Disentangling competitive processes to better understand their drivers and consequences in a native grassland community

by

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ABSTRACT

Competition is often highlighted as a major force influencing community structure. However, there are multiple facets of competition that may have independent and differential impacts, making the understanding of what drives competition and how it structures communities difficult. In this thesis, I disentangle two facets of competition, competitive intensity and size-asymmetry, to better understand their drivers and relative importance for community assembly. First, I test the assumption that competition for soil nutrients is size-symmetric. I find that the modification of soil nutrient abundance and distribution can alter the degree of competitive size-asymmetry independent of competitive intensity, suggesting that competitive size-asymmetries may be more common than originally thought. Second, I indirectly test the importance of competitive size-asymmetries for species diversity by examining how the incorporation of community size-structure increases the explanatory power of the productivity-diversity relationship. I find that variation in size structure is common, even in a typically non-light limited system, and its incorporation can increase the explained variance of the productivity-diversity relationship by up to 30%. Next, I directly test the relative importance of competitive intensity and size-asymmetry for species turnover. I find that competitive size-asymmetries are associated with increased species loss and decreased species gain, while competitive intensity has no impact. Finally, I test an alternative mechanism that may promote increased beta-diversity in a landscape: whether the removal of vegetation, which is often associated with changes to competitive processes, results in distinct seedbank communities. I find that vegetation removal leads to distinct seedbank communities by decreasing seed rain and increasing germination rates. Overall, the results of this thesis promote new understanding of how competition structures communities, the mechanisms of competitive size-asymmetry, and the mechanisms that support beta-diversity.

PREFACE

This thesis is an original work by Charlotte Brown.

Chapter 2 of this thesis has been published in *Functional Ecology* in 2019:

> Brown, C., Oppon, K.J., Cahill Jr, J.F. 2019. Species-specific size vulnerabilities in a competitive arena: Nutrient heterogeneity and soil fertility alter plant competitive size-asymmetries. *Functional Ecology,* 33(8):1491-1503.

I was responsible for idea conception, data collection, analysis, and manuscript writing. KJO assisted with the collected data on foliar nitrogen and carbon content as well as provided feedback on the manuscript. JFC provided significant input on the conception of the ideas and feedback on the manuscript. Data deposited in the University of Alberta Dataverse:

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To my family and friends,
it has been quite an adventure,
and for all the small plants out there

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Chapter 1: General Introduction

A primary focus in ecology is to understand the underlying mechanisms that influence species co-occurrence, distribution, and overall community structure. One of the early mechanisms that was considered a critical force in driving community structure was the competitive interactions between species. This is driven by a rich history of theory, from Darwin's 1859 *The Origin of Species* to Gause's 1934 competitive exclusion principle, that has influenced many foundational ideas in ecology and evolution (e.g. limiting similarity (Macarthur & Levins 1967) and character displacement (Brown & Wilson 1956)). Over time, mechanistic understanding of how communities assemble has evolved from being primarily focused on competition to incorporating other biotic interactions (e.g., facilitation, parasitism, and herbivory) as well as additional factors such as regional species pools, dispersal, and environmental filters (see review HilleRisLambers *et al.* 2012). However, competition remains a primary assembly mechanism (Schoener 1983; Aarssen & Epp 1990; Goldberg & Barton 1992; Gurevitch *et al.* 1992).

Within plants, the importance of competition in structuring communities has been highly debated (Grime 1973; Newman 1973; Tilman 1982; Grace 1991; Brooker *et al.* 2005; Craine 2005); however, there are four dominant hypotheses that differ depending on which resource plants are competing for, the productivity of the system, and the relative importance of other assembly factors. Tilman’s resource ratio hypothesis suggests that competition is always an important structuring force for communities (Tilman 1982). In contrast, Grime’s C-S-R triangle indicates that competition is only important in high productivity systems as stress should be the dominant structuring force at low productivity (Grime 1973, 1979). In the middle of the debate, Newman's light asymmetry hypothesis proposes competition is always acting, regardless of productivity level, but the resources that plants are competing for determines its signature on community structure (Newman 1973). A more modern theory, Chesson's 2000 coexistence theory, generalizes those above to suggest that the role competition plays in community structure is dependent on the dynamic between stabilizing (e.g., niche partitioning) and equalizing mechanism (e.g., fitness differences), such that species loss due to competition should only occur when fitness differences (e.g., competitive ability) are greater than stabilizing mechanisms. In this thesis, I aim to build on the hypotheses above to better understand how resources alter competitive processes and how competition alters community dynamics, including species diversity, species turnover, and seedbank dynamics. However, in order to fully understand how competition structures communities, we first need to break down its complexity and examine how the different facets of competition may differ in drivers and consequences.

The multiple facets of competition

Competition is the aggregate of multiple processes: *the intensity of interactions*, or the degree to which competition for a limited resource reduces plant performance (Welden & Slauson 1986), *the size-asymmetry of interactions*, or the degree to which individuals obtain a disproportionate amount of resources relative to their size (Hara 1986; Weiner 1990), *and the transitivity of interactions*, or the degree to which a species in a community follow a perfect hierarchy (Laird & Schamp 2006). In theory, all of these processes may be independent of one another, ultimately having different drivers and consequences for community dynamics. In this thesis, I separate two of these competitive processes, competitive intensity and size-asymmetry, to test their independence, under which conditions they are strongest, and their consequences for community structure.

Resource competition

Most plants compete for the same three major classes of resources: soil nutrients, water, and sunlight (Craine & Dybzinski 2013; Aschehoug *et al.* 2016). However, plants differ in their ability to uptake and utilize those resources (Chapin 1980; Grace 2012), likely due to differences in their traits (Aerts 1999). Thus, a large part of resource competition is a plant's ability to find, reach, and uptake (i.e., pre-empt) a limiting resource before its neighbours (Novoplansky 2009). It is well understood that a plant's size is directly related to its ability to pre-empt sunlight, such that larger individuals are able to overtop and shade-out their neighbours (Schwinning & Weiner 1998). Consequently, aboveground competition is typically size-asymmetric. However, less is known about the preemptive nature of belowground resources or the symmetry of belowground competition (though it is often assumed to be size-symmetric (Schwinning & Weiner 1998; Schenk 2006)), ultimately limiting our mechanistic understanding of how plants compete. In chapter 2, I seek to fix this discrepancy by directly testing whether altering the abundance and distribution of soil nutrients can alter the degree of size-asymmetric competition within experimental plant communities (Fig. 1-1).

The degree of competitive size-asymmetry experienced by an individual, however, may not be consistent across species as they differ in their strategies to respond to and tolerate resource reduction (Novoplansky 2009). For example, smaller species that are constantly shaded out by larger neighbours can adapt a shade-avoidance response (Poorter, 2001; Weinig, 2000) that allows them to tolerate and persist in low-light environments. Thus, a shade-tolerant species would respond differently to reduced light levels than a shade-intolerant species. Ultimately, this potential for differential species responses to size-asymmetric competition could permit the coexistence of small and large individuals, even under strongly size-asymmetric competition. In chapter 2, I examine whether the degree of size-asymmetric competition experienced is dependent on a species identity (Fig. 1-1).

Competition, productivity, and species diversity

The importance of competition for species diversity can be directly related to the productivity of a system. Competition is often the mechanism used to explain the well-documented and unimodal relationship between diversity and productivity (Grime 1973; Newman 1973). With an increase in productivity, there is a decrease in light availability, promoting increased size-asymmetric competition for light (Hautier *et al.* 2009; DeMalach *et al.* 2017). Since increased size-asymmetry gives larger individuals a disproportionate advantage over smaller individuals (Schwinning & Weiner 1998), this is thought to promote the competitive exclusion of smaller species under high productivity (Newman 1973). However, an underlying assumption of this hypothesis is that there is a change in size structure along a productivity gradient, such that more individuals are bigger and the minimum size to survive in the community is larger in high productivity areas. In chapter 3, I examine vegetative size structures along a productivity gradient to test the relationship between size inequality and species diversity and whether the incorporation of size structures can increase the diversity-productivity relationship (Fig. 1-1).

Most studies on competition and community assembly evaluate how changes in competitive intensity alter species diversity, with mixed results (e.g, Lamb & Cahill 2008; Hautier *et al.* 2009; Lamb *et al.* 2009; Mitchell *et al.* 2009; Bagousse-Pinguet *et al.* 2014; Martorell & Freckleton 2014; Michalet *et al.* 2015). However, this ignores the potential role of other competitive processes. There is increasing evidence that the competitive size-asymmetry of interactions may have more substantial impacts on species diversity than intensity alone (DeMalach *et al.* 2017). Thus, different competitive processes may be better linked to species diversity than intensity. In chapter 4, I examine the relative importance of competitive intensity and size-asymmetry for species loss in plant communities.

Competition and seedbank dynamics

When scaling up from local to landscape-level assembly, different competitive dynamics between local communities may promote increased beta-diversity (i.e., variability in species composition among local communities in a given area (Anderson *et al.* 2006; Tuomisto 2010)). For example, small-scale disturbances have been linked to the maintenance of plant diversity by promoting the coexistence of competitive and subdominant species in a community (Levins & Culver 1971; Horn & MacArthur 1972; Huston 1979; Levine & Rees 2002; Cadotte 2007). A primary mechanism for this coexistence is that there are different competitive dynamics between established local communities (e.g., experience consistent competitive dynamics) and those that have been disturbed (e.g., experience reduced or changed dynamics) (Suding 2001; Suding & Goldberg 2001).

Competition can have a strong filter on seedling establishment in communities, evidenced by an increase in germination rates following the removal of vegetation (an indirect measure of potential competition) (e.g.Isselstein *et al.* 2002; Jutila & Grace 2002; Ruprecht *et al.* 2010). However, the removal of vegetation can also alter abiotic properties and seed dispersal, which may alter germination rates, seed predation rates, and seed rain (Baskin & Baskin 1989). Thus, another possible mechanism for increased beta-diversity with small-scale disturbances can be changes to seedbank composition and assembly, ultimately impacting the species available for reestablishment. In chapter 5, I test how the removal of vegetation through small-scale disturbances alter seed inputs (i.e. seed rain) and outputs (i.e. germination and predation) as well as seedbank composition (Fig. 1-1).

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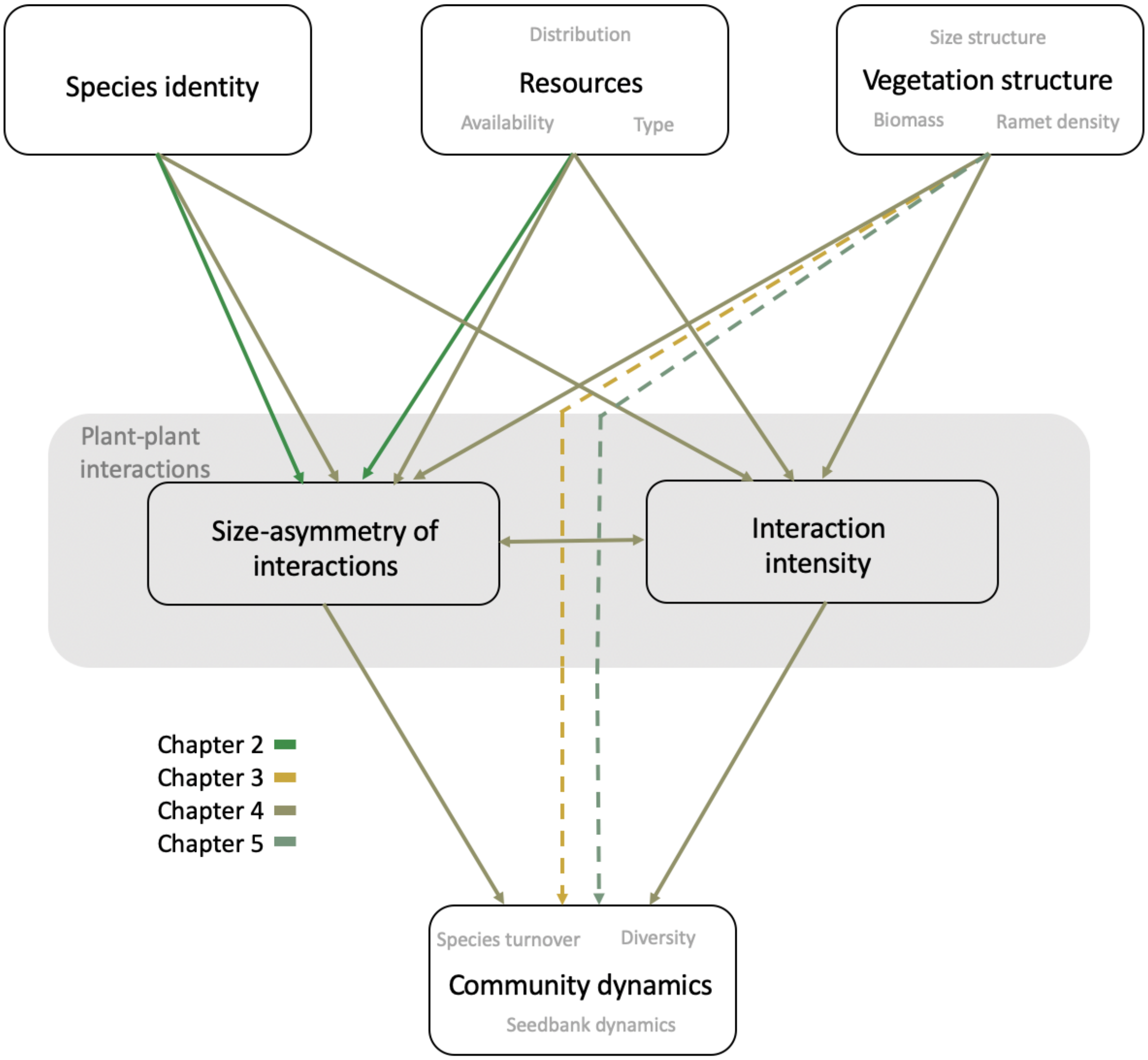

Figure 1–1. Conceptual diagram showing direct (solid line) and indirect (dashed line) linkages between the elements of the thesis. Arrows color coded by chapter number.

Chapter 2: Species-specific size vulnerabilities in a competitive arena: Nutrient heterogeneity and soil fertility alter plant competitive size-asymmetries

INTRODUCTION

Living with neighbours can impact a plant's reproductive output (Keddy, 2001; Weiner, Campbell, Pino, & Echarte, 2009, but see Klinkhamer, Meelis, de Jong, & Weiner, 1992) and growth (Enquist *et al.* 1999; Keddy 2001), which can ultimately influence population and community dynamics (Goldberg & Barton 1992). These competitive interactions between individuals are often defined by the intensity of competition (Weigelt & Jolliffe 2003); however, there is increasing evidence that the size-dependence of these interactions can influence ecological dynamics without changes to the overall intensity of competition (DeMalach *et al.* 2016). Size-asymmetric competition, in which larger individuals take up a disproportionate amount of resources relative to their size (Harper 1967; Begon 1984; Schwinning & Weiner 1998), gives larger individuals a competitive advantage and could lead to the competitive exclusion of smaller and slow-growing species (DeMalach *et al.* 2016). However, despite the possible exclusion of smaller individuals, they tend to have a higher abundance within communities (Niklas *et al.* 2003; Moles *et al.* 2009; Tracey *et al.* 2017). Thus, there must be mechanisms allowing the coexistence of small and large individuals despite the occurrence of size-asymmetric competition.

Most proposed mechanisms behind this coexistence involve trade-offs between plant size and fitness (e.g. Aarssen, 2015; Schamp & Aarssen, 2014; Tracey & Aarssen, 2014). However, another possible explanation is that species differ in their vulnerability to size-asymmetric competition. Under similar environmental conditions, competitive suppression and tolerance between species can be variable (Goldberg & Werner 1983; Goldberg & Fleetwood 1987; Miller & Werner 1987), likely due to differences in species competitive strategies (Novoplansky 2009). Many small species have adopted tolerant behavioural strategies (e.g. shade-tolerance) (Poorter, 2001; Weinig, 2000), such that they are less harmed by competition than species that do not exhibit these behaviours. Thus, it is possible that under size-dependent interactions species too could differ in their suppression and tolerance such that small plants are not always the losers of these interactions, ultimately promoting the coexistence of small and large species. However, a plant's competitive strategy is typically dependent on its environment (Novoplansky 2009), thus these responses of species to size-asymmetric competition may vary based on the contested resource.

Typically, competition for light is size-asymmetric, while competition for soil resources is size-symmetric (Hara, 1986, 1993; Schwinning & Weiner, 1998; Weiner, 1990). However, such a binary outlook disregards that size-dependent interactions occur on a spectrum, ranging from completely symmetric to size-asymmetric (Weiner 1990; Hara 1993; Schwinning & Weiner 1998) and is primarily based on trends within plant populations. When looking within communities, the drivers of size-asymmetric competition could differ from that of populations due to greater size (Connolly & Wayne 1996), growth, or uptake rates between species.

Soil fertility and distribution could promote size-asymmetric competition directly, by switching root competition from size-symmetric to size-asymmetric (Schwinning & Weiner 1998), or indirectly, by enhancing the size-asymmetry of shoot competition (Cahill 1999). A switch in the size-dependence of competition could occur when resources are heterogeneously distributed (Schwinning & Weiner 1998; Fransen *et al.* 2001; Rajaniemi & Reynolds 2004; Rasmussen *et al.* 2019), if larger individuals are better able to reach and uptake a nutrient patch before their smaller neighbours (Schwinning & Weiner 1998; Craine & Dybzinski 2013). Additionally, the presence of microbial communities (Schwinning & Weiner 1998; Merrild *et al.* 2013) could switch the size-dependence of competition if larger individuals have more microbial associations that increase their nutrient uptake (Schwinning & Weiner 1998) or if the presence of microbes leads to resource sharing within the community (Simard *et al.* 1997; Beiler *et al.* 2010), where larger individuals give resources to smaller individuals (Beiler *et al.* 2010). However, the mechanisms that lead to disproportionate resource utilization belowground would also indirectly increase the degree of size-asymmetric competition for light as the amount of resources a plant obtains belowground regulates its growth aboveground. Thus, it is important to consider the interactive effects of root and shoot responses when determining the effects of soil resources on size-asymmetric competition.

Plant size is typically measured aboveground (Weiner 1985; Bourdier *et al.* 2016), which could inhibit the detection of size-asymmetric competition for soil resources. Plants can have different responses to aboveground and belowground stimuli (Poorter & Nagel, 2000), which may lead to differences in shoot and root production. In response to competition, plants can alter their biomass allocation (Aerts *et al.* 1991; McConnaughay & Coleman 1999), shoot:root ratio (Gedroc *et al.* 1996), and shoot and root architecture (Aphalo *et al.* 1999; Belter & Cahill 2015). Thus, it is possible that an individual which has a size advantage belowground may not have a size advantage aboveground, so measuring size with shoot biomass alone could mask the degree of size-asymmetric competition within the community. Partitioning plant size between shoot, root, and whole plant biomass is necessary to separate these dynamic processes and to determine what resources can alter size-asymmetric competition.

Here, using experimental mesocosms, we manipulated soil fertility, nutrient heterogeneity, and soil microbial presence as well as initial size inequalities in a three-species community to address the following questions:

- Does the degree of size-asymmetric competition vary as a function of species identity?
- Do soil fertility, nutrient distributions and the presence of microbial communities alter the degree of size-asymmetric competition?
- Does defining plant size as shoot, root, or total biomass alter the size-dependence of competitive interactions?

METHODS

Experimental design

Experimental mesocosms were constructed containing nine individuals (3 species x 3 different starting sizes) that were grown in azalea pots (20.3 x 14.1 cm) filled with 4.2 L of a 1:3 topsoil to sand mixture (Canar Rock Products Ltd in Edmonton AB, Canada). Mesocosms received one of five soil treatments which varied in soil fertility (low vs. high), nutrient heterogeneity (homogeneous vs. heterogeneous), or level of initial microbial community suppression (no suppression vs. suppression) (Fig. 2-1). Each soil treatment was replicated 20 times, for a total of 100 mesocosms. A full factorial design was not used as we were ultimately testing the effects of soil fertility, nutrient heterogeneity and microbial community suppression alone and not in combination.

To determine each species maximum growth potential under each soil treatment and starting size, plant species and sizes found in each multispecies mesocosm were grown alone in each soil treatment. Individually grown plants were replicated 13 times per soil treatment and starting size, for a total of 585 mesocosms (13 replicates x 3 species x 3 sizes x 5 soil treatments). In total, the experiment consisted of 685 mesocosms that were arranged in a completely randomized design within a 3.5 x 13 m area on the roof of the University of Alberta Biotron in Edmonton AB, Canada.

Study species

Agrostis scabra, Gaillardia aristata, and *Erigeron speciosus* were chosen for this study based on the following criteria: 1) they are all native to local grasslands in central Alberta (Moss 1983); 2) they have non-clonal growth; 3) they have similar average sizes (Wang et al. 2010); and 4) they are non-nitrogen fixing. Seeds of *Agrostis scabra* were collected from wild populations at the Roy Berg Kinsella Research Ranch in Kinsella AB, Canada. Seeds of *Gaillardia aristata* and *Erigeron speciosus* were collected from a local seed supplier (Wild About Flowers, Calgary AB, Canada).

Creation of size classes and planting design

A key requirement in this study was the generation of initial size variability among individuals within each species. This size variation was created by germinating plants 10, 8, 6, or 4 weeks before transplantation; four rather than three time points were used to ensure we had enough individuals despite low germination rates. Estimated initial biomass for all individuals was calculated using species-specific biomass regressions. Regressions were created from destructive harvests of a subset of individuals one week before transplantation (Appendix 2-S1). To ensure representation of intraspecific size variation, individuals within each species were ranked by estimated biomass and assigned to one of three size classes: small (bottom third of rankings), medium (middle third of rankings), or large (top third of rankings), which resulted in significant size differences between classes (Appendix 2-S2) but not between species (Appendix 2-S3A).

However, these rankings were only used in the experimental setup, for all analyses an individual's size was evaluated relative to all individuals within a mesocosm regardless of species identity. Although size is confounded with age in this experiment, we eliminated priority effects of early germination by transplanting all individuals into the experimental mesocosms at the same time. The effects of small age differences on size-asymmetric competition are unknown and could be an important factor but are likely limited in this study as all individuals were in the same development phase (i.e. pre-reproductive) and are perennials, so a few weeks difference in growth is only a small fraction of their typical life-span.

