, J. 1996. "Is the Humped Relationship between Species Richness and Biomass an Artefact Due to Plot Size?" *Journal of Ecology* 84: 293–5.

Rajaniemi, T. K. 2003. "Explaining Productivity-Diversity Relationships in Plants." *Oikos* 101: 449–57.

Rajaniemi, T. K., and H. L. Reynolds. 2004. "Root Foraging for Patchy Resources in Eight Herbaceous Plant Species." *Oecologia* 141: 519–25.

Rasmussen, C. R., A. N. Weisbach, K. Thorup-Kristensen, and J. Weiner. 2019. "Size-Asymmetric Root Competition in Deep, Nutrient-Poor Soil." *Journal of Plant Ecology* 12: 78–88.

Schwinning, S., and J. Weiner. 1998. "Mechanisms Determining the Degree of Size Asymmetry in Competition among Plants." *Oecologia* 113: 447–55.

Smith, M. D., and A. K. Knapp. 2003. "Dominant Species Maintain Ecosystem Function with Non-random Species Loss." *Ecology Letters* 6: 509–17.

Soliveres, S., F. T. Maestre, W. Ulrich, P. Manning, S. Boch, M. A. Bowker, D. Prati, et al. 2015. "Intransitive Competition Is Widespread in Plant Communities and Maintains their Species Richness." *Ecology Letters* 18: 790–8.

Suding, K. N., S. L. Collins, L. Gough, C. Clark, E. E. Cleland, K. L. Gross, D. G. Milchunas, and S. Pennings. 2005. "Functional- and Abundance-Based Mechanisms Explain Diversity Loss Due to N Fertilization." *Proceedings of the National Academy of Sciences of the United States of America* 102: 4387–92.

Tilman, D. 1982. *Resource Competition and Community Structure.* Princeton, NJ: Princeton University Press.

Valladares, F., and Ü. Niinemets. 2008. "Shade Tolerance, a Key Plant Feature of Complex Nature and Consequences." *Annual Review of Ecology, Evolution, and Systematics* 39: 237–57.

Weigelt, A., and P. Jolliffe. 2003. "Indices of Plant Competition." *Journal of Ecology* 91: 707–20.

Weiner, J. 1986. "How Competition for Light and Nutrients Affects Size Variability in Ipomoea Tricolor Populations." *Ecology* 67: 1425–7.

Weiner, J. 1990. "Asymmetric Competition in Plant Populations." *Trends in Ecology & Evolution* 5: 360–4.

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