One individual from each species-specific size class was randomly selected and transplanted into each mesocosm, such that there were nine individuals (3 species x 3 size classes) per multispecies mesocosm (Fig. 2-1A). Individuals were arranged in a circle 5 cm from the center of the mesocosm to ensure that all individuals were equidistant to nutrient patches when they were present. To minimize confounding effects of neighbour identity and size on competition, the order of the nine plants around the mesocosm was randomly selected. In total, there were nine unique combinations. For alone-plant mesocosms, each individual was randomly placed 5 cm from the center of the mesocosm.

Soil treatments

We used five soil treatments (Fig. 2-1B): low nutrient-homogeneous, low nutrient-heterogeneous, low nutrient-initial suppression of microbial community, high nutrient-homogeneous, and high nutrient-heterogeneous. Low nutrient and high nutrient treatments received 4 and 32 g m^{-2} NPK respectively, in the form of Nutricote ®13-13-13 slow release pellets. Fertilizer was evenly distributed throughout the mesocosm in the homogeneous soil nutrient treatments. To determine the effects of both high-quality and low-quality patches, nutrient distributions varied between the low-nutrient and high-nutrient heterogeneous treatments. In the low nutrient-heterogeneous soil treatment, fertilizer was distributed in the center of the mesocosm within a 5 cm area (high-quality patch). In the high nutrient-heterogeneous soil treatment, fertilizer was distributed along the outside of the mesocosm with no nutrients placed in the center of the mesocosm (low-quality patch). For the initial microbial suppression treatment, soil was autoclaved at 121°C for 3 hours (Chagnon *et al.* 2018) prior to nutrient addition to reduce any positive effects of sterilization on nutrient concentrations (Powlson & Jenkinson 1976). Although autoclaving soil prior to nutrient addition cannot fully control for differences in nutrient concentrations among sterilized and non-sterilized treatments, this should be minimized here due to the low fertility of the soil mixture (Powlson & Jenkinson 1976). Consequently, any difference among these treatments should be due to the presence or absence of microbial communities and not to nutrient differences.

Harvest

After 10 weeks of growth (mid-June to the end of August 2016), plants were clipped at the soil surface, dried and weighed. Roots were separated by individual, washed over a 1mm sieve, dried and weighed. At the time of harvest, it was visually obvious that roots had reached the center of the pot in all replicates, regardless of the soil treatment. Unfortunately, species determination of root fragments (Taggart *et al.* 2010) was not feasible.

Light and foliar nitrogen measurements

To obtain estimates of resource availability, photosynthetically active radiation (PAR) and foliar nitrogen (% nitrogen) were measured. PAR was measured once at the center of each mesocosm immediately before the harvest. PAR was measured simultaneously above and below the plant canopy using an Accu-Par light meter with attachment (Decagon, Pullman, WA). Light penetration was estimated as the amount of PAR available below the canopy relative to PAR above the canopy. Foliar nitrogen was measured on a subset of pots: 106 alone pots, selected semi-randomly to allow for variation in initial size per treatment (between 20 and 23 individuals per treatment), and 15 multi-species pots (3 replicates x 5 soil treatments), selected randomly and all individuals within a pot were analyzed. Three leaves from each plant were randomly selected, pooled, and ground using a beadmill (Qiagen TissueLyser II) for analysis. Percent nitrogen (%N) was measured using flash combustion (Thermoscientific FLASH 2000 combustion Elemental Analyzer) with tobacco leaves as standards.

Measure of competitive response

Competitive response, which is a commonly used competition metric that represents the relative performance of an individual grown with and without neighbours (Weigelt & Jolliffe 2003), was measured as the log-response ratio (Cahill, 1999). For each plant, competitive response was measured at the end of the experiment separately as a function of shoot, root, and total biomass. Due to the fully randomized design, plants grown in multispecies mesocosms were not paired with alone plants. Instead, the log-response ratio for each individual within a multispecies mesocosm was calculated separately for each replicate of alone plants in the same species, size class, and soil treatment combination and then averaged (Lamb & Cahill 2006). Between 4 and 13 replicates of each alone-plant mesocosm were used in this calculation due to differences in germination and mortality rates among species.

Mesoscosm-level competitive response was calculated by averaging the competitive responses of all individuals in the mesocosm. There was only about 3% mortality within multispecies mesocosms and since competitive response cannot be calculated for dead plants (log(0)= -Inf), they were excluded from this average.

Measure of the degree of size-asymmetric competition

To date, there is no standard metric to measure size-asymmetric competition within communities. There are multiple facets of size-asymmetric competition: size-asymmetric resource uptake, size-asymmetric growth (Rasmussen & Weiner 2017), size-asymmetric resource assimilation, and size-asymmetric mortality; the latter three being an outcome of size-asymmetric resource uptake. The majority of studies that examine size-asymmetric competition focus on size-asymmetric resource uptake and are theoretical models, many of which are hard to fit to empirical data due to the difficulty of measuring particular model parameters (e.g. zones of influence in zone-of-influence models models (e.g. Gates & Westcott, 1978; Weiner, Stoll, Muller-Landau, & Jasentuliyana, 2001). Many of the other metrics used to examine size-asymmetric competition measure size-asymmetric growth, where empirical data is fit to a growth function with a size-asymmetric parameter (e.g. Connolly & Wayne, 1996; Coomes & Allen, 2007; Damgaard, 1999).

In this study, we focus on size-asymmetric growth and how it varies as a function of soil treatment, but also examine size-asymmetric mortality and size-asymmetric resource assimilation (using foliar nitrogen concentration (%N) as a proxy). In our measure of size-asymmetric growth, we include competitive response in order to separate competitive and intrinsic differences in an individual's performance. This separation is necessary for accurately measuring the size-asymmetry of competition (Schwinning & Weiner 1998), but is not always done in previous metrics of size-asymmetric growth (Weiner & Damgaard 2006).

The degree of size-asymmetric competition (°SAC) was measured as the slope of the logarithmic regression between an individuals' competitive response and relative initial size calculated using least squares estimation (Fig. 2-2). Relative size was used instead of absolute size as a relative measure is needed to determine the effects of larger versus smaller neighbours. For example, a small individual can end up having a relatively low competitive response under size-asymmetric competition if its neighbours are also small. Relative initial size was calculated as the proportion of the total mesocosm biomass that individual's biomass contributes ($\text{Biomass}_{\text{individual}}/\text{Biomass}_{\text{total mesocosm}}$). The °SAC is positive under size-asymmetric competition, negative under symmetric competition and zero under size-symmetric competition (Table 2-1, Fig. 2-2). This metric was validated using simulated data with known degrees of size-asymmetric competition (Appendix 2-S4). The degree of size-asymmetric resource assimilation was calculated using this method, but using a log-response ratio in %N instead of competitive response (i.e. biomass).

Statistical analysis

To test for soil treatment effects on size-asymmetric growth, mortality, and resource assimilation mixed models were fit with competitive response, mortality, or the log-response ratio for % foliar nitrogen as response variables respectively. For each response variable, two models were fit: one examining mesocosm-level effects, where relative initial size and soil treatment were fixed effects and species identity and mesocosm were random effects, and another examining species-level effects, where species identity was instead fit as a fixed factor. Linear mixed models were used for competitive response and % foliar nitrogen models, while a binomial generalized mixed model was used for mortality models. Due to differences in germination and mortality rates among species, 18 replicates per soil treatment were used in the analysis.

To determine whether soil treatments led to a shift in the degree of size-asymmetric competition, the relative initial size by soil treatment interaction (mesocosm-level model) and relative initial size by soil treatment by species identity interaction (species-level model) for each planned comparison (Fig. 2-1B) were used. To determine whether partitioned plant size altered the size-dependence of competitive interactions, competitive response models were run using either shoot, root or total biomass. For species-level models, p-values for each planned comparison were corrected using the Bonferroni correction (Dunn 1961) as specific species-level hypotheses were not set prior to experimental setup. For all models, denominator degrees of freedom were estimated using Satterthwaite's approximation (Satterthwaite 1946). Relative initial size was log-transformed for all size-asymmetric growth and nutrient assimilation estimates. Two outliers were removed from the size-asymmetric resource assimilation analysis. All analyses were run using the lmerTest (Kuznetsova *et al.* 2017) and lsmeans (Lenth 2016) packages in R (v 3.4.3).

RESULTS

Soil treatments altered mesocosm-level biomass and competitive response while the presence of neighbours altered mortality and resource assimilation of individuals. Mesocosms receiving higher levels of fertilization produced more shoot, root, and total biomass than those with lower levels of fertilization (Fig. 2-3, Appendix 2-S5). However, the low nutrient-microbial suppression treatment also produced more biomass than the low nutrient-homogeneous treatment for shoot and total biomass (Fig. 2-3). High levels of nutrients applied homogeneously decreased mesocosm-level competitive responses (Fig. 2-3). All other soil treatments had more complex effects on competitive response and varied as a function of how plant size was partitioned (Fig. 2-3); however, in all soil treatments, the presence of neighbours reduced resource assimilation by plants (log-response ratio (mean ± se): -0.51 ± 0.02). Overall mortality was low during the experiment, only 3% in multispecies mesocosms and 8% in alone-plant mesocosms and did not vary as a function of soil treatment (X^2_6= 4.675, p=0.586) nor species identity (X^2_2= 4.357, p=0.113).

Species-specific responses to size-asymmetric competition

Species differed in how soil treatments affected size-asymmetric growth (Fig. 2-4), but not size-asymmetric mortality (X^2_8= 1.825, p=0.986; Fig. 2-5) nor resource assimilation ($F_{8,\ 74.43}$=0.635, 0=0.75; Fig. 2-6). For size-asymmetric growth, all treatments resulted in differing competitive size-asymmetries between species except for the low-nutrient homogeneous and low-nutrient autoclaved treatments, where competition was size-asymmetric for all species (Fig. 2-4A). *E. speciosus* and *A. scabra* typically responded similarly to treatments except under the high-nutrient homogeneous treatment, where competition was size-asymmetric for *E. speciosus* but size-symmetric for *A. scabra* (Fig. 2-4A). *G. aristata* continually displayed opposite responses to the heterogeneous soil treatments from *E. speciosus* and *A. scabra,* where the presence of high- and low-quality patches led to size-symmetric and size-asymmetric competition in *G. aristata* respectively but size-asymmetric and size-symmetric competition in *E. speciosus* and *A. scabra* (Fig. 2-4A).

Effects of soil characteristics on the degree of size-asymmetric competition

At the mesocosm-level, growth was size-asymmetric in all soil treatments except the high nutrient-heterogeneous treatment (Fig. 2-4A). Soil treatments had a significant effect on the degree of size-asymmetric growth ($F_{4,\ 806}$=2.979, p=0.019; Fig. 2-4B) and resource assimilation ($F_{4,\ 90.7}$=5.198, p>0.001; Fig. 2-6), but not mortality (X^2_4= 2.043, p= 0.728; Fig. 2-5). For size-asymmetric growth, there were no significant differences among the a priori comparisons (Fig. 2-4B; Appendix 2-S6), while for size-asymmetric resource assimilation, the presence of a high-nutrient patch significantly reduced the degree of size-asymmetric assimilation ($t_{91.45}$=3.837, p>0.001; Fig. 2-6). However, the effects of soil treatment significantly varied by species ($F_{8,786}$=3.886, p>0.001) for size-asymmetric growth but not resource assimilation ($F_{8,60.48}$=0.674, p=0.712). Overall, at the mesocosm and species level, we found (Fig. 2-4B, Appendix 2-S6, Appendix 2-S7, see Appendix 2-S8 for relationships in log-space):

1. Increased soil fertility reduced or had no effect on competitive size-asymmetry relative to low amounts of nutrients when applied homogeneously.
2. Nutrient heterogeneity (high-fertility patch) either reduced or had no effect on competitive size-asymmetry when contrasted with equal amounts of nutrients applied homogeneously.
3. Nutrient heterogeneity (low-fertility patch) increased or had no effect on competitive size-asymmetry relative to equal quantities of nutrients applied homogeneously.
4. Initial suppression of soil microbial communities had no impact on competitive size-asymmetries.

Effects of partitioned plant size on the degree of size-asymmetric competition

Measuring competitive response with shoots or roots versus total biomass led to consistent effects of soil treatments on the degree of size-asymmetric competition in half of the comparisons at the mesocosm level, all comparisons within *E. speciosus,* and 3 out of 4 of the comparisons in *G. aristata* and *A. scabra* (Appendix 2-S6, Appendix 2-S6). At the mesocosm level, measuring plant size with shoots, rather than at the whole-plant level, resulted in increased soil fertility significantly reducing the degree of size-asymmetric competition, while measuring plant size with just roots, led to nutrient heterogeneity (low-quality patch) significantly reducing the degree of size-asymmetric competition (Appendix 2-S6, Appendix 2-S9, Appendix 2-S10). At the species level, measuring size with just roots, led to differences in the effects of nutrient heterogeneity (low-quality patch) for both *G. aristata* and *A. scabra* when compared to measuring size at the whole plant level; having no effect of treatment in *G. aristata* and significantly reducing the degree of size-asymmetric competition in *A. scabra* (Appendix 2-S7, Appendix 2-S9).

DISCUSSION

Overall, we found that soil heterogeneity and fertility can alter the degree of size-asymmetric competition, while microbial communities do not. However, soil heterogeneity and fertility altered size-asymmetric competition in ways not previously predicted and their effects were dependent on species identity. For example, increased soil fertility decreased size-asymmetric competition in *G. aristata,* such that competition was size-symmetric, but increased size-asymmetric competition in *E. speciosus*. Thus, the same environment can not only lead to different degrees of size-asymmetric competition experienced by species but also change the type of competition experienced (e.g. size-symmetric vs. size-asymmetric).

Species-specific responses to competitive size-asymmetries

The intensity of competition changed in response to the soil treatments (Fig. 2-3); however, the degree to which competition was size-asymmetric depended on which species was examined (Fig. 2-4A). This suggests that species have varying degrees of sensitivity to size-asymmetric competition which could provide an explanation behind why the relative abundance of small plants is higher than large plants in natural communities (Niklas *et al.* 2003; Moles *et al.* 2009) despite the popular 'size-advantage' hypothesis (Grime 1973; Goldberg 1996). When plants are actively competing for a limiting resource in time and space, an increased body size would be beneficial if plants display confrontational competitive strategies, such that interactions result in a "race" towards the contested resource (Novoplansky 2009); however, this is just one of multiple competitive strategies a plant can adopt. Under competition, plants can also display tolerant competitive behaviors, where they adapt strategies to maximize their performance under competition with neighbours (Novoplansky 2009). If plants exhibit more tolerant strategies they may be better adapted to utilize the disproportionately less amount of resources they receive during size-asymmetric competition, making them less vulnerable and keeping them from being competitively excluded. Thus, it is possible that a species vulnerability to size-asymmetric competition may depend on the competitive strategy of itself and its neighbours and that these differing vulnerabilities could promote coexistence of large and small individuals.

However, all species experienced size-symmetric competition under certain soil treatments (Fig. 2-4A), which suggests that in certain environments smaller individuals may not be at a competitive disadvantage, providing an alternative answer to why there are more small individuals than large in a community. Surprisingly, some cases of size-symmetric competition occurred under high nutrient treatments, suggesting that despite receiving up to 50% less sunlight than in low nutrient treatments (Appendix 2-S11), smaller individuals still responded to competition similarly to their larger neighbours. This suggests that competition for light alone may not be a driver of size-asymmetric competition but that there is an interaction between above and belowground resource competition that results in size-asymmetric competition (Harpole *et al.* 2017).

Effects of soil characteristics on the degree of size-asymmetric competition

At the mesocosm and species level, increased soil fertility under homogenous conditions either had no effect or decreased the degree of size-asymmetric competition (Fig. 2-4B). This contradicts the common prediction that increasing soil fertility can indirectly increase size-asymmetric competition by promoting increased shoot growth, switching competition from belowground to aboveground (Cahill 1999; Hautier *et al.* 2009; Lamb *et al.* 2009). The high soil fertility treatment did lead to an increase in shoot production (Fig. 2-3) and a decrease in light availability (Appendix 2-S11); however, it did not correspond with an increase in size-asymmetric competition. Nevertheless, when a low-nutrient patch was present within a matrix of high nutrients, this led to an increased degree of size-asymmetric competition in *G. aristata*. This suggests that a patchy nutrient environment may be driving the competitive advantage of larger individuals and the degree of size-asymmetric competition under high soil fertility.

The theory of how larger individuals gain benefits from nutrient patches is that large individuals can pre-empt high-nutrient patches (Schwinning & Weiner 1998), usually through root foraging (Craine & Dybzinski, 2013). However, we found that the presence of a high-nutrient patch either had no effect or decreased the degree of size-asymmetric competition (Fig. 2-4B), which has also been seen in plant populations (Rasmussen *et al.* 2019). Although our experiment did not look at root placement of individuals, a potential mechanism for the presence of high-quality patches reducing size-asymmetric competition could be that smaller individuals are more precise foragers than larger individuals (Campbell et al., 1991; Wijesinghe, John, Beurskens, & Hutchings, 2001, but see Kembel & Cahill, 2005), where the higher proportion of their root systems they are able to place in nutrient patches would reduce their competitive response, which is consistent with the scale-precision hypothesis (Campbell *et al.* 1991). This could explain why size-asymmetric resource assimilation decreased under this treatment, such that smaller individuals had significantly higher percent nitrogen in their leaves than larger individuals (Fig. 2-6). However, the presence of a low-nutrient patch increased the degree of size-asymmetric competition within *G. aristata* and had no effect on size-asymmetric resource assimilation, which suggests that foraging precision may be dependent on the location of the nutrient patch relative to an individual's neighbours (Wijesinghe *et al.* 2001; Cahill *et al.* 2010). Larger individuals may have the competitive advantage under heterogeneous conditions where high-nutrient soils are already occupied by provoking an avoidance response in smaller individuals, such that smaller individuals proliferate roots into nutrient-poor patches to avoid interactions with a larger neighbor. This phenomenon of root proliferation in low-nutrient patches when neighbours are present has been seen previously (McNickle *et al.* 2016), but the dependency on plant size may depend on the location of neighbour roots in relation to the high-nutrient patches. Thus, the consequences of nutrient heterogeneity for the degree of size-asymmetric competition are likely dependent on the quality of the patch, whether or not patches are already occupied, and the responsiveness of a plant to its environment.

We found no evidence that the initial suppression of microbial communities alters the degree of size-asymmetric competition at the mesocosm level or within any of the species studied. This goes against previous hypotheses on how microbial communities could increase or decrease size-asymmetric competition. This could be because: 1) nutrient sharing among individuals through microbial interactions is uncommon (He, Critchley, & Bledsoe, 2003; Robinson & Fitter, 1999, but see Selosse, Richard, He, & Simard, 2006), 2) benefits of microbial associations are not size-dependent (Eissenstat & Newman 1990), or 3) larger individuals may obtain more microbial associations, but these associations are not all beneficial but also parasitic (Thrall *et al.* 2007). It is possible that the role of microbial communities on the degree of size-asymmetry could be reliant on nutrient heterogeneity, where access to nutrients is not equal among individuals within the community; however, this was not tested in this study.

Most responses to soil treatments were found within *G. aristata.* This could be because *G. aristata* is more responsive to changes in the soil environment than the other species or because *G. aristata* was the species with largest difference between small and large individuals at the beginning of the experiment (Appendix 2-S3A). Since this responsiveness was only found in one species, it is not possible to determine why it occurred. However, *G. aristata* was not the largest species at the end of the experiment (Appendix 2-S3B) and *A. scabra,* which showed intermediate initial size differences compared to *G. aristata* and *E. speciosus*, did not have an intermediate response to soil treatments, suggesting responses to soil treatments were due to inherent properties within *G. aristata* and not larger initial size differences.

Partitioned plant size and the degree of size-asymmetric competition

Our results were typically consistent regardless of the how size was defined; however, there were some differences when size was measured as shoot, root, or whole plant biomass at the mesocosm level and within *G. aristata* and *A. scabra* (Appendix 2-S6, Appendix 2-S7). This reinforces the idea that plants that have the size-based competitive advantage aboveground may not have the size-based competitive advantage belowground and vice versa. Typically, measuring the size of a plant with only shoots or roots led to significant changes in the degree of size-asymmetric competition not seen when measured at the whole plant level (Appendix 2-S6, Appendix 2-S7), so measuring the size of a plant with only shoots or roots may exaggerate the degree of size-asymmetric competition occurring. Thus, it is important to consider the interactive effects between shoot and root responses when determining the degree and consequences of size-dependent competitive interactions between individuals.

Species identity determines its vulnerability to and the drivers of size-dependent competition. Overall, soil fertility and nutrient heterogeneity can promote size-asymmetric competition in one species but size-symmetric competition in another species. This challenges the current understanding that competition for soil resources is always size-symmetric, but also suggests a novel mechanism as to how species coexist. Differential tolerances of species to size-asymmetric competition suggest smaller species may not always be outcompeted by larger species and as such, may not necessarily promote the loss of small species.

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Table 2-1. Parameter values for the degree of size-asymmetric competition in reference to the definitions from Schwinning and Weiner 1998 and in the context of competitive response.

Term	**Definition from Schwinning and Weiner 1998**	**Definition in context of competitive response**	**Parameter value**
Partial size-asymmetry	“Uptake of resources increases with size, and larger plants receive a disproportionate share”	Larger individuals gain more resources than smaller individuals, resulting in larger individuals having the competitive advantage and smallest competitive response	°SAC>0
Size-symmetry	“Uptake of resources proportional to size”	All individuals gain a proportional amount of resources. Although larger individuals obtain a larger quantity of total resources, they also require more resources to survive and grow, and thus do not gain a competitive advantage over smaller individuals. As a result, the competitive advantage and competitive response is equal among all individuals regardless of size.	°SAC=0
Partial symmetry	“Uptake of contested resources increases with size, but less than proportionally”	Smaller individuals gain more resources than they need relative to larger individuals, resulting in smaller individuals having the competitive advantage and smallest competitive response	°SAC<0

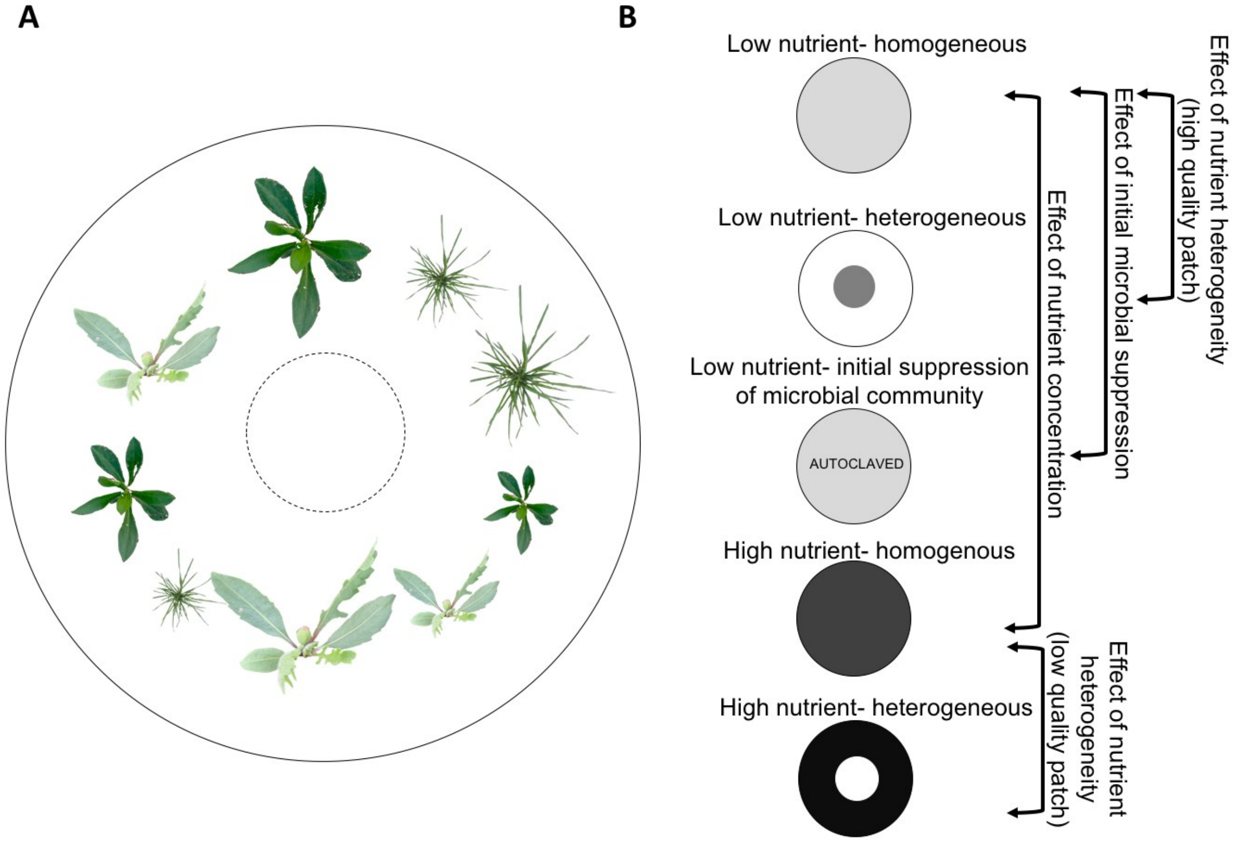

Figure 2–1. Planting design (A) and experimental soil treatments (B) for multispecies mesocosms. Nutrient patch or void (depicted by the dashed line) was 5 cm in diameter and placed at the center of the mesocosm. Planting design represents one of nine total planting orders. Brackets among soil treatments correspond to *a priori* comparisons. Mesocosms consisted of 20.3 cm azalea pots planted with three species of three different size classes that were randomly placed 5 cm from mesocosm edge. Plants in the picture are not to scale.

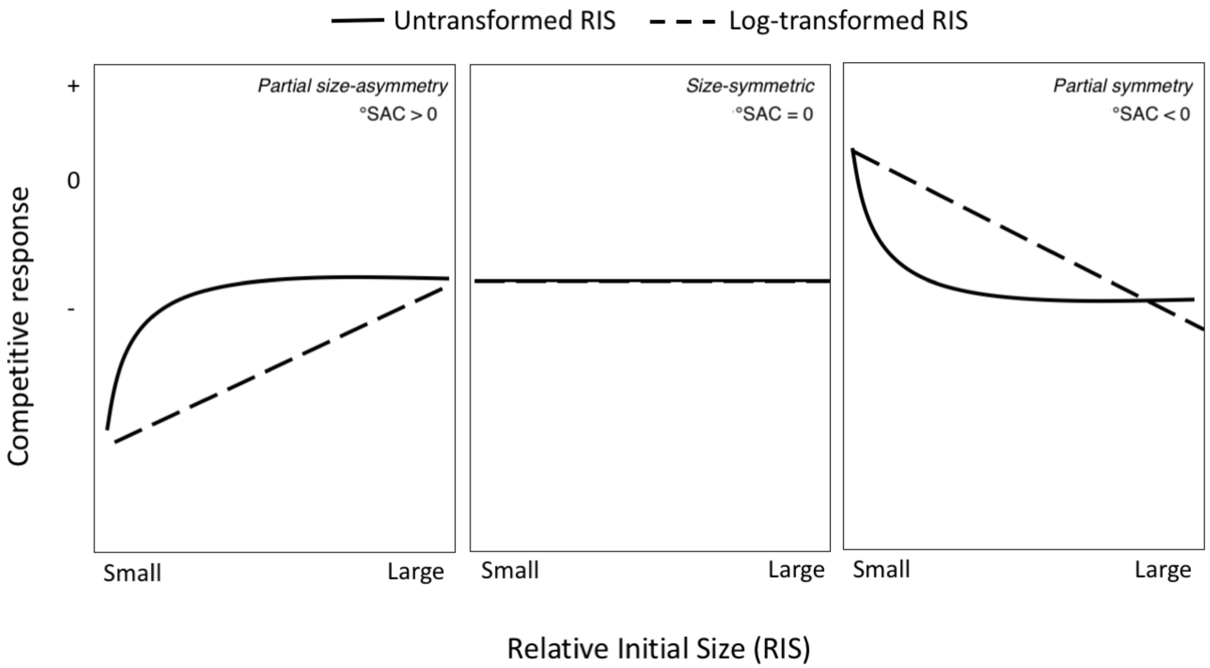

Figure 2–2. Conceptual model of how the relationship between relative initial size and competitive response depicts the degree of size-asymmetric competition. Relationship shown for when relative initial size is untransformed (solid line) and log-transformed (dashed line). A positive slope represents partial size-asymmetric competition (left panel), a slope of zero represents size-symmetric competition (middle panel) and a negative slope represents partial symmetry (right panel). See Table 2-1 for more explanation on relationships.

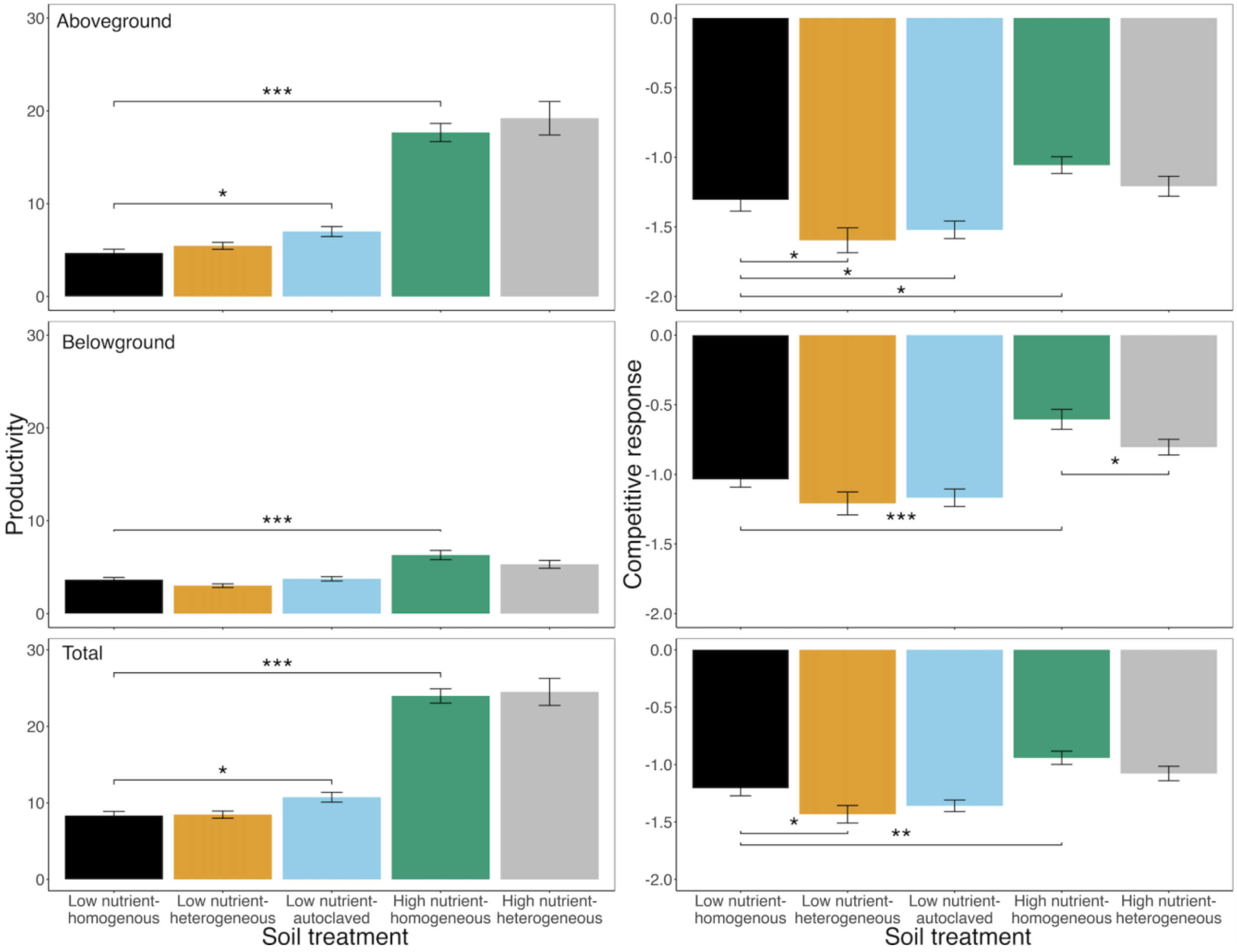

Figure 2–3. Average mesocosm-level productivity and competitive response (mean ± standard error) of each soil treatment. Productivity and competitive response were measured with aboveground (top panel), belowground (middle panel), and total (bottom panel) biomass. A more negative competitive response indicates stronger competition. Significant differences between *a priori* comparisons depicted (* < 0.05, ** < 0.01, *** < 0.001).

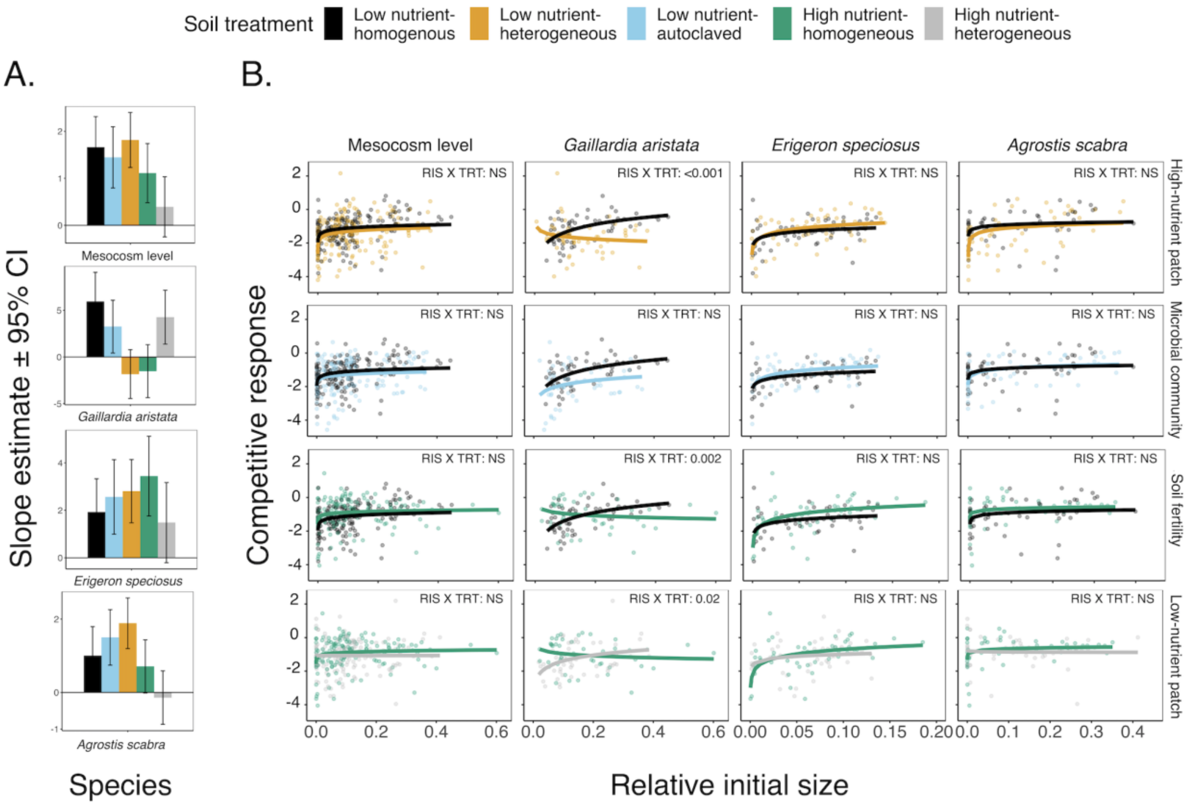

Figure 2–4. The degree of size-asymmetric competition at the mesocosm and species level under each soil treatment. Panel A depicts the degree of size-asymmetric competition estimate (regression slope estimate ± 95% confidence intervals) calculated as the slope of the logarithmic relationship between an individual's competitive response and relative initial size from a linear mixed model (panel B). A positive value represents size-asymmetric competition, a negative value represents partially symmetric competition, and a zero represents size-symmetric competition. For panel B, each row represents one of the four *a priori* comparisons (see Fig. 2-1B). RIS X TRT corresponds to the significance values for the relative initial size by soil treatment interaction from the mesocosm-level and species-level mixed linear models (NS= nonsignificant). Species-level p-value estimates were corrected using a Bonferroni correction (***α*** * 4). To facilitate comparison within species, the slope estimate axis (panel A) and relative initial size axis (panel B) has been adjusted to better represent the ranges of each species.

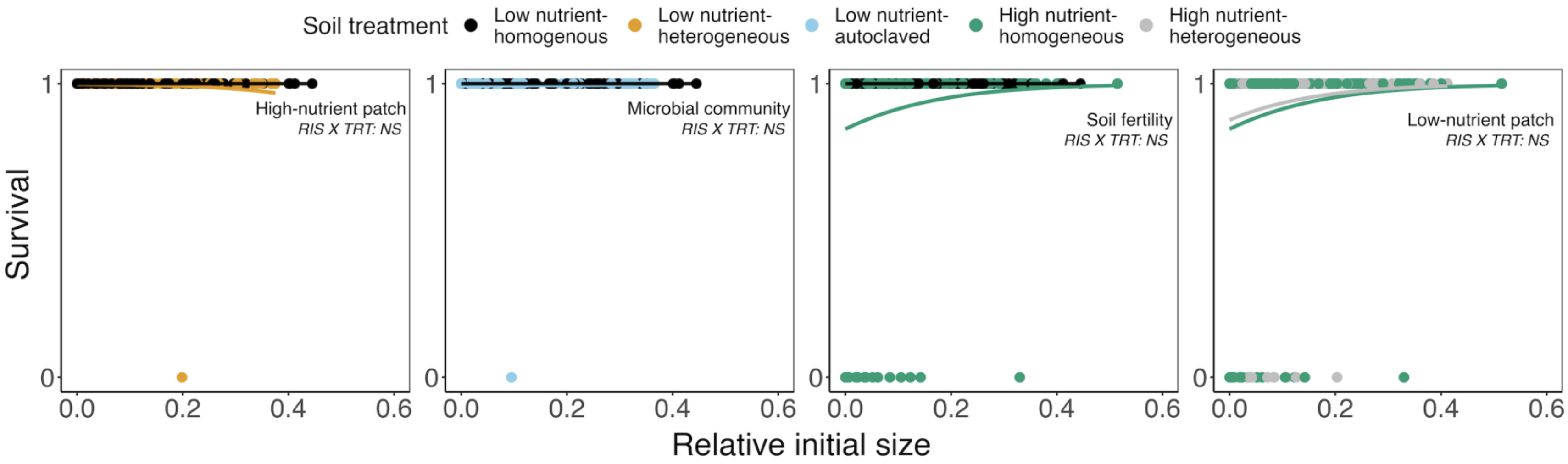

Figure 2–5. Size-dependent mortality within multispecies mesocosms as a function of soil treatment. Each panel represents one of the four a priori comparisons (see Fig. 2-1B). Survival measured at the end of the experiment: 0=dead and 1=alive. Regression line represents the relationship between relative initial size and survival from a binomial generalized linear mixed model. RIS X TRT corresponds to the significance values for the relative initial size by soil treatment interaction (NS= nonsignificant).

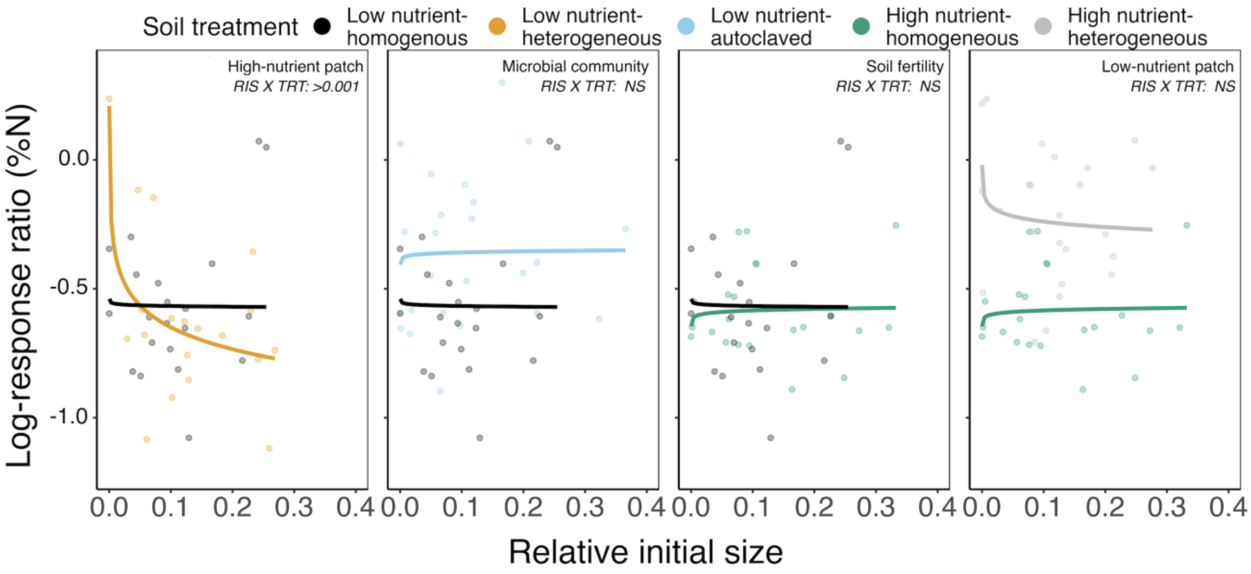

Figure 2–6. Size-dependent resource assimilation within multispecies mesocosms as a function of soil treatment. Each panel represents one of the four *a priori* comparisons (see Fig. 2-1B). Resource assimilation was measured as the log-response ratio of % foliar nitrogen at the end of the experiment. Regression line represents the relationship between relative initial size and the log-response ratio from a linear mixed model. RIS X TRT corresponds to the significance values for the relative initial size by soil treatment interaction (NS= nonsignificant).

Chapter 3: 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

INTRODUCTION

The role of size in a plant's performance is multifaceted and may dictate the function of an individual by affecting their competitive ability (Harper 1977; Gaudet & Keddy 1988), risk of herbivory (Noy-Meir *et al.* 1989; Diaz *et al.* 2001; Osem *et al.* 2004), or stress tolerance (Grime 1977). As such, the distribution of plant size within a community may be linked to the function and diversity of a system. For example, the importance of plant size within plant populations and forested stands is well understood and size inequalities within these systems have been linked to productivity (Hardiman *et al.* 2011; Zhang & Chen 2015; Bourdier *et al.* 2016), genetic diversity (Weiner & Solbrig 1984; Weiner & Thomas 1986), and species diversity (Niklas *et al.* 2003; Hardiman *et al.* 2011; Zhang & Chen 2015). However, size distributions within herbaceous communities do not typically receive the same amount of attention and are often overlooked when describing patterns within these communities (but see Schamp & Aarssen 2009; Moles et al. 2009; Waugh & Aarssen 2012). This shortage of studies could reflect a lack of meaningful function of size variation within herbaceous communities, or simply be a knowledge gap within the literature; however, due to size distributions being an important predictor in other systems, this suggests they too could be important for herbaceous community assembly.

Herbaceous communities vary in their magnitude of potential height differences between individuals, ranging from smaller differences of absolute height in short-statured alpine grasslands to larger differences in tall grass prairies. However, even small height differences between plants can impact a plant's responses to neighbours (Purves & Law 2002; Mullen *et al.*

2006) due to the prevalence of size-dependent processes, suggesting vertical size structure in a variety of herbaceous communities could play a functional role in determining community assembly. For example, when plants experience size-asymmetric competition for light, taller individuals gain the competitive advantage as they are able to pre-empt sunlight (Harper 1977; Weiner 1990), leading to their increased growth, and the possible reduction and removal of the shorter individuals (DeMalach *et al.* 2016). Further, the height distributions among species may also dictate the long-term performance of a species by impacting an individual's fitness (Weiner & Solbrig 1984; Aarssen & Taylor 1992; de Jong & Klinkhamer 1994) possibly through controlling its visibility to herbivores or pollinators (Klinkhamer et al. 1989 but see Klinkhamer & de Jong 1993). Consequently, a tall individual may gain more sunlight and visitations by pollinators compared to its shorter neighbours, but it is also may be more likely to be eaten by herbivores (Noy-Meir et al. 1989). Thus, height inequalities within communities may provide information on the processes acting in assembly.

Due to the relationship between vertical size structure and community assembly mechanisms, height distributions are likely to vary along a productivity gradient as limiting resources change from low to high productivity areas (Newman 1973; Tilman 1982). Under high productivity, light can be limiting (Grime 1973b; Newman 1973; Tilman 1982), and the overall size-asymmetry of competition may be high (Newman 1973; DeMalach *et al.* 2016); however, the effects of this on the vertical size structure of a system can be dependent on the stage of assembly (e.g. transient or stable states) as well as the strategies of the species in that system. Size-asymmetric competition is a multi-stage process. Initially, the acquisition of a disproportionate amount of resources by the taller individuals leads to a positive-feedback loop that results in their increased growth but the stunting of shorter individuals' growth, increasing height inequalities (Harper 1977; Hara 1986; Weiner 1990). Conversely, the final or stable state, in theory, is the removal of these smaller individuals as they do not receive enough sunlight (Weiner 1990), shifting the vertical size structure of the community such that more individuals are taller and the minimum height to survive in the community is larger. However, the competitive loss of small individuals is not equal among species (Brown *et al.* 2019) and an individual's height can be plastic, changing based on its environment (Smith 1982; Weinig 2000). As such the relationship between productivity and diversity is likely dependent upon the height inequalities within a community as well as the height plasticity and size-dependent competitive tolerance of the species within the community.

Although the productivity-diversity relationship is well established (Grime 1973a; Adler *et al.* 2011; Fraser *et al.* 2015), its explanatory power is quite low (Tredennick *et al.* 2016), suggesting that critical drivers of species loss and coexistence are missing from this model. The inclusion of vertical size structure may strengthen this relationship due to the potential causal associations between productivity, height inequalities and species diversity (Newman 1973; Rajaniemi 2003). Height inequalities typically increase with increased productivity (Weiner *et al.* 2001; Zhang & Chen 2015; Bourdier *et al.* 2016); however, the presence of height inequalities could increase species diversity through complementarity (Morin *et al.* 2011) or decrease diversity through size-asymmetric competition (DeMalach *et al.* 2016). Under complementarity, the increase of size inequalities results in an increase in niches of available sunlight that allows for the coexistence of species that require full sunlight and those that are shade-tolerant (Macarthur & Levins 1967), ultimately increasing diversity under high productivity (Morin *et al.* 2011). Conversely, under the transient stage of size-asymmetric competition, where height inequalities are exaggerated, the disproportionate distribution of sunlight between individuals would lead to the exclusion of shorter species, ultimately reducing diversity under high productivity (DeMalach *et al.* 2016). Many of the hypotheses as to why there is a productivity-diversity relationship are dependent on size-dependent processes within the community, and as such the inclusion of size structure parameters in these models may increase their explanatory power by incorporating biological information that is currently missing.

Plant size can be measured in many different ways including height, dry biomass, volume, and leaf size (Harper 1977; Weiner & Thomas 1986; Rösch *et al.* 1997; Schamp *et al.* 2013; Tracey *et al.* 2016). Here, we focus on height as much of the theory behind how size inequalities alter species diversity is based on light availability and are thus directly linked to plant height; however, we do recognize that other measures of plant size could produce similar or different results depending on the mechanisms in which they may impact diversity. By measuring individual's heights within local communities and accounting for intraspecific height variation, we examine the vertical size structure within a short-stature grassland to answer the following questions:

1. Is there variability in vertical size structures within a short-stature grassland?
2. Does vertical size structure vary along a productivity gradient?
3. Does vertical size structure vary with diversity and does its addition enhance the understanding of the underlying diversity-productivity relationship?

METHODS

Study site

This study was conducted within a 50 ha area of the Roy Berg Kinsella Research Ranch in Kinsella AB, Canada (53°5'N, 111°33'W) located within the aspen parkland ecoregion, which is characterized as a savannah habitat with mixed-grass prairie (dominated by *Hesperostipa curtiseta* (Hitchc.) Barkworth*, Festuca hallii* (Vasey) Piper *and Poa pratensis* L.) and patches of aspen (*Populus tremuloides* Michx.). The grasslands of the aspen parkland are a good system to test the importance of height distributions on community dynamics due to their low-statured nature compared to many other grasslands, herbaceous communities, or biomes (Knapp & Smith 2001; Moles *et al.* 2009). For example, the maximum height of vegetative growth we observed in our system is ~0.8 m when the maximum height can get up to ~10 m in other herbaceous communities and 100m in woody communities (Moles *et al.* 2009). Thus, if height effects are found here, they should also be found in other systems that have a greater magnitude and variation of heights.

Our study system is primarily dominated by graminoids, but much of the species diversity is found within forbs (Appendix 3-S1); local community composition varies with local environmental conditions (e.g. soil nitrogen and topographic position) and plant biomass (Lamb & Cahill 2008). Biomass production is primarily limited by water and nitrogen (Lamb *et al.* 2007). Historically this site has been grazed by cattle with the most recent grazing event occurring in the fall two years before this study began.

Study design

Sixteen blocks were distributed across the largest continuous grassland patch at the study site (~250 m x 350 m). Within each block, two 50 cm x 50 cm plots were established approximately 1 m away from each other. At each 50 cm x 50 cm plot, percent cover and vertical size structure (see below) were measured. Each plot was raked to remove litter biomass then clipped at the soil surface to measure standing biomass. Litter and standing biomass were dried and weighed separately. Species richness was calculated as the total number of unique species per plot.

Species evenness was calculated for species abundance using Pielou's evenness index (Pielou 1975).

Vertical size structure estimation

To estimate vertical size structure within each plot, three 50 cm transects were placed 10, 25, and 40 cm from and parallel to one of the plot's edges (Appendix. 3-S2); transects were pooled for analysis. Vegetative height and species identity were recorded for all ramets that touched each transect (~5900 ramets were measured in total with an average of 53 ramets/plot) during peak biomass to ensure the majority individuals had reached maturity. Height was measured using the methods outlined in (Perez-Harguindeguy *et al.* 2013; Cornelissen *et al.* 2014) to ensure height measures captured the maximum height in which plants actively photosynthesize and were comparable to other studies. Due to many of the species in our system being rhizomatous (Moss 1983), the identification of genets was not possible and vertical size structure estimation was performed on individual ramets. For the rest of the manuscript, individual ramets will be referred to as individuals.

For each plot, vertical size structure was measured using four metrics: average height and the Gini coefficient, which are common when examining size distributions in herbaceous plant populations (Weiner & Solbrig 1984), and the shape and scale parameters from a two-parameter Weibull distribution, which are common when examining size distributions in forested stands (He *et al.* In prep; Bailey & Dell 1973). All metrics were calculated using the height of all individuals within a plot; maximum likelihood estimation was used to determine the shape and scale parameters after fitting the height data with a Weibull distribution (Bailey & Dell 1973). The shape parameter of a Weibull distribution determines it's skewness (Rennolls *et al.* 1985) and is typically inversely related to the Gini coefficient such that a higher shape parameter corresponds to lower size inequality (Newby 1980; Knox et al. 1989, Appendix 3-S3). The scale parameter of a Weibull distribution is related to the distribution range (Rennolls *et al.* 1985) and mean (Knox *et al.* 1989) and as such can be correlated with a plot's average height (Appendix 3-S3). Despite these correlations, we decided to use all four measures in order to examine all common measures of vertical size structure regardless of the study system (herbaceous vs. forested stands).

Statistical analysis

To test whether size structure varies within a short-stature grassland, we ran Kolmogorov-Smirnov tests to compare height distributions between local communities with the most variable shape and scale parameters (see distributions in Fig. 3-1). We ran a total of six Kolmogrov-Smirnov tests, each comparing local communities with the following height distributions: 1) largest versus smallest shape parameter, 2) largest versus smallest scale parameter, 3) largest versus average shape parameter, 4) smallest versus average shape parameter, 5) largest versus average scale parameter, 6) smallest versus average scale parameter. For these tests, we focused on the shape and scale parameter, but due to the high correlation between these factors and average height and Gini coefficient (Appendix 3-S3), these tests also incorporated local communities with the most variable average height and Gini coefficient.

To determine whether size structure varies with productivity, we ran linear mixed models with productivity as a fixed factor, block as a random factor, and each of the four size structure parameters as response variables in four separate models. To address the potential importance of litter driving patterns related to productivity (Adler *et al.* 2011; Fraser *et al.* 2015), we ran two sets of models, one examining living productivity, where productivity was measured using standing living biomass, and another examining total productivity, where productivity was measured using standing living biomass and litter.

To determine whether the addition of size structure parameters improve the diversity-productivity relationship, we first tested the associations between the size structure parameters and species diversity, then we tested whether the inclusion of each size structure parameter individually increased the parsimony and explained variance of the diversity-productivity models. Due to the high correlations between the size structure parameters (Appendix 3-S3), we fit separate models for each size structure parameter rather than using model selection on a global model with all size structure parameters included. To determine whether size structure varies with diversity, we ran linear mixed models with either richness or evenness as a fixed factor, block as a random factor, and each of the four size structure parameters as predictors in eight separate models. To determine the most parsimonious model, we compared the AICc values between 1) each diversity-productivity model, where either richness or evenness was the response variable, productivity was a fixed factor, and block was a random factor, and 2) each diversity-productivity-size structure model where each of the size structure parameters were added separately to the diversity-productivity models as an additional fixed factor. To determine the explained variance of each of these models, pseudo-R-Squared values for each linear mixed model were calculated using the methods outlined in (Nakagawa & Schielzeth 2013)). All statistical analyses were performed in R (v 1.1.419) using the Mass (Venables & Ripley 2002), lmerTest (Kuznetsova *et al.* 2017) and MuMIn (Barton 2009) packages.

RESULTS

Variation in vertical size structure

Overall, variation among local communities was between 15 and 23% for all size structure parameters (Table 3-1). Local communities varied from having many short individuals (as low as 5cm) and few tall individuals to a more equal distribution of medium-height individuals (Fig.1). Differences in height distributions among local communities were significant when comparing the extreme and mean values of shape and scale parameters (Fig. 3-1): largest versus smallest shape parameter ($D=0.54$, $p<0.001$), the largest versus smallest scale ($D=0.52$, $p<0.001$), the largest versus average shape ($D=0.35$, $p<0.001$), the smallest versus average shape ($D=0.30$, $p<0.001$), the largest versus average scale ($D=0.42$, $p<0.001$), and the smallest versus average scale ($D=0.31$, $p<0.001$).

Variation in vertical size structure along a productivity gradient

Size structure parameters varied across a productivity gradient; however, the direction of the relationship was dependent on the size structure parameter as well as the response variable. An increase in productivity was associated with an increase in the local community's average height ($t_{19.87}=5.12$, $p<0.001$) and scale parameter ($t_{25.94}=2.99$, $p=0.006$) (Fig. 3-2), and a decrease in the local community's height inequality (Gini: $t_{25.56}=-2.84$, $p=0.009$, scale: $t_{25.94}=2.99$, $p=0.006$) (Fig. 3-2). Whether productivity was measured as living biomass or total biomass (living plus litter) had no significant effects on these relationships (Fig. 3-2).

Vertical size structure and the diversity-productivity relationship

A local community's richness or evenness had no association with its average height or scale parameter; however, increased height inequality was found in more species-rich communities ($t_{28.57}=-2.14$, $p=0.041$ and $t_{27.98}=2.02$, $p=0.053$) (Fig. 3-3)). There was evidence for plasticity in species and individual height characteristics as average, minimum and maximum height, as well as variation in height, varied with diversity (Appendix. 3-S4). To test whether species loss was size-dependent, we compared height characteristics for all species found within a plot versus species only found in both high and low diversity areas (Appendix 3-S4). We found there was a significant decrease in a species' minimum height at high levels of diversity for both species found at high and low diversity areas as well as all species found in a plot (Appendix 3-S4). In combination, these results suggest that species loss associated with a decrease in height inequality was not due to the exclusion of small species but the plasticity of species heights between high and low diversity areas. However, as described below, the strength of these relationships between diversity and size structure is impacted by the underlying diversity-productivity relationship.

Alone, productivity explained 12.02% and 2.92% of the variation in species richness and evenness respectively. However, the addition of any vertical size structure parameter increased the explanatory power of the productivity-richness relationship by 42.0-46.3% while increasing its parsimony (Table 3-2). Conversely, although, the addition of any size structure parameter increased the explanatory power of the productivity-evenness relationship by 12.7-24.5%, only the addition of the Gini coefficient increased its parsimony (Table 3-2). Overall, height inequality parameters resulted in the most parsimonious models for the diversity-richness and diversity-evenness models (Table 3-2).

As single predictors for diversity, all of the size structure parameters were more parsimonious in explaining variation in diversity than productivity; however, only the size inequality parameters resulted in the most parsimonious models with the highest explained variance (Table 3-2). However, the explained variance of the combined predictor models is more than the sum of its parts (Table 3-2), suggesting that the correlation between productivity and the size structure parameters (Fig. 3-2) results in added explained variation.

DISCUSSION

Vertical size structure significantly varied within this short-stature grassland, ranging from being comprised of many short individuals and a few tall individuals to a more equal distribution of medium-height individuals (Fig. 3-1). Although the trend of short individuals being more abundant in herbaceous communities seems to be widespread (Moles *et al.* 2009), the presence of a fairly equal distribution of medium-height individuals is rarely reported. This could be due to the fact that the majority of studies looking at height distributions do not incorporate the variation of heights within a species, as they typically link species abundance data with maximum height data from trait databases (e.g. Schamp & Aarssen 2009; Moles et al. 2009; Waugh & Aarssen 2012) to reduce problems with the indeterminate growth of plants and capture height relationships between fully matured plants (Moles *et al.* 2009). However, a species' height characteristics can vary as a function of diversity (Appendix 3-S4) and limitations to seedling establishment can impact diversity (Gilbert *et al.* 2009), thus capturing the plasticity in plant height between mature individuals as well as incorporating seedling and juvenile plant measures may be necessary to fully determine the consequences of height structure on plant diversity.

The vertical size structure of a local community can be directly associated with its productivity and species diversity (Fig. 2 & 3) likely because it represents the consequences of resource competition and species loss. Overall, the height inequality of a local community seems to be more important than the average height of its individuals for inferring patterns of productivity and species diversity (Table 3-2). As the productivity of a system increases, the average height of individuals increases while height inequality decreases (Fig. 3-2), which is indicative of what would be expected under size-asymmetric competition for light after exclusion occurs (Weiner 1990). However, it is unclear whether light availability is the mechanism driving height inequalities in this system. Another potential mechanism could be a decrease in soil nutrient heterogeneity with increasing productivity, which would also result in a decrease in height inequality with increased productivity either directly by altering individual plant access to nutrients (Casper & Cahill 1998) or indirectly by altering the degree of size-asymmetric competition (Brown *et al.* 2019; Rasmussen *et al.* 2019).

A decrease in size inequality leading to a loss of species richness could be the result of two processes: size-asymmetric competition (DeMalach *et al.* 2016) and assemblage-level thinning (Stevens & Carson 1999). Distinguishing between the two has important implications for the predictability of species loss, as one process is the result of trait-based exclusion, while the other is random. Under size-asymmetric competition, larger, fast-growing species (Rajaniemi 2003; DeMalach *et al.* 2016) or those more tolerant to size-asymmetric competition (Brown *et al.* 2019) will survive. While, under assemblage-level thinning, each species, through intraspecific competition, competitively excludes its smaller individuals and the coinciding reduction in density promotes species loss due to chance (Stevens & Carson 1999). In our system, there is a significant difference between minimum heights in high and low diversity areas for all species in the community as well as those only found in high and low diversity areas (Appendix 3-S4). This suggests that loss did not target shorter species and that variation in minimum heights between high and low diversity areas is due to the plasticity of individuals. As a result, in our system, assemblage-level thinning is likely the mechanism behind species loss with decreased height inequality.

Determining the mechanisms behind why increased height inequalities are associated with increased species diversity, however, is more nuanced. Size inequalities can promote species diversity through complementarity by providing more niche spaces for light and nutrients

(Morin *et al.* 2011) or, in the absence of density-dependent mortality, by promoting facilitation between individuals (Chu *et al.* 2009); however, size inequalities can also infer the early stages of size-asymmetric competition before thinning or exclusion (Weiner 1985). Thus, it is possible that diversity is higher under larger height inequalities because these local communities are younger and have not undergone species loss or thinning yet or because height inequalities confer more niche space. As such, the relationship between size inequality and diversity may be dependent on the successional stage of the system and whether local communities are in a transient or stable state. However, in our study, since grassland systems are maintained through disturbance they are typically in transient states (Collins & Wedin 2000), suggesting that size-asymmetric competition had not led to thinning yet. However, spatial heterogeneity in community composition is high in these systems (Collins & Smith 2006), suggesting that not all communities may be undergoing the same assembly mechanisms such that both niche creation and size-asymmetric thinning could occur within the same landscape.

The relationship between size inequality and species loss, however, may be dependent on the strategies of species within the community. When light is the limiting resource, plants can exhibit more bold strategies, increasing growth to try to pre-empt the resource (e.g. shade-avoidance response), or tolerant strategies, allowing them to compensate for receiving a lower proportion of resources (Novoplansky 2009). In communities with large size inequalities, if shorter species display bold strategies they will not be able to compete with the taller individuals for light and thus will be competitively excluded from the community, resulting in species loss. However, if short species display tolerant strategies, an increase in size inequality will not confer species loss as the shorter species will be able to tolerate the reduced amount of resources. Further, these strategies can be plastic within a plant, changing based on an individual's neighbours and its environment which can have consequences for species coexistence (Weinig 2000). This plasticity in strategy is higher in high diversity areas, such that intraspecific variation in height is significantly higher in high versus low diversity areas (Appendix 3-S4), suggesting that a plants ability to alter its competitive strategy based on its environment could be a mechanism for species coexistence, potentially combating the negative effects of size-asymmetric competition (Schwinning & Weiner 1998). As such, not only can height inequality be linked to diversity but can also provide information on the strategies of species within the community.

Although many of the inferences of how height inequality is tied to species loss are dependent on productivity (Newman 1973; Tilman 1982), productivity alone did not explain variation in species richness as well as the vertical size structure parameters (Table 3-2) and the inclusion of height inequality measures as well as average height measures improve the diversity-productivity relationship (Table 3-2). Furthermore, although there is no well-established hypotheses or evidence for a productivity-evenness relationship, the inclusion of size structure parameters can improve this relationship up to six times compared to using productivity alone (Table 3-2). These findings suggest that vertical size structure is an important pattern related to community assembly that is missing from current theory and models. The strength of vertical size structure as predictor likely comes from its ability to provide information on both the properties of a system, such as its density (Weiner *et al.* 2001; Stoll *et al.* 2002), productivity (Hardiman *et al.* 2011; Zhang & Chen 2015; Bourdier *et al.* 2016) , or diversity (Niklas *et al.* 2003; Hardiman *et al.* 2011; Zhang & Chen 2015), as well as the mechanistic determinants of a systems' assembly, such as resource availability (Schwinning & Weiner 1998), the degree of competition (Weiner 1990) or facilitation (Chu *et al.* 2009) as well the plasticity and strategies of individuals within the community (Appendix 3-S4). Thus, understanding the causality between the size-structure-productivity and size-structure-diversity relationships can provide insight into the assembly and structure of systems. If size structure causes changes to productivity and diversity, rather than being a product of it, this could provide potential tools to manage systems through manipulating their size structure. As such, future work should be done to determine the causality behind these relationships. Further, size inequalities can indicate processes of either light or nutrient competition; thus, future studies determining the effects of both light and nutrient availability on size inequalities are needed to fully understand the mechanisms driving patterns in size structure and diversity. Overall, vertical size structure adds to our understanding of the diversity of a system, and in some cases may be more powerful than productivity. Future studies should incorporate size structure to incorporate a more mechanistic understanding of a systems' properties.

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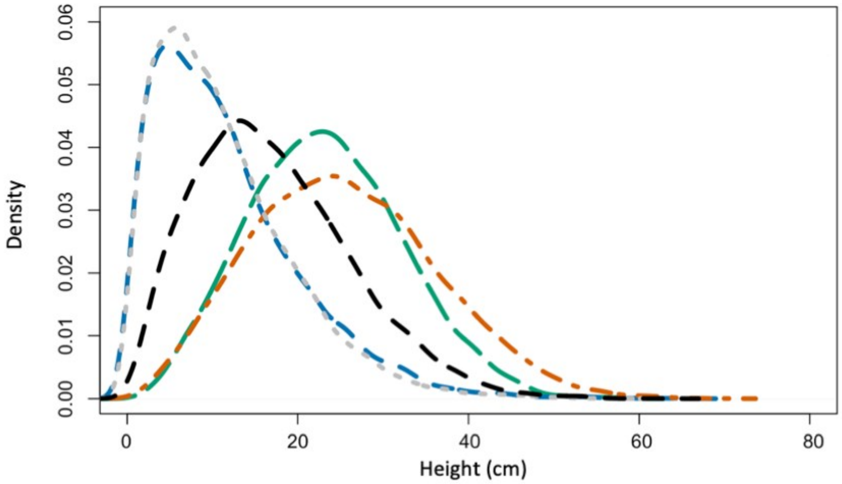
Table 3-1. Variation in vertical size structure parameters, productivity and species diversity among local communities.

Parameter	**Minimum**	**Maximum**	**Average**	**Coefficient of Variation**
Average height (cm)	11.40	25.50	17.20	21.80
Gini coefficient	0.23	0.40	0.31	15.50
Shape parameter	1.38	2.77	1.97	20.00
Scale parameter	12.48	28.77	19.29	22.30
Productivity (g/m^2)	89.72	453.52	255.88	31.10
Productivity with litter (g/m2)	233.70	672.20	411.90	22.70
Richness (# species)	7.00	21.00	12.00	23.84
Evenness	0.67	0.93	0.82	8.56

Table 3-2. Akaike information criterion with small sample correction (AIC_c) and explained variance (R^2) for each diversity-productivity model and size structure parameter. The most parsimonious models are bolded for combined and single predictors. Most parsimonious models were determined by having the lowest AICc value that was at least two less than another model. The explained variance for all models corresponds to the marginal R^2, which represents the variance explained by the fixed factors alone, calculated using the methods outlined in (Nakagawa & Schielzeth 2013)). Species richness was measured as the total number of unique species per plot. Species evenness was measured using Pielou's evenness index (Pielou 1975).

Explanatory variables	**Response variable**			
	Richness		**Evenness**	
	AICc	**R^2**	**AICc**	**R^2**
Single predictors				
Productivity	172.3	12.0	-51.9	2.9
Average height	167.4	7.1	-57.23	1.1
Gini coefficient	**157.3**	10.9	**-68.9**	8.5
Shape parameter	161.1	12.2	-64.6	8.3
Scale parameter	167.5	7.5	-57.0	1.1
Combined predictors				
Productivity + Average height	163.0	44.9	-42.6	12.7
Productivity + Gini coefficient	**155.9**	42.0	**-55.6**	24.5
Productivity + Shape parameter	**157.7**	46.3	-51.4	23.9
Productivity + Scale parameter	162.5	46.2	-42.4	13.0



Line	Community	Most common height (cm)	Average height (cm)	Gini coefficient	Shape parameter	Scale parameter
— –	Largest shape	21.5	23.07	0.23	2.77	25.87
– –	Smallest shape	4.8	11.69	0.40	1.38	12.79
· —	Largest scale	22.5	25.45	0.25	2.54	28.77
· · ·	Smallest scale	4.6	11.42	0.38	1.41	12.48
—	Average shape and scale	12.2	17.16	0.30	1.97	19.29

Figure 3–1. The range in vertical size structure observed within a short-stature grassland represented by a two-parameter Weibull distribution. To visually display the range of size-variability observed within local communities, here we present height distributions for the local communities with the largest and smallest shape and scale parameters. The black line represents the average of shape and scale parameters observed among all community and thus does not represent the actual distribution of a single community. Due to the correlation between size structure parameters, this also depicts the local communities with the largest and smallest average height and Gini coefficient.

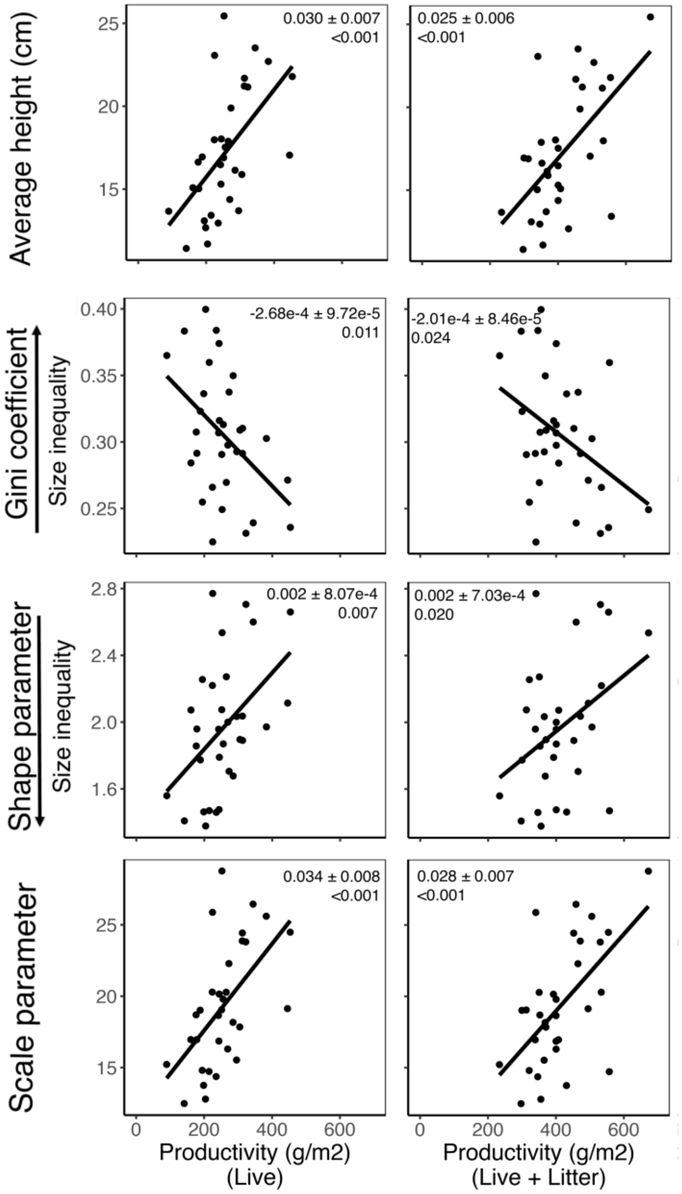


Figure 3–2. The relationship between productivity and size structure parameters. Regression slope estimates and p-values from each linear mixed model are shown in the upper left or right corner of each plot. Productivity represents the total living biomass (Live) or total living plus litter (Live + Litter) found within a plot at peak biomass.

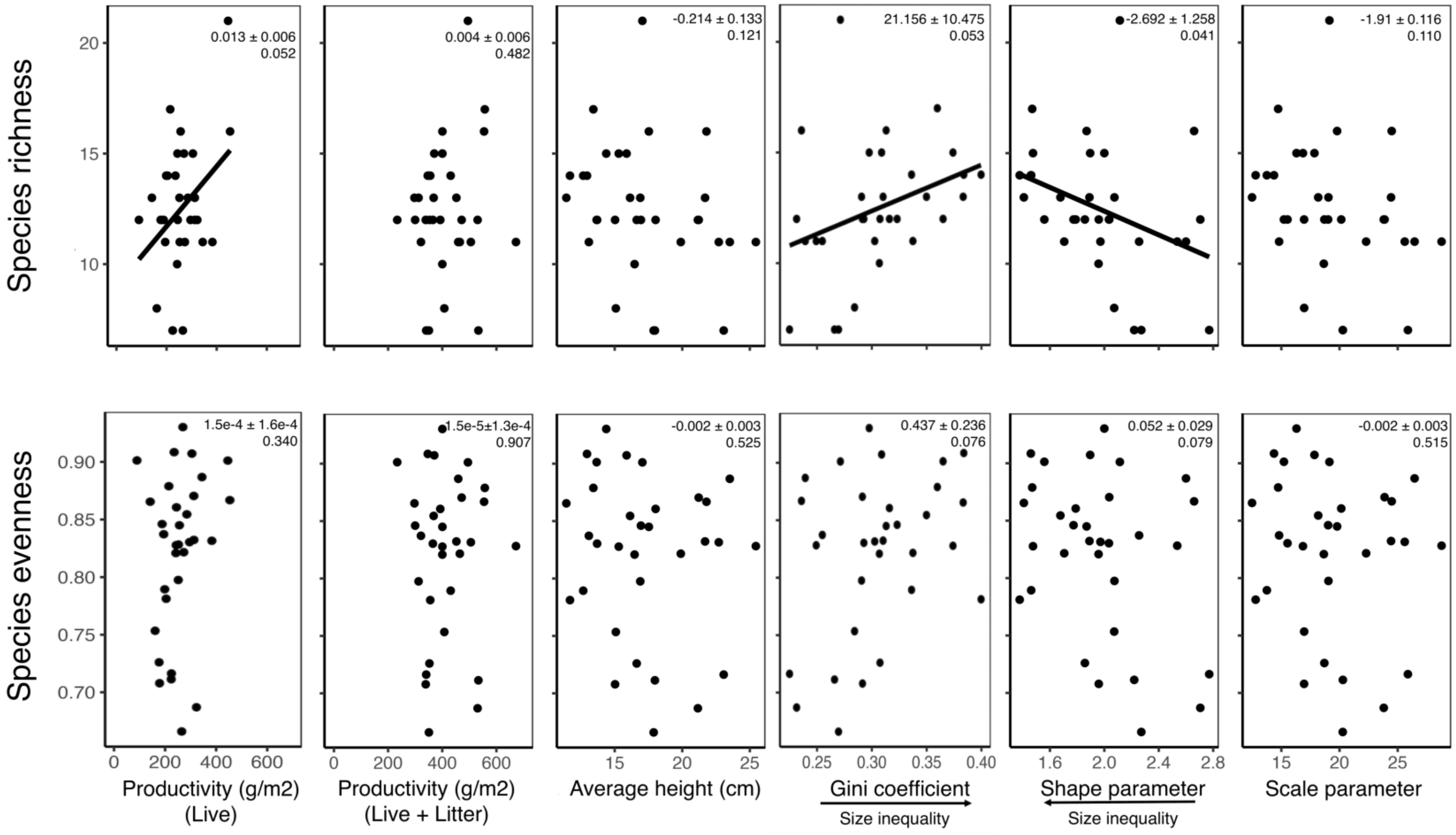


Figure 3–3. The relationship between productivity and size structure parameters with species richness and evenness in a short-stature grassland. Regression slope estimates and p-values from each linear mixed model are shown in the upper right corner of each plot. Species richness was measured as the total number of unique species per plot. Species evenness was measured using Pielou's evenness index (Pielou 1975). Regression lines were included if there was a significant relationship between variables.

Chapter 4: Competitive size-asymmetry, not intensity, leads to short-term species loss in a native grassland community

INTRODUCTION

Competitive interactions are common in natural communities (Schoener 1983); however, the role competition plays in community assembly and diversity maintenance remain unclear (Goldberg & Barton 1992; Gurevitch *et al.* 1992; Schenk 2006). Complicating understanding of how competition structures communities is that there are multiple facets of competition, including the intensity (i.e., the degree to which competition for a limited resource reduces plant performance (Welden & Slauson 1986)), size-asymmetry (i.e., the degree to which individuals obtain a disproportionate amount of resources relative to their size (Hara 1986; Weiner 1990)), and transitivity (i.e., the degree to which a species in a community follow a perfect hierarchy (Laird & Schamp 2006)) of competition, which may have independent and differential impacts on community assembly. There has been a historical focus on the relationship between competitive intensity and species diversity, likely due to the prevalence of the competitive exclusion principle, which states species exclusion is the necessary outcome of intense competition among species (Tansley 1917; Gause 1934; Hardin 1960). Yet, consistent empirical support for whether intense competition does (Hautier *et al.* 2009; Lamb *et al.* 2009; Martorell & Freckleton 2014; Michalet *et al.* 2015) or does (Lamb & Cahill 2008; Mitchell *et al.* 2009; Bagousse-Pinguet *et al.* 2014) not alter species diversity is lacking. There is increasing evidence for the potential importance of competitive size-asymmetry for species diversity (Hara 1993; DeMalach *et al.* 2016). For example, competition for light (a size-asymmetric process) is thought to be a major mechanism for species loss under high productivity (e.g., Newman 1973, Rajaniemi 2003). However, there are only a few empirical studies that test the impact of competitive size-asymmetry (e.g., Goldberg and Miller 1990, Hautier et al. 2009, DeMalach et al. 2017) on species diversity, and less is known about the relative importance of competitive size-asymmetry and intensity for species loss.

Competitive size-asymmetry is a potentially strong driver of species loss because it leads to a positive feedback loop where larger individuals keep getting larger while stagnating the growth of, and eventually competitively excluding, smaller individuals (Weiner 1990). Thus, competitive size-asymmetry may target species that are particularly sensitive to size differences (Brown *et al.* 2019), leading to differential but persistent species loss. On the other hand, competitive intensity should lead to consistent species loss only in situations where there are clear competitive hierarchies among species (Laird & Schamp 2006). However, completely transitive hierarchies seem to be rare in nature (Keddy and Shipley 1989, Taylor and Aarssen 1990, Shipley 1993, Soliveres et al. 2015), likely because of intraspecific aggregation (Stoll & Prati 2001), variation in intraspecific competitive abilities (Lichstein *et al.* 2007; Hart *et al.* 2016), or the independence of a species' ability to tolerate competition and competitively suppress its neighbours (Goldberg & Landa 1991; Wang *et al.* 2010). Thus, an increase in competitive intensity should not necessarily cause consistent loss of competitive inferior species, but may instead alter dynamics within numerous submodules of an interaction network (Laird & Schamp 2006), leading to less predictable impacts on coexistence.

Size-asymmetric competition may be more common than once thought, making the understanding of its role in community assembly critical. There is increasing evidence that size-asymmetric competition is not restricted to environments with intense competition, high productivity, and low light availability, as previously thought (reviewed in Schwinning and 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 (DeMalach *et al.* 2016; Brown *et al.* 2019; 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, to test the relative influence of competitive intensity and size-asymmetry on species turnover, we experimentally manipulated the size structure within 57 native grassland communities and monitored the growth of eight focal species over three growing seasons. Overall, we had five experimental treatments: a control, where no vegetation was removed, a total neighbor removal, where all vegetation except focal plants were removed, and three size structure manipulations, where 30% of the community's biomass was removed by size class (i.e., small, medium and large individuals). By combining the selection of focal individuals and size-dependent thinning treatments, we were able to experimentally create a substantial variation in the relative size of our focal individuals compared to the established vegetation that is needed to measure competitive size-asymmetries (Weiner 1990; Brown *et al.* 2019). Species turnover was measured as temporal beta-diversity and broken down into the proportion of species gains and losses over the three years (Legendre 2019). To examine what factors are both aspects of competition, we measured environmental variables, including light availability, soil pH, soil inorganic nitrogen, and soil moisture.

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.

Experimental design

Fifteen experimental blocks were set up within one of the largest contiguous grassland patches (~250 m x 350 m) at the study sites in May 2016. Blocks were established to ensure at least three focal plant species occurred within the block (Appendix 4-S1). Two hundred fifty-five focal plants were selected semi-randomly (needed to appear healthy) and represent the most dominant species at the study site (Lamb & Cahill 2008; Brown & Cahill 2019). Focal species included eight species from four families: Asteraceae (*Artemisia frigida* Willd. and *Artemisia ludoviciana* Nutt.), Poaceae (*Festuca hallii* (Vasey) Piper, *Hesperostipa curtiseta* (Hitchc.), and *Poa pratensis* L.), Rubiaceae (*Galium boreale* L.), and Rosaceae (*Geum triflorum* Pursh and *Rosa arkansana* Porter.). Established individuals were used rather than transplants due to the system being dominated by long-living perennials. Thus transplants typically do not fully reflect established vegetation responses in these systems (Lamb & Cahill 2006). By using established individuals, we may have unintentionally selected individuals that have already successfully passed through biotic and abiotic filters within the community, which may underestimate the effects of competition on the community. For example, if competition has the strongest filter during the recruitment stage. However, since this study is not purely observational, and we manipulated community size structure, we expect there to be changes to the acting filters and species performance, which is supported by the fact that there is a differential amount of gains as a result of thinning treatment ($F_{3,39.26}$=2.953, p=0.044).

Measuring size-asymmetric competition requires variation in individuals' initial sizes relative to the neighbouring vegetation (Weiner 1990; Brown *et al.* 2019). To create size variation, we imposed a series of thinning treatments within each block. We experimentally removed 30% of the community's biomass by size class (i.e., small, medium, and large individuals). We also had a control treatment, where we kept all vegetation intact, and an all neighbor removal treatment, where we removed all individuals but the focal individuals to estimate focal plant performance in the absence of neighbours. In total, there were five experimental removal treatments per block: a control, total removal, and three partial neighbor removals by size class (Fig. 4-1). When manipulating the size structure in a community, you can control for community-level ramet density or shoot biomass, not both. Although our thinning treatments resulted in different ramet densities between plots in a block, they allow biomass between plots in a block to stay relatively equal. Changes in ramet density can be important for competitive size-asymmetry as they may indicate that it is acting (Weiner 1986). However, much of the theory behind the link between size-asymmetry and species loss is dependent on productivity (e.g., Newman 1973), so we prioritized controlling for biomass. Additionally, we measured ramet density throughout the experiment to determine if it altered our observed levels of competition.

In May 2016, removal treatments were created by clipping individuals at the soil surface and then painting the cut stems with Glyphosate herbicide to ensure complete plant death. Root and rhizome connections were severed to a depth of 15 cm between each experimental plot and the surrounding vegetation to reduce belowground interactions between treatments (Lamb & Cahill 2008). To ensure focal individuals within the all neighbor removed treatment had continued growth without neighbours, we reapplied glyphosate herbicide every month during the growing season. All plots were 80 cm by 80 cm except for the total neighbor removal plots, which were 80 cm by 320 cm to reduce interactions between focal individuals in the plot.

In August 2018, after three growing seasons, we harvested the aboveground biomass of each focal plant. 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 4-S1 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 performance of the focal individuals within each plot. For this measure, we averaged the competitive intensity and degree of size-asymmetry experienced by each focal individual in each plot (see Appendix 4-S2). As a result of our blocked design, block incorporated much of the variation due to differences in focal species identity between plots (see Appendix 4-S3). 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 the analysis.

The intensity of competition was measured as competitive response, which represents the relative performance of an individual grown with neighbours to one grown without (Cahill 1999;

Weigelt & Jolliffe 2003). For each focal individual, competitive response was measured at the end of the experiment using aboveground biomass. The average competitive response was used for each focal plant in a neighbor treatment (e.g., partial removal or control) by calculating separate competitive responses for each replicate of "alone" plants of the same species, regardless of block, then averaging them (Lamb & Cahill 2006). The community-level intensity of competition was estimated by averaging the competitive response of each individual in each local community (see Appendix 4-S2 for more details).

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 (Brown *et al.* 2019). The degree of size-asymmetric competition experienced by individuals was calculated as the derivative of the species-level regression equation, or:

$$CSA_{ind} = CSA_{spp}\ x\ \frac{1}{IS_{ind}},$$

where CSA_{ind} is the degree of competitive size-asymmetry experienced by an individual, CSA_{spp} represents the degree of competitive size-asymmetry experienced by a species (values reported in Appendix 4-S4), and IS_{ind} represents the initial size of an individual (see Appendix 4-S2 for more details). An individual experiences size-asymmetric competition if $CSA_{ind} > 0$, size-symmetric competition if $CSA_{ind} = 0$, and partial symmetry if $CSA_{ind} < 0$ (as defined by Schwinning & Weiner 1998 and Brown *et al.* 2019).

To test the sensitivity of this measure to how initial size is defined, the degree of size-asymmetric competition was calculated three different ways, each with different measures for initial size (*relative initial average biomass* is used in the manuscript, and the others are referenced in the supplementals):

1. *Absolute initial biomass,* estimated using species-specific biomass regressions created from destructive harvests of individuals found outside of the experimental treatments (see Appedix S5),
2. *Relative initial total biomass,* calculated as the absolute initial biomass of a focal individual divided by the total biomass of the plot it was found in,
3. *Relative initial average biomass*, calculated as the absolute initial biomass of a focal individual divided by neighboring plants' average initial biomass. The average initial biomass of neighbor plants was calculated by dividing the plot's total biomass by the ramet density in the plot, which resulted in differing average initial biomass of neighbouring plants between thinning treatments (Appendix 4-S6).

The community-level measure of the degree of size-asymmetric competition was calculated by averaging the degree of size-asymmetric competition experienced by all focal species in each plot (see Appendix 4-S2 for more details).

Temporal beta-diversity and environmental measures

To determine the impacts of competition on species turnover, we measured the presence and absence of species within a 50 cm by 50 cm region of each experimental plot at the beginning (i.e., June 2016) and end (i.e., August 2018) of the experiment. Temporal beta-diversity and the relative contributions of gains and losses for each plot between June 2016 and August 2018 were calculated using the Jaccard dissimilarity (Legendre 2019). Temporal beta-diversity is a measure that examines the relative number of species that are lost, gained, and shared between two time points (Legendre 2019). A species gain would occur if a species was not present at the first time point (i.e., June 2016) but was present at the second time point (i.e., August 2018). A species loss would occur if a species was present at the first time point but no longer there at the second time point.

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). Light availability was measured as the ratio of photosynthetically active radiation (P.A.R.) 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 cm by 20 cm soil core taken in the middle of each plot. Roots were then washed over a 2 mm sieve. All biomass samples were dried at 65°C for 48 hours 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 the relative importance of competitive intensity versus the degree of competitive size-asymmetry for species gain, loss, and turnover, we ran three linear mixed models with either the relative contributions of gains or losses, or the temporal beta-diversity index 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). However, the quadratic term was never significant, and subsequently removed from the models for analysis. To determine whether species loss was a consequence of an individual's initial size or abundance, two binomial generalized linear models were fit with either initial size or abundance as fixed factors and whether or not that individual 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 plant identity, measured as two axes of a non-metric multidimensional scaling with focal plant 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

We found contrasting effects of competitive intensity and size-asymmetry on species turnover over three growing seasons. Counter to the standard model, increased competitive intensity was not associated with community instability, species loss, or species gain (Fig. 4-2). In contrast, though competitive size-asymmetry was not associated with community instability, it was associated with increased species loss, where species loss was more likely to occur when larger individuals had the competitive advantage, and weakly associated with decreased species gains, where species gain was more likely to occur when small individuals had the competitive advantage (Fig. 4-2). Contrary to expectations, the probability of loss was independent of a species' initial height but increased with a species' rarity (Fig. 4-3); the rarity of a species was independent of its initial height (Appendix 4-S7).

The relationship between competitive size-asymmetry and species turnover was consistent among the three metrics of competitive size-asymmetry in terms of significance (at $\alpha=0.05$) and sign (positive or negative relationship) except for species gains (Appendix 4-S8). For species gains, whether the p-value was under 0.05 varied among the three metrics of competitive size-asymmetry (relative average biomass: $p=0.038$, relative total biomass: $p=0.079$; and absolute biomass: $p=0.352$); however, the sign stayed consistent among them all. Due to this inconsistency in the degree of significance and a lack of strong relationship based on visual observation of the graph (Fig. 4-2), we conclude that there is only a weak negative relationship between competitive size-asymmetry and species gains.

Competitive intensity and size-asymmetry were not correlated within local communities (Appendix 4-S9) and were associated with different environmental factors (Fig. 4-4, Appendix 4-S10). 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 (mean ± SE: -0.233 ± 0. 0.622; Appendix 4-S11). 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 (-0.309 ± 0.148, $F_{1,42.34}$=4.354, p=0.043) in low litter environments (Fig. 4-4). However, the degree of competitive size-asymmetry was also weakly associated with nitrogen availability, being more size-asymmetric in high nitrogen environments (0.269 ± 0. 137, $F_{1,37.71}$=3.886, p=0.056; Fig. 4-4). Further, the degree of competitive size-asymmetry was associated with focal species identity, suggesting that vulnerability to competitive size-asymmetry is species-specific (Fig. 4-4, Appendix 4-S10). Contrary to prior beliefs, neither light availability nor standing biomass (shoot or root) was associated with changes in the intensity or size-asymmetry of competition (Fig.4-4, Appendix 4-S10).

DISCUSSION

Contrary to expectations (Gause 1934; Grime 1973; Tilman 1988), competitive intensity was not associated with species loss or gains (Fig. 4-2). Competitive size-asymmetry, on the other hand, was independent of competitive intensity (Appendix 4-S9) and associated with increased species loss and reduced species gain (Fig. 4-2). These results help clarify the role competition plays in the assembly of plant communities by demonstrating that different aspects of competition have independent and differential influence on species turnover. In some communities, competitive size-asymmetry may be a stronger assembly mechanism than competitive intensity as it is more directly linked to species loss and gain. However, the lack of association between either competitive intensity or size-asymmetry and overall species turnover (i.e., TBI, Fig. 4-2) suggests that competition alone is not the only structuring force in community assembly (despite the occurrence of intense or highly size-asymmetric competition). This result reinforces the issue of the importance of competition for community structure (*sensu* Welden and Slauson 1986).

Species loss and gains are likely more strongly associated with the degree of size-asymmetric competition because competitive size-asymmetries capture the inequalities among species. In contrast, competitive intensity captures the overall growth reduction experienced by a community. The importance of inequalities for preventing coexistence has been shown with competitive intransitivity (Laird & Schamp 2006; Soliveres *et al.* 2015). Coexistence occurs when there is a breakdown in competitive hierarchies (i.e., competitive intransitivity), while species loss occurs when there are clear hierarchies (i.e., competitive transitivity) (Laird & Schamp 2006). 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 (Chesson 2000). The size-asymmetry of competitive interactions is essentially a special case of competitive transitivity where competitive dominance stems from particular traits (i.e., an individual's size). For those species that are particularly sensitive to size differences (Brown *et al.* 2019), the disproportionate allocation of resources within competitively size-asymmetric communities may lead to the competitive exclusion of these vulnerable species as well as potentially prevent other vulnerable species from establishing in the community.

Whether small or large individuals have competitive advantage dictates the amount of species gain or loss within a community (Fig. 4-2). Species gains are highest when small individuals have the advantage within a community (i.e., under partially symmetric competition) (Fig. 4-2), 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) (Fig. 4-2). 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 (Newman 1973; Goldberg & Miller 1990; 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 (Fig. 4-3), 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), competitive abilities (Gaudet & Keddy 1988; Aarssen 1992; Goldberg 1996), and ability to tolerate or avoid competition or resource limitations (Novoplansky 2009; Craine & Dybzinski 2013). 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; Smith & Knapp 2003; Mouillot *et al.* 2013; Jain *et al.* 2014), 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 4-S7).

The recognition that size-asymmetric competition is critical for species loss is mostly limited to high productivity environments where light is limited (Grime 1973; Newman 1973; Tilman 1982; Hautier *et al.* 2009); 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 but slightly increased with soil fertility (Fig. 4-4; Appendix 4-S10). This suggests that the role of fertility in promoting size-asymmetric competition may be due to belowground mechanisms rather than aboveground mechanisms (Brown *et al.* 2019) or the interaction between the two. For example, small and large individuals may have differential soil resource preemption or uptake rates (Schwinning & Weiner 1998; Fransen *et al.* 2001; Rajaniemi & Reynolds 2004; Craine & Dybzinski 2013). 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 4-S11), where smaller individuals have a competitive advantage and receive a larger proportion of resources compared to their larger neighbours (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 neighbours. 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 versus nutrients) may alter the consequences of size-asymmetric competition.

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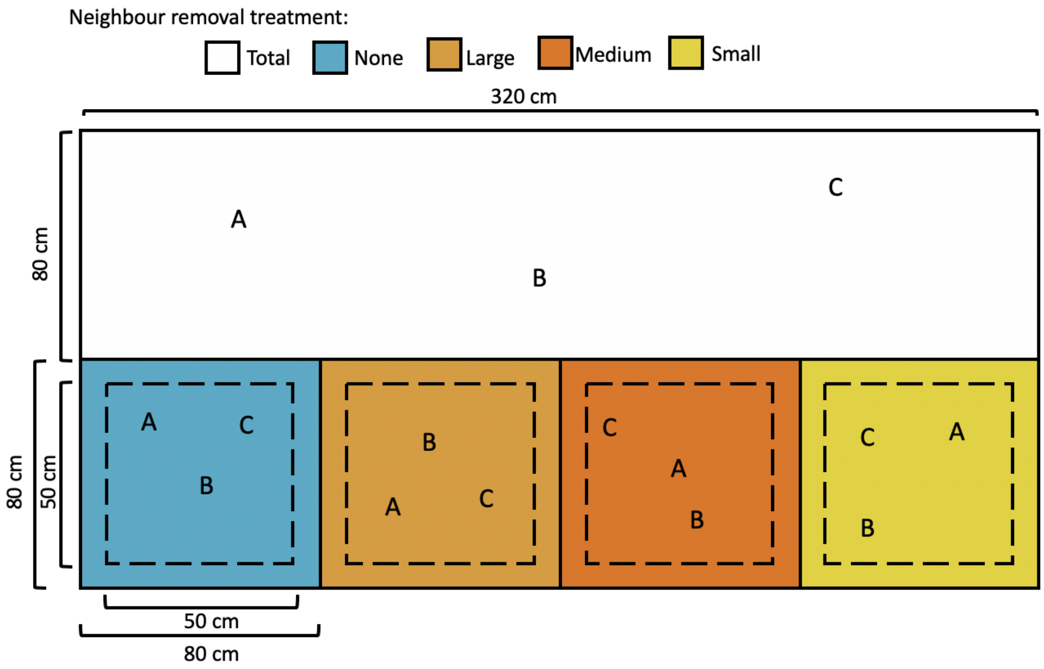

Figure 4–1. Schematic representation of the experimental thinning treatments. "A", "B", and "C" represent different focal species within each plot. The five treatments were "total" (all neighbours removed"), "none" (no neighbours removed), "large" (30% of the biomass removed using large individuals), "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.

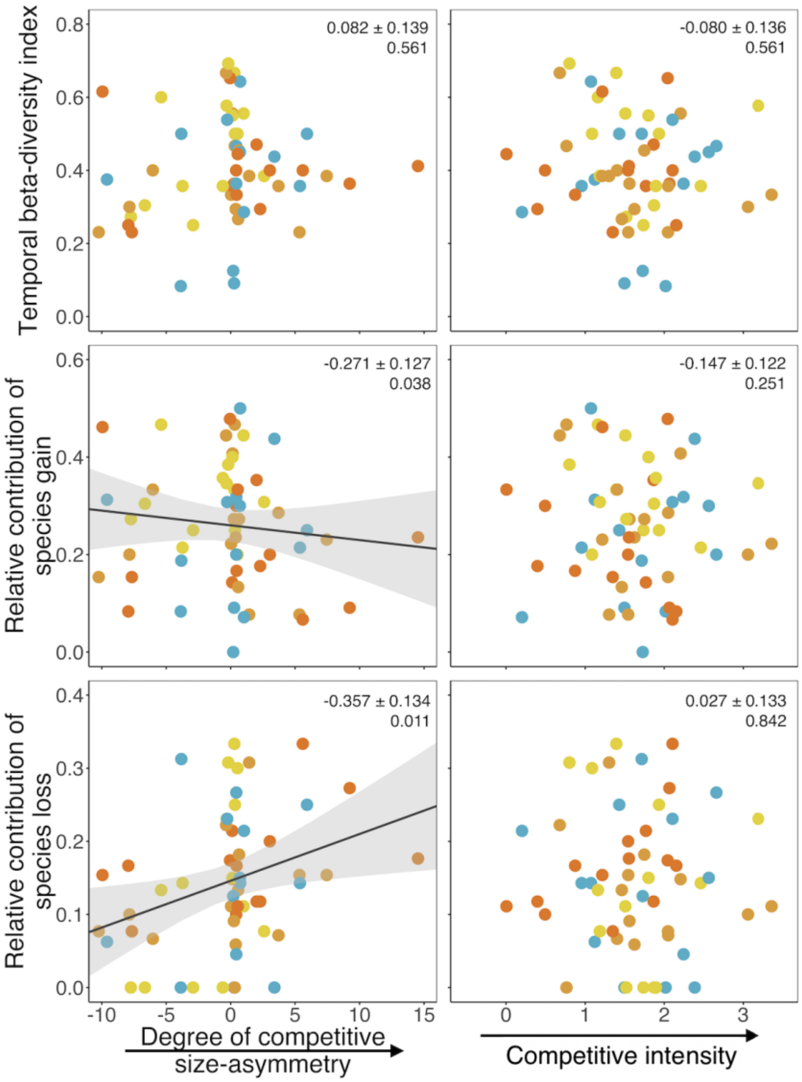

Figure 4–2. The relationship between competitive intensity and size-asymmetry and temporal beta-diversity, species gains, and losses. For the degree of size-asymmetric competition, values < 0 represent partial symmetry, values = 0 represent size-symmetric competition, and values > 0 represent size-asymmetric competition. For competitive intensity, values < 0 represent facilitation, values = 0 represent no competition, and values > 0 represent competition. Regression estimate and corresponding significance value 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.

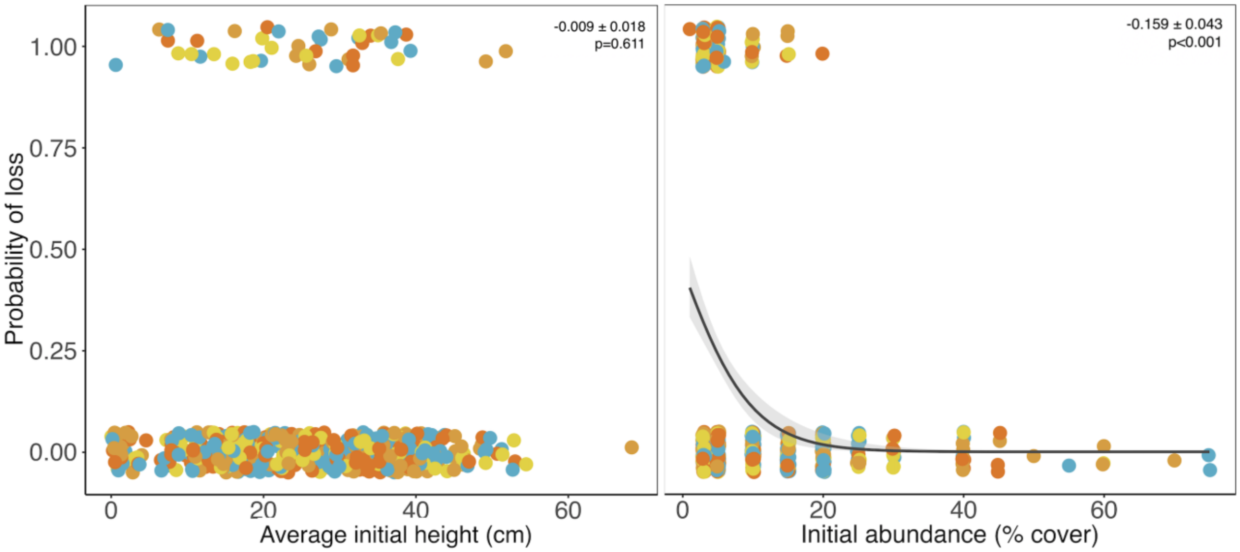

Figure 4–3. The probability of loss as a function of a species' initial size and abundance. Regression estimate and corresponding significance value displayed in the top-right corner. Regression lines are included when there was a significant relationship relationship at the 0.05 significance level. The color of points corresponds to neighbor removal treatments.

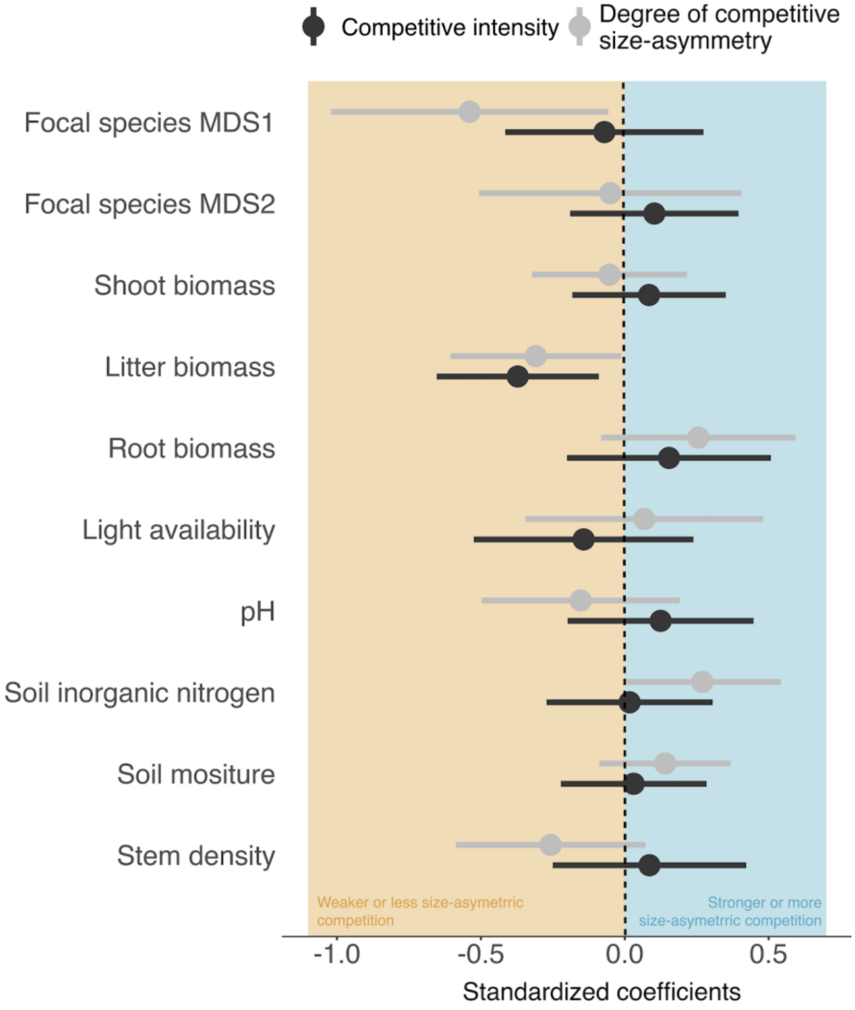

Figure 4–4. Standardized effect sizes linking environmental factors with competitive intensity and degree of size-asymmetric competition. Shown are the effect sizes ± 2 S.E. Variables were standardized to have a mean of 0 and a standard deviation of 1. Effect sizes represent the coefficients from two 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 4-S10.

Chapter 5: Standing vegetation as a coarse biotic filter for seedbank dynamics: effects of gap creation on seed inputs and outputs in a native grassland

INTRODUCTION

Changes to plant community composition following small-scale disturbances have been well documented (Huston 1979; Lavorel *et al.* 1994); with potential mechanisms for this change including reduced competition (Grime 1973), changes to the competitive hierarchy (Suding 2001; Suding & Goldberg 2001), and alterations to the abiotic properties (Suding & Goldberg 2001). Depending upon the processes involved, these patches of altered community composition within a matrix of more established communities can increase the diversity of a system (Petraitis *et al.* 1989), through increasing the beta diversity, here defined as the variability in species composition among local communities in a given area (Anderson *et al.* 2006; Tuomisto 2010). Assuming there is a competition-colonization tradeoff, the presence of gaps within a landscape promotes coexistence over time and space as the removal of stronger competitors within gaps allows more competitively inferior species to rapidly colonize and persist (Levins & Culver 1971; Horn & MacArthur 1972; Huston 1979; Levine & Rees 2002; Cadotte 2007). As such, determining the mechanisms behind these community shifts will enhance understanding of the mechanisms that promote diversity in a system. Many of the proposed mechanisms of why composition changes with a disturbance focus on interactions occurring between individuals in the standing vegetation and do not consider potential compositional shifts due to changes to seedbank processes (but see Goldberg 1987; Bullock et al. 1995). Despite the lack of focus on seedbanks, they are one of the primary species pools for community reestablishment after a disturbance or through species turnover (Bullock *et al.* 1995; Kalamees & Zobel 2002), suggesting they may play an important role in community assembly and impact beta diversity.

Small-scale disturbances within grasslands are prevalent (see review by Loucks et al. 1985) and can be the result of natural causes, such as selective grazing by herbivores and small mammal mounds, or anthropogenic causes, such as invasive species introduction and herbicide usage, all of which result in differing degrees of disturbance intensity, or the degree of vegetation removal (sensu Grime 1979). Disturbances not only have the potential to change the assembly mechanisms of the reestablished community (Belyea & Lancaster 1999; Chase 2003; Martin & Wilsey 2012), but also likely change the assembly of the seedbank through altering local seed input (i.e. seed rain) and output rates (i.e. seedling establishment and predation), that future reestablishment occurs from. However, these effects of standing vegetation removal could be complex as they may differ in magnitude and direction for seed inputs versus outputs. For example, if the removal of vegetation increases inputs while decreasing outputs, this would lead to an overall net increase in seed density and richness within the seedbank. However, if the removal of vegetation led to an increase in both inputs and outputs, assuming the degree of each increase is equal, no net change in seed density within the seedbank would occur. Consequently, gap creation through its potential influence on seedbank composition could alter plant community composition (Fig. 5- 1), but this is dependent on how it changes seed inputs and output rates.

Seed entry to the seedbank is the result of multiple factors including the dispersal abilities of individuals (Bakker *et al.* 1996) and environmental conditions, such as the direction and velocity of wind (Chambers & MacMahon 1994); however, gap creation may also alter input rates. For example, if inputs are predominately sourced from the local standing vegetation or standing vegetation acts as a seed trap (Bullock & Moy 2004), the removal of standing vegetation would likely reduce inputs to the local seedbank. Conversely, if standing vegetation acts as a physical barrier inhibiting the input of seeds, then the removal of standing vegetation would increase inputs to the local seedbank. However, the seeds found within the local seedbank are not just the product of seed inputs as many seeds are lost to the system through seed outputs (Fig. 5- 1).

Unlike seed inputs, the effects of gap creation on seed outputs have the potential to be more nuanced as there are a variety of ways seeds can be removed from the local seedbank, including seed germination (Baskin & Baskin 1989), mortality and predation (Louda 1989), each of which may respond to vegetation removal differently. The removal of standing vegetation is likely to increase germination rates by opening niche space (e.g. regeneration niche sensu Grubb (1977)), reducing competition from neighbours (Grime 1973; Southwood 1988), or providing favourable environmental conditions such as increased light availability or changes to soil temperature and water infiltration (Baskin & Baskin 1989). However, it could decrease germination if facilitation by neighbours is needed for establishment (e.g. Lortie & Turkington 2008; Soliveres et al. 2010) or vegetation removal results in a shift in the microbial community (Jasper *et al.* 1991) that may impede establishment, either through altering germination or mortality rates. In terms of seed predation, there is some evidence that vegetation removal reduces seed predation (Mittelbach & Gross 1984) as it is indirectly linked to predation risk (Manson & Stiles 1998; Orrock *et al.* 2004); however, in cases where disturbance leads to an increase in seed density, seed predation may be consequently higher when vegetation is removed (Platt 1976), and other factors, such as time of day, are also important (Manson & Stiles 1998). Overall, there is evidence that gap creation may be important for seedbank dynamics, but there is little empirical evidence that examines its impacts on relative changes to seedbank inputs and outputs and what consequences this has for seedbank composition.

The role gap creation plays on seedbank dynamics could be influenced by the total removal of all neighbours, or it can be an indirect consequence of the removal of particularly influential species or community traits. Since plants differ in their ability to alter the chemical and biotic composition of soils (Kulmatiski *et al.* 2008), attract seed predators (Janzen 1971), and produce seeds (Moles *et al.* 2004), seed inputs and outputs could differ depending on the composition of the standing vegetation community. Further, certain traits of plants can alter the abiotic environment, which might also impact seed input and output rates. For example, if plants in a community have large leaf areas, there may be more shading or vegetation cover which could decrease germination rates or increase predation rates respectively. As such, the species or trait composition of a community may have a larger impact on seedbank dynamics than the complete removal of standing vegetation. Here, we examine how seedbank composition and net seed inputs and outputs change as a function of experimental gap creation to determine:

1) Does gap creation alter seedbank composition? If so, are these seedbanks increasingly dissimilar to the composition of the original standing vegetation before the disturbance as well as the surrounding vegetation?,
2) How does gap creation alter seed inputs and outputs within a local community?, and
3) Outside of gaps, does the community or trait composition of the standing vegetation also impact seed input and output rates?

METHODS

Study site

This study was conducted at the Roy Berg Kinsella Research Ranch in Kinsella AB, Canada (53°5'N, 111°33'W). This study site falls within the aspen parkland ecoregion, characterized as a mosaic of mixed-grass prairie and trembling aspen (*Populus tremuloides* Michx.), and has a mean annual temperature and precipitation of 2.29°C and 222.45 mm respectively (Alberta Agriculture and Forestry, 2018). Our field site is located within the grassland area of the aspen parkland and is primarily dominated by graminoids (*Hesperostipa curtiseta* (Hitchc.) Barkworth*,* *Festuca hallii* (Vasey) Piper *and Poa pratensis* L.); however, much of the diversity is within the forbs (Appendix 5-S1). Historically, the site has been grazed by cattle; the last grazing event occurring in the fall four years before the study began.

Experimental design

The effects of gap creation on seedbank composition, net seed inputs, seedling establishment, and seed predation by small mammals were measured in sixteen blocks comprised of two paired plots throughout the study site (Fig. 5- 2). To determine the effects of gap creation on these factors, each plot within the pair received one of two removal treatments: no removal, where standing vegetation was kept intact, and total removal, where standing vegetation was removed by first clipping it at the soil surface and then painting stems with glyphosate herbicide (Roundup ©) to ensure plant death. It is possible that some glyphosate got into the soil during application. There is mixed evidence whether glyphosate can reduce germination rates (Campbell 1974; Blowes *et al.* 1985; Yenish & Young 2000); however, in our experiment, germination rates were higher in plots where glyphosate was applied, which is the opposite of what you would expect if there was a negative effect of glyphosate. Nevertheless, if the glyphosate application did reduce germination rates, our measured germination rates would be underestimates and our conclusions would not change. Plots were 50 cm x 50 cm with a buffer of

30 cm on each side. Removal treatments occurred in May 2016 and to ensure gaps stayed open for the duration of the experiment, glyphosate was reapplied to the total removal plots, except for within the seed trays, once a month during the growing season. Seed addition, seed predation, and seedbank studies started in October 2017, two growing seasons after removal treatments were implemented. These treatments do not simulate any specific natural disturbance (e.g. animal disturbance, fire, etc.) but instead are intended to show the effects of relatively small-scale neighbour removal on seedbank dynamics.

Seedbank determination

To measure the effects of gap creation on seedbank composition, we sampled seedbank composition in each paired plot at three timepoints: at the end of the growing season (October 2017), after snowmelt (May 2018), and right after peak biomass (August 2018). Within each plot, at each sampling time, one soil core (8 cm wide by 3.5 cm deep; total volume 175.9 cm^3) was taken including litter to obtain a measure of the persistent and transient seedbank (Thompson & Grime 1979) (Fig. 5- 2). The soil was then washed successively through two sieves (6.3 mm and .25 mm mesh) to separate seeds from coarse and fine soil and debris (Heerdt *et al.* 1996; White *et al.* 2012). The smaller sieve size should capture the majority of seed sizes found at this site (White *et al.* 2012), but we recognize that some may have passed through. Seeds and soil trapped in the sieves were then spread thinly over 3 cm of sterilized potting soil in 12 cm square pots that were 6.5 cm deep. The soil in each pot was turned twice during the duration of the study to ensure seeds originally buried deeper than others had equal opportunity to germinate (White *et al.* 2012). To confirm seedlings coming up in pots were from the seedbank and not contaminants from the greenhouse, three control pots with the same 3 cm of sterilized potting soil were dispersed among the treatment pots. No seedling emergences occurred within control pots throughout the experiment. In total, the experiment consisted of 35 pots per sampling period that were arranged in a completely randomized design and were randomly rearranged biweekly in the greenhouse of the University of Alberta Biotron in Edmonton AB, Canada.

Emerging seedlings from seeds captured in the sieves were counted and identified to species at regular intervals, with unidentifiable seedlings transplanted into pots and grown until identifiable. Seed density was measured as the total number of seedling emergences, as this represents the density of viable seeds in the soil, which is how seedbanks are commonly defined (Harper 1977). Species richness was measured as the total number of unique species that emerged. During the duration of the study, pots received supplemental heating and lighting and were watered every two to three days. Seedbank studies for each sampling period lasted approximately six months, which was when emergences rates slowed to between zero and one emergence per month.

Seed addition and predation experiment

To measure net seed inputs and outputs, within each study block, five seeds of nine different species (Table 5-1) were added to three different seed trays: a seed rain collection tray, a seed predation tray, and a seedling establishment tray. Seed trays consisted of 7.5 cm wide by 3 cm deep PVC pipe that was drilled 2.5 cm into the ground and installed in each paired plot in October 2017 and remained there until the end of the experiment in August 2018 (Fig. 5- 2). Species were selected based on the following criteria: 1) they are present in this field site, 2) they represent a range in phylogenetic relatedness, seed size and relative abundance at the field site (Table 5-1), and 3) seed availability. Seeds were obtained by a local seed supplier (Wild About

Flowers, Calgary AB, Canada) and covered with a sterilized 3:1 sand to topsoil mixture to prevent them from blowing away during the study period.

Net seed inputs were measured as net seed rain. To measure net seed rain, landscape fabric was glued to the seed rain collection tray at the soil surface to capture seeds while still allowing water drainage. Seed rain collection trays were measured twice, once in May 2018, after snowmelt, and once in August 2018, at the end of the growing season. For both measurements, seeds were collected from each tray and separated from the sand:topsoil mixture using water and visual inspection under a dissecting microscope (similar to (Malone 1967). Seeds were identified to species where possible but are reported as the total number of seeds recovered from each seed rain collection tray irrespective of species identity. Though some seeds were added to seed rain trays at the beginning of the experiment, the same number of seeds were added to both vegetation intact and removed treatments, so any difference between treatments at the end of the experiment should be due to net seed rain. Seed rain collection trays were open to small mammal use and some germination did occur, so net seed rain represents total seed rain minus seed loss from predation and germination.

Net seed outputs were measured as seedling establishment and predation rates. To measure seedling establishment, the seedling establishment tray had a 50 mm metal mesh over the top to obtain a germination measure independent of seed predation. The mesh size used excluded small mammals but still allowed ants and other small insects entry. We focused on small mammal seed predation as they have strong impacts on plant recruitment in grasslands (Bricker *et al.* 2010), but small insect predation does occur. Although our seedling establishment measure is obtained from germination rates, because we did not apply any fungicide or other treatments that would inhibit seed mortality, differences in seed germination between removal treatments could be due to changes to seed mortality or alterations in seed germination conditions. Consequently, our germination rate estimate is a measurement of how gap creation may alter the establishment of seedlings, either by altering germination rates, mortality rates or both. To measure seed predation, the seed predation tray was left open and had no mesh overtop to allow small mammal predation. Seed predation was measured as the number of germinations in open (seed predation tray) versus enclosed (seed germination tray) seed trays regardless of species identity.

Standing vegetation characterization

To determine how gap creation alters the compositional similarity between the seedbank and standing vegetation, community composition of the standing vegetation was measured in a 50 cm x50 cm plot within the removal plot treatment in May 2016 before vegetation removal occurred. To determine how gap creation impacts the similarity between seedbank composition and the surrounding vegetation, community composition of the standing vegetation was measured in a 50 cm x 50 cm plot within the non-removal treatment in August 2018.

To determine the effects of gap creation on seed bank dynamics are independent of changes to the community or trait composition of the standing vegetation, we examined how community and trait composition of the standing vegetation altered seed input and output rates within the non-removal plots. Community composition was measured as the percent cover of each species in a 50 cm x 50 cm plot within each of the non-removal plots in August 2018. Trait composition was estimated by weighting site-specific trait values by the relative abundance of species that made up at least 80% of the community composition (Pakeman & Quested 2007) except *Carex* spp., which we were unable to identify to species. Overall, we had trait data for approximately 90% of the species found within our plots (see Appendix 5-S1 for a list of trait data we had for each species). Trait data for each species were measured on semi-randomly selected plants (had to be mature and healthy) within the field site in July and August 2018. Traits measured included those typically associated with competitive ability, including height, longest width, specific leaf area (SLA), as well as those associated with competition-stress-tolerance trade-offs including SLA and specific stem density (SSD). Traits were measured using the methods outlined in Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013).

Statistical analysis

To determine the effects of gap creation on seedbank composition, we tested its effects on seed bank seed density, richness, and composition. The effect of gap creation on seed density was tested using linear mixed models with seed density as response variables, removal treatment and time of year as fixed factors, and block and block:removal treatment as a random factors. The effect of gap creation on species richness was tested using a generalized linear model with a Poisson distribution (log link). Richness was the response variable, removal treatment and time of year were fixed factors, and block and block:removal treatment were random factors. The effects of gap creation on seedbank composition were tested using a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations. Removal treatment and time of year were predictor variables and to incorporate the blocked design, we constrained randomization to within each removal treatment within block. To meet the assumptions of the linear mixed models, one outlier was removed from the seed density data prior to analysis. The removal did not change our overall conclusions (Appendix 5-S2).

To determine the effects of gap creation on net seed inputs and seedling establishment, generalized linear mixed models were used with a Poisson distribution (log link) and either net seed input or germination number as response variables, respectively. For each response variable, removal treatment was fit as a fixed factor and block was fit as a random factor. One net seed input sample was lost prior to processing and was not included in the analysis. To determine the effects of standing vegetation on seed predation, a generalized linear mixed model was used with a Poisson distribution (log link) and germination number as the response variable, tray exclosure type (i.e. open or closed) and removal treatment as fixed factors, and block as a random factor. We determined whether predation occurred through the significance of the tray exclosure type term (i.e. if seed germination was significantly different in the open versus closed trays). To determine whether gap creation altered predation rates, we used the removal treatment by tray exclosure type interaction term, such that if there was a significant difference in germinations between open versus closed trays in the non-removal but not removal treatment, we would conclude gap creation reduced predation rates since predation occurred in the non-removal treatment but not the removal treatment.

To determine whether the effects of standing vegetation on seed inputs and outputs are independent of the standing vegetations' community or trait composition, community and trait composition were estimated using the axes loadings from five separate non-metric multidimensional scaling (NMDS) ordinations of community, height, longest width, SLA and SSD composition respectively. Bray-Curtis dissimilarity was used to create distance matrices. 30 separate models were then fit (3 response variables x 5 compositions x 2 axes), with either net seed rain, seed germination, or seed predation as a response variable, axis 1 or 2 from one of the five NMDS ordinations as a fixed factor and block as a random factor. Seed rain and germination models were fit as generalized linear models with a Poisson distribution (log link). Seed predation rate models were fit as linear models. All analyses were run using the lme4 (Bates *et al.* 2015), lsmeans (Lenth 2016), and vegan (Dixon 2003) packages in R (v 3.4.3).

RESULTS

Overall, gap creation decreased seed bank seed density ($F_{1,73.77}$=5.754, p=0.019; Fig. 5- 3) and richness (χ^2_1=14.035, p<0.001; Fig. 5- 3) as well as altered seedbank composition ($F_{2,87}$ =2.206, p=0.005). Seedbanks within gaps were significantly different from seedbanks where standing vegetation was kept intact and had a composition more dissimilar to the standing vegetation (Fig. 5- 4). Time of collection also had significant effects on richness and composition (χ^2_2= 11.537, p=0.003 and $F_{2,87}$=2.972, p=0.001 respectively; Fig. 5- 3); however, there was a slight interaction between gap creation and time of collection for seed density ($F_{1,73.76}$=2.504, p=0.019, p=0.089; Fig. 5- 3) but not richness (χ^2_2= 1.308, p=0.520; Fig. 5- 3) or composition ($F_{2,87}$=0.905, p=0.654). Seed bank seed density was significantly lower in gaps in May, right after snowmelt, but not during or after the growing season in August and October (Fig. 5- 3).

Gap creation altered net seed inputs (χ^2_1=11.074, p<0.001) and seedling establishment (χ^2_1= 22.638, p<0.001) but not predation (χ^2_1=0.048, p= 0.827); however, its effects on net seed inputs were dependent on the time of year (χ^2_1=29.091, p<0.001). Gap creation led to a significant increase in net seed inputs during the growing season in August (Z=6.249, p<0.001) but not right after snowmelt in May (Z=-1.054, p=0.292; Fig. 5-5). Overall germination rates were low (Appendix 5-S3); however, gap creation significantly increased seedling establishment but did not affect seed predation during the growing season (Fig. 5-5). In fact, there were no significant levels of seed predation detected in either standing vegetation present or absent plots (χ^2_1=0.017, p=0.895; Fig. 5-5).

The impacts of standing vegetation on seed inputs were dependent on community and trait composition; however, the effects of standing vegetation on seed outputs were not (Table 5-2; Appendix 5-S4). Seed inputs were highest in communities comprised of individuals that were, on average, taller with narrower canopies, lower SLA, and SSD (Appendix 5-S5). Changes to standing vegetation traits typically associated with competitive ability (i.e. plant height, canopy size, and specific leaf area) or competition-stress-tolerance trade-off (i.e. specific leaf area and specific stem density) did not alter net seed germination or predation rates (Table 5-2).

DISCUSSION

Overall, gap creation alters the assembly mechanisms of seedbanks by altering net seed inputs and seedling establishment (Fig. 5- 5- 3 & 5-5). As a consequence, following a disturbance, seedbank composition becomes increasingly dissimilar to that of the previous or surrounding standing vegetation over time (Fig. 5- 4). As such, changes to small-scale disturbance regimes could alter seedbank dynamics ultimately having consequences for community assembly, beta diversity, and resilience, particularly in instances where the local community would be reestablished from the local seedbank. Further, seed output rates are consistent regardless of standing vegetation community or trait composition (Table 5-2), suggesting that standing vegetation acts as a coarse biotic filter and the removal of standing vegetation through gap creation may be more important than compositional changes in preserving the local seedbank.

Changes to the seedbank is an additional mechanism that could explain a switch in plant community composition following a disturbance. Within gaps, seedbank composition shifts further away from the composition of the standing vegetation and has a unique composition compared to a seedbank where the standing vegetation is kept intact (Fig. 5- 4). This has two potential consequences if reestablishment primarily occurs from the seedbank: increased beta-diversity or decreased community stability, which are likely dependent on the scale of the disturbance. If disturbances occur at a smaller scale, reestablishment from the seedbank in these gaps could result in a community that is unique to the standing vegetation, ultimately increasing the beta diversity within the area (Petraitis *et al.* 1989; Rydgren *et al.* 1998; Uys *et al.* 2004; Smart *et al.* 2006; Myers *et al.* 2015). Conversely, the reestablished community having a unique composition to the original community could have negative consequences for community stability if disturbances occur at a wide-scale removing the majority of the original community. However, dissimilarities between seedbanks in and outside of gaps seem to damper throughout the growing season (Fig. 5- 3), suggesting that the processes driving seedbank assembly as well as the effects of disturbance on these processes differ as a function of time of year (Bekker *et al.* 2000; Ma *et al.* 2013; Royo & Ristau 2013). This means that the potential role seedbanks have on community reestablishment, resilience and diversity may be reliant on when disturbances occur during the year.

Small-scale disturbances are likely needed to increase community diversity, not only by promoting the persistence of ruderal species (Levins & Culver 1971; Tilman 1994) but also by enabling novel seeds to reach the community. Local communities are typically seed limited, such that the addition of seeds results in increased local species richness (e.g. Myers & Harms 2009). However, we found that the presence of standing vegetation significantly reduces the amount of net seed inputs into the local seedbank (Fig. 5- 5), though the community and trait composition of the standing vegetation also impacts net seed inputs (Table 5-2). This suggests that although seeds may be able to establish in local communities when experimentally added (see review by Myers & Harms 2009), the standing vegetation may naturally limit the entry of these seeds, potentially having an overall negative impact on species diversity. As such, a species chance of reaching a novel area may not only be due to its seed traits and random chance but also the presence of standing vegetation. This is consistent with the competition-colonization trade-off (Levins & Culver 1971; Tilman 1994), as the presence of neighbours limits the likelihood of seeds reaching an area. However, it appears that local communities may differ in how much they limit seed inputs (Table 5-2). Consequently, in the short term, it seems like the presence of standing vegetation could limit species diversity through limiting dispersal and establishment of non-resident species.

The negative effects of standing vegetation on seedbank species diversity, however, may dampen or even reverse over time as seeds accumulate in the seedbank. Standing vegetation limiting seedling establishment (Fig. 5- 5) is a common phenomenon (e.g., Isselstein *et al.* 2002; Jutila & Grace 2002; Ruprecht *et al.* 2010) and is likely why we see an increase in seed density and richness within the seedbank when standing vegetation is present (Fig. 5- 3) because seed inputs are also reduced (Fig. 5- 5), so the increased density cannot be due to increased inputs. As a result, the presence of standing vegetation leads to a seed reserve that can add to the standing vegetation community through species turnover or more commonly through gap regeneration (Rusch & van der Maarel 1992; Milberg & Hansson 1994; Kalamees & Zobel 2002; Shinoda & Akasaka 2019). However, the longer gaps are left exposed, seedbank composition becomes increasingly dissimilar to the composition of standing vegetation (Fig. 5- 4), changing the species pool available for reestablishment. Thus, the composition of the reestablished community will be significantly different from that of the original community, which may have different consequences depending on management goals. For example, if the goal is to increase diversity, this new reestablished community could increase the overall beta diversity of the system; however, if the goal is to maintain the current community, for instance, if it was a rare or functionally diverse community, the transition of this community to the reestablished one could reduce the services gained from this unique original community. Overall, the frequency of disturbances in an area likely influences the stability of a community, especially if reestablishment is dependent on the seedbank.

The removal of vegetation, through disturbance or gap creation, may be more important for altering seedbank dynamics than changes to standing vegetation community or trait composition. Standing vegetation, regardless of its community or trait composition, had a consistent impact on seed outputs (Table 5-2). This suggests that standing vegetation acts as a coarse biotic filter on seedbank output processes. As such, traditional trait-based assembly mechanisms, such as trait similarity or phylogenetic relatedness (see review by HilleRisLambers et al. 2012), do not seem to alter seedbank dynamics through seedling establishment. However, gap creation not only alters biotic interactions but also modifies abiotic conditions, so it is not possible to fully determine whether changes seedbank dynamics are the result of changes to biotic or abiotic conditions. For example, an increase in seedling establishment following gap creation (Fig. 5- 5) could be due to changes to the abiotic conditions, such as increased temperature or light levels (Baskin & Baskin 1989), or changes to the biotic conditions, such as changes to the soil biotic community (Bartelt-Ryser *et al.* 2005) or the competitive environment (Weinig 2000). Nevertheless, these results suggest that small-scale, total vegetation removal may be necessary to promote increased beta diversity through seedbank regeneration rather than more minute changes to the community and trait composition of the standing vegetation. However, the gap size (Bullock *et al.* 1995; Burke & Grime 1996) and intensity of disturbance (Burke & Grime 1996; Myers & Harms 2009) also impact regeneration rates. Overall, gap creation promotes a distinct seedbank composition that differs from both the standing vegetation as well as seedbanks where standing vegetation is kept intact. This suggests that changes to seedbank composition with gap creation could be a potential mechanism for higher heterogeneity and beta diversity within communities.

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Table 5-1. Species identity and their associated traits used in the seed addition study. Average abundance and frequency refer to their presence in the standing vegetation. Average abundance is the average percent cover of species in all non-removal plots. Frequency is the proportion of plots species are found in.

Species	**Family**	**Seed size (seed/g)**	**Average abundance**	**Frequency**
Achillea millefolium L.	Asteraceae	7462	1.97	0.56
Agrostis scabra Willd	Poaceae	11023	0.43	0.06
Anemone cylindrica A. Gray	Ranunculaceae	1544	0.00	0.00
Campanula rotundifolia L	Campanulaceae	15037	0.04	0.06
Geum triflorum Pursh	Rosaceae	838	1.57	0.25
Hesperostipa curtiseta (A.S. Hitchc.)	Poaceae	250	25.56	1
Koeleria macrantha (Ledeb.) Schult	Poaceae	4232	2.50	0.44
Sisyrinchium montanum Greene	Iridaceae	1209	0.00	0.00
Symphyotrichum falcatum (L.) A. Love & D. Love	Asteraceae	1002	4.19	0.69

Table 5-2. The relationships between seedbank processes and standing vegetation community and trait composition.

Process	df	Community composition		Height composition		Plant width composition		SLA composition		SSD composition	
		X^2/F	p	X^2/F	p	X^2/F	p	X^2/F	p	X^2/F	p
Seed germination	1	1.062	0.303	1.101	0.294	0.434	0.510	0.819	0.365	0.307	0.579
Seed predation	1,14	0.074	0.7896	0.200	0.662	3.674	0.076	2.245	0.156	0.678	0.424
Net seed inputs	1	9.906	**0.002**	17.645	**<0.001**	7.507	**0.006**	9.972	**0.002**	5.1793	**0.023**

Note: Composition values represent the axes loadings from NMDS axis 1 (see Appendix 5-S4 for relationships with loadings from NMDS axis 2). SLA is the specific leaf area. SSD is the specific stem density. Traits were measured using the methods outlined in Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013).

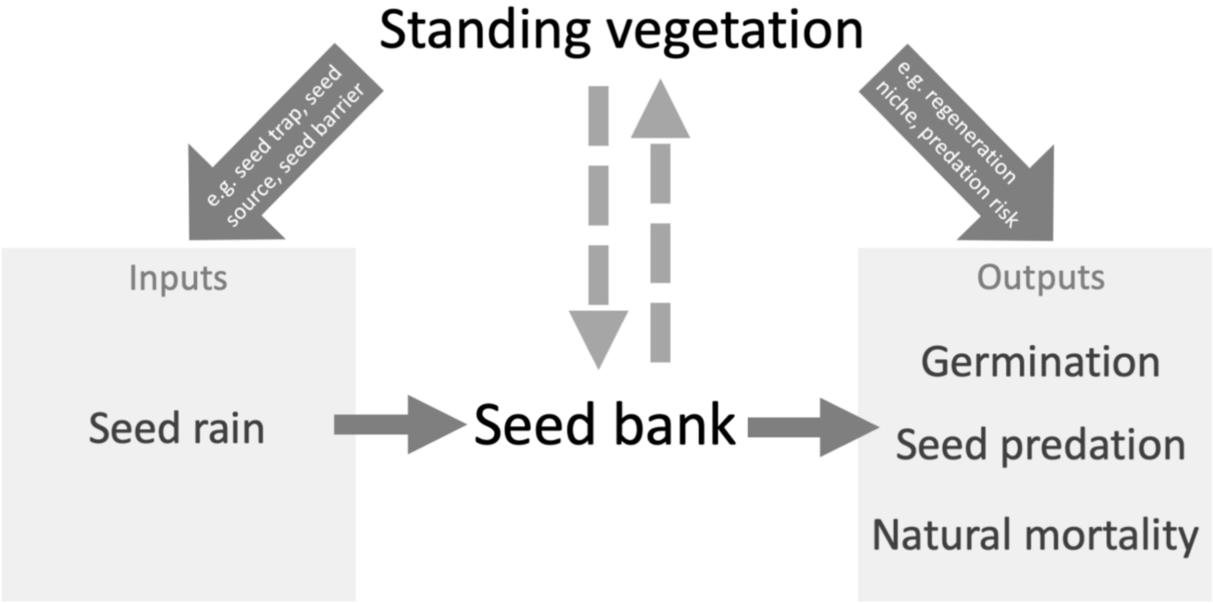

Figure 5–1. Conceptual diagram showing the direct (solid arrows) and indirect (dashed arrows) relationships between standing vegetation, seed inputs and outputs, and the seedbank. Standing vegetation indirectly influences the seed bank by directly impacting seed input and output rates. Some proposed mechanisms for how standing vegetation may alter seed inputs and outputs are listed within the arrows.

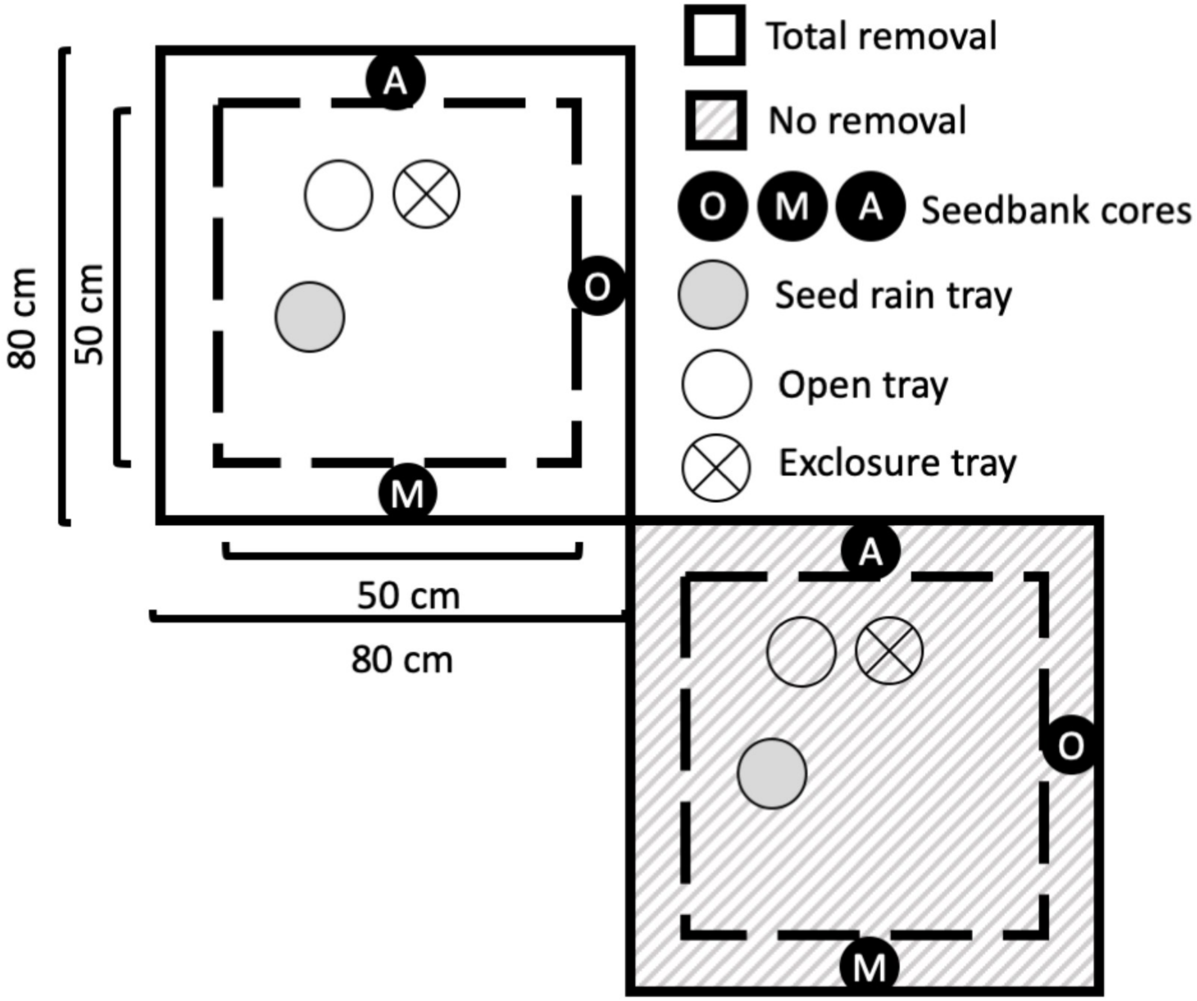

Figure 5–2. Experimental design of the seedbank, seed addition, and seed predation experiments. Soil cores for the seedbank study were 8cm wide by 3.5 cm deep and collected in October 2017 (O), May 2018 (M) and August 2018 (A). Seed trays for the seed addition and seed predation experiment were 7.5 cm wide by 3 cm deep. Seed rain trays included landscape cloth at the soil surface to collect seeds while allowing water drainage. Exclosure trays had a 50 mm metal mesh over the top to exclude small mammals. Image is not to scale.

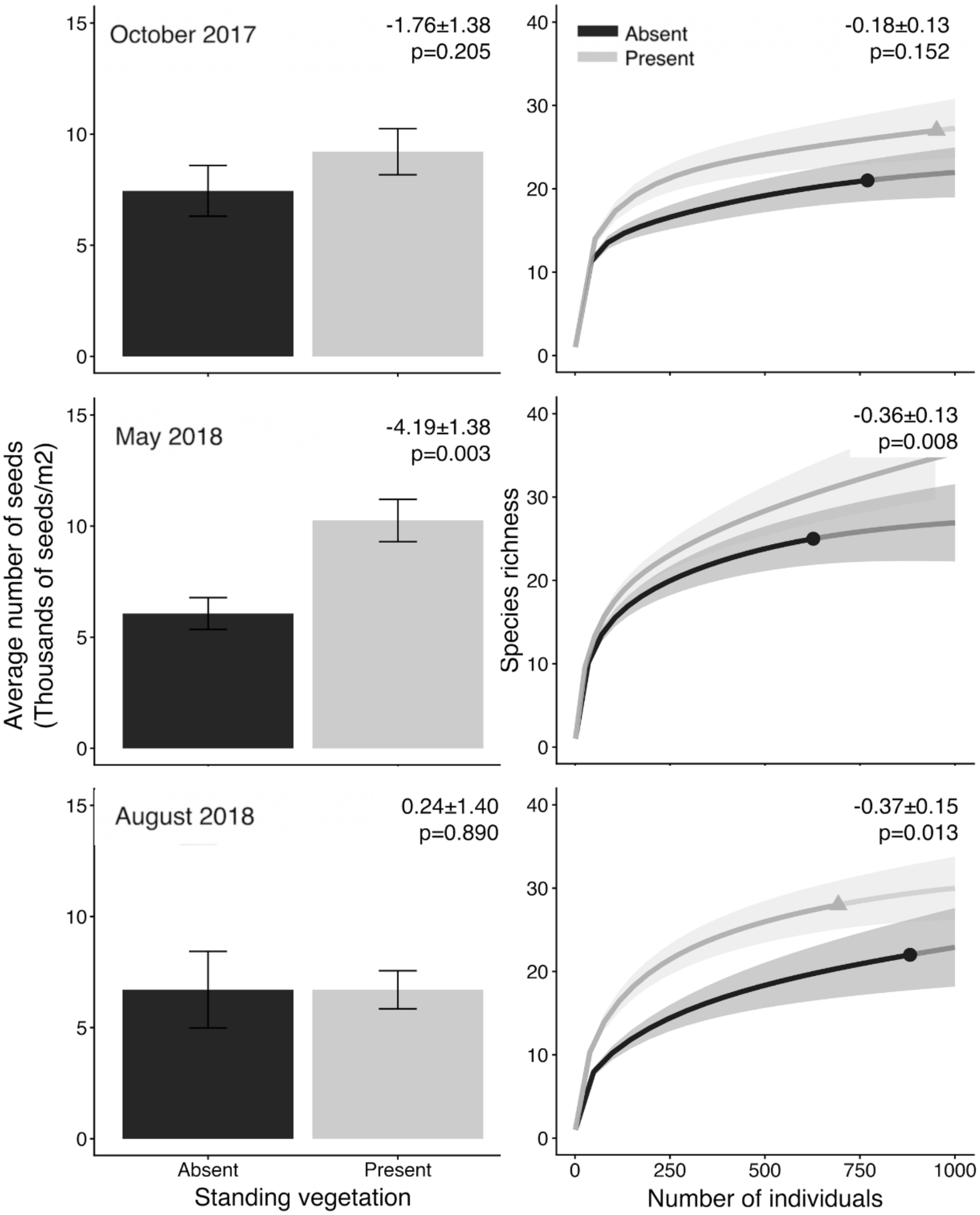

Figure 5–3. Effects of standing vegetation presence on seedbank seed density (left panels; mean ± SE) and richness (right panels) overtime. Regression estimates and significance levels for each pairwise comparisons are shown in the upper right corner of each panel. To account for differences in seed density between standing vegetation treatments, species richness is represented through a rarefaction curve; however, statistics correspond to differences in mean observed values.

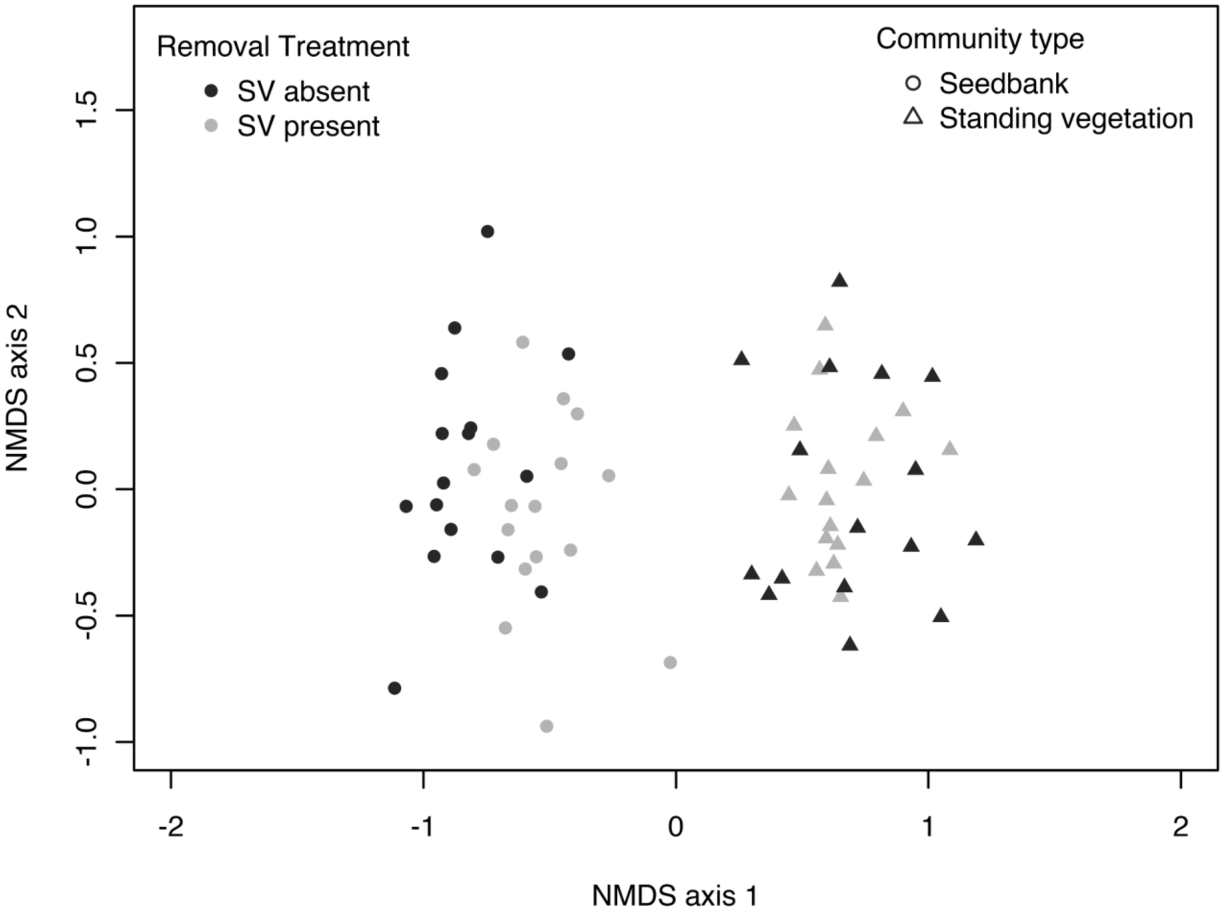

Figure 5–4. Non-metric multidimensional scaling ordination of seedbank and standing vegetation community composition for each of the 16 paired plots. Community composition was separated by standing vegetation presence. Community composition of the seedbank was determined from a greenhouse seedbank experiment. Community composition of the standing vegetation was measured in the field before removal in May 2016 for the removal treatment plots (SV absent) and at the end of the experiment in August 2018 for the non-removal treatment plots (SV present). Stress= 0.173.

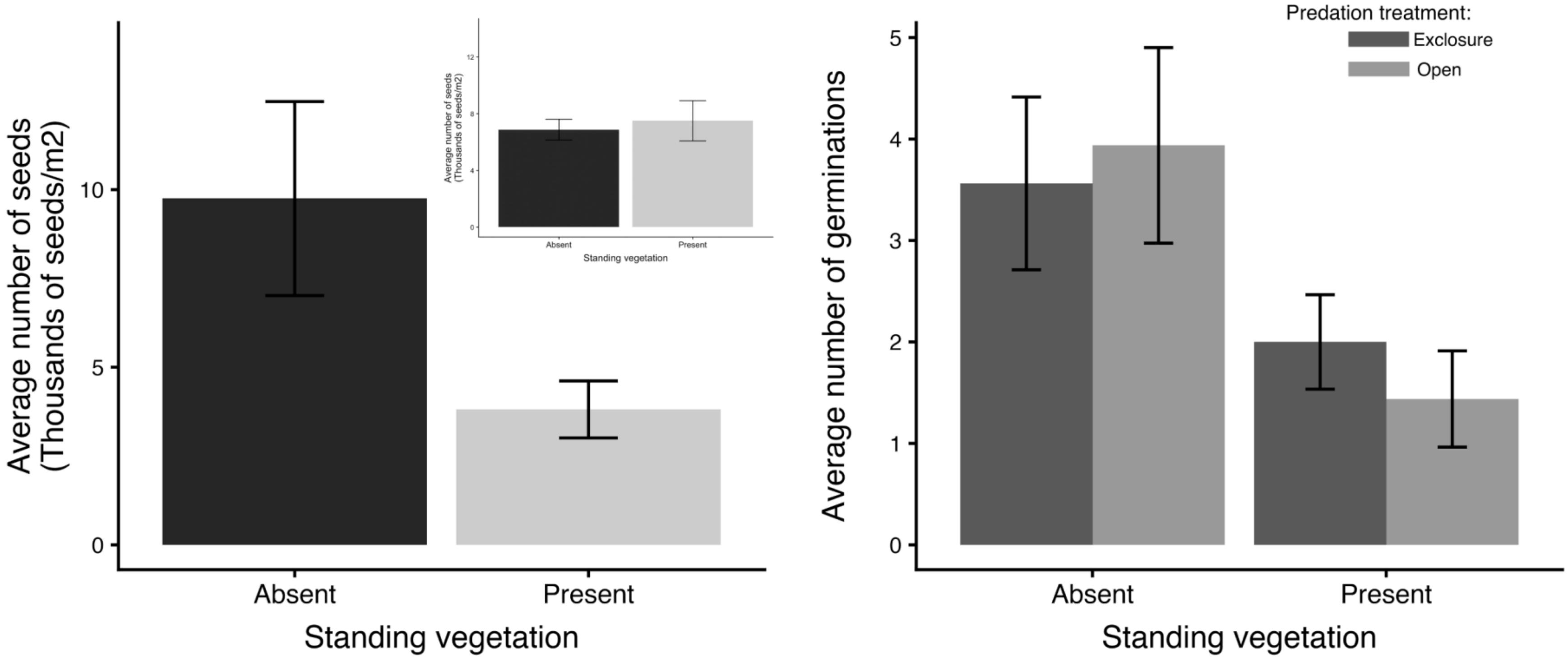

Figure 5–5. The effects of standing vegetation presence on net seed inputs and outputs (mean ± SE). Net seed inputs were measured as the average number of seeds captured in the seed rain tray measured at peak biomass (main figure) and right after snowmelt (inset graph). Net seed outputs were measured as the average number of germinations in both the open and enclosure trays at peak biomass. Germination rate was measured as the number of germinations in the enclosed trays to obtain germination measures independent of seed predation. Seed predation rate was measured as the number of germinations in open versus enclosed seed trays regardless of species identity.

Chapter 6: General Discussion

The primary objective of this thesis was to disentangle competitive processes to better understand their drivers and relative importance for community assembly. The historical focus on competitive intensity is slowly starting to progress as evidence for the importance of competitive size-asymmetry (Hautier *et al.* 2009; DeMalach *et al.* 2016, 2017) and intransitivity (Laird & Schamp 2006, 2008; Allesina & Levine 2011) emerges. Through this thesis, I advance this work by providing indirect and direct evidence that the size-asymmetry of competitive interactions is an important mechanism in plant community assembly, sometimes more so than competitive intensity. This importance is further reinforced by the finding that competitive size-asymmetries are likely more common than once thought, occurring during aboveground and belowground competition, as opposed to the traditional view that only aboveground competition is size-asymmetric. In this general conclusion, I summarize some of the most important findings of this thesis.

Competitive size-asymmetry is associated with species loss

With the formalization of the competitive exclusion principle (Tansley 1917; Gause 1934; Hardin 1960), there developed a concerted effort in ecology to explain why we observe species coexistence if exclusion is the necessary outcome of intense competition between species (Hutchinson 1959). Most mechanisms to explain coexistence focus on factors that may reduce the impact of competition. For example, coexistence mechanisms typically require that either stabilizing differences (e.g., niche differentiation) are greater than fitness differences (e.g., competitive ability) (Chesson 2000) or disturbances preclude exclusion (Grime 1973, 1979; Keddy 2001). However, there is increasing recognition that there may be aspects of competitive interactions that may have differential impacts on species coexistence, without changing the relative importance of competitive interactions. For example, models have shown that the intransitivity (Laird & Schamp 2006) or degree of competitive size-asymmetry (DeMalach *et al.* 2016) can promote coexistence. In Chapter 4, through empirically testing the association of competitive size-asymmetry and species diversity, I find that an increase in competitive size-asymmetry, but not competitive strength, was tied to species loss in a native plant community (Fig. 4-2). The importance of size-asymmetries for community dynamics was further reinforced by the finding that the incorporation of size inequalities into productivity-diversity models increased their explained variance by 30% (Table 3-2). These results suggest that different aspects of competitive interactions not only have differential impacts on community assembly but may differentially contribute to species diversity and coexistence. This finding promotes further questions such as, under what conditions are the various facets of competition most important? Are particular facets of competition more important for preserving ecosystem services? Do these different facets of competition interact to have stronger consequences on community and ecosystem dynamics?

Soil resources can alter the degree of competitive size-asymmetry

Counter to prior understanding, size-asymmetric competition occurs not only through competition for light but also soil resources (Chapter 2) and is not restricted to environments with intense competition (Chapter 2 & 4). Together, these results suggest that competitive size-asymmetries may be more ubiquitous than once thought and that we are still in the early stages of understanding how it works in communities. The most common way soil resources are thought to promote competitive size-asymmetries is indirectly through increasing aboveground productivity and competition for light (Newman 1973; Schwinning & Weiner 1998). However, I find that nutrient heterogeneity is needed for soil fertility to promote size-asymmetric competition (Fig. 2-4). This suggests that light competition alone does not cause size-asymmetric competition and that there is some interaction between belowground and aboveground processes promoting competitive size-asymmetries. This is further supported in the field, when I find that the degree of competitive size-asymmetry is not associated with light availability or aboveground biomass but does weakly increase with total soil nitrogen (Fig. 4-4). These results do not oppose the well-documented evidence that size-asymmetric competition for light is important for community assembly (Hautier *et al.* 2009; DeMalach *et al.* 2017). Rather, they demonstrate the importance of considering the role of aboveground-belowground interactions when examining the mechanisms and consequences of competitive size-asymmetries.

The impact of nutrient heterogeneity on competitive size-asymmetries was the opposite of what was expected by theory (Schwinning & Weiner 1998). The primary mechanism thought to promote size-asymmetric competition is the pre-emption of resources by larger individuals (Schwinning & Weiner 1998). Thus, it was expected that the presence of a high-quality resource patch may increase the degree of size-asymmetric competition (Schwinning & Weiner 1998). However, when nutrient heterogeneity had an effect, the presence of a high-quality patch reduced the degree of size-asymmetric competition. In contrast, the presence of a low-quality patch increased it (Fig. 2-4). This suggests that resource pre-emption may not be the only mechanism behind size-asymmetric competition, as increased size-asymmetry occurred when all individuals were already in a high-resource environment. Instead, an additional mechanism that may promote competitive size-asymmetry is potential avoidance behavior by smaller individuals. Small individuals may have proliferated more roots in the low-quality patch to reduce interactions with larger individuals in the high-quality patch. Overall, these results suggest that there are multiple different resource environments and mechanisms that may drive size-asymmetric interactions that were not previously considered. Moving forward, more work needs to be done to understand the mechanisms and drivers of size-asymmetric competition, especially given its importance for species loss and diversity (Chapter 3 & 4).

Reassurance for the small species: species-specific vulnerabilities to competitive size-asymmetry

Competitive size-asymmetries were initially discovered in plant populations (Kuroiwa 1960; Ford 1975; Hara 1986; Weiner & Thomas 1986), where small individuals are the losers of competition. Thus, it makes sense that when moving it into a community perspective, we assumed that smaller species would be the losers of competition, especially since competitive ability is regularly associated with plant size (e.g., Grime 1977; Keddy 2001). However, smaller species are typically more abundant in natural communities than larger species (Niklas *et al.* 2003; Moles *et al.* 2009; Tracey *et al.* 2017) and do not seem to have a higher chance of being lost from a system (Fig. 4-3, Suding *et al.* 2005), despite the expectation that they are inferior competitors. Consequently, there must be a mechanism allowing smaller species to persist.

In Chapter 2, I find that species have differential vulnerabilities to competitive size-asymmetry that may promote their coexistence with smaller individuals. This species-specific response was further supported in the field, as the degree of competitive size-asymmetry was associated with focal plant identity (Fig. 2-4). The presence of differential vulnerabilities likely occurs because unlike in populations, where there is somewhat limited variability among individuals (at least relative to interspecies variability (Siefert *et al.* 2015)), within communities, species can differ greatly in their resource requirements and strategies to deal with competition (Novoplansky 2009). Small species could have particular traits (e.g., shade avoidance) that allow them to persist despite a reduction in resources. Additionally, I found that partially symmetric competition (i.e., when smaller individuals have a competitive advantage) is not necessarily uncommon (Appendix 4-S11). Overall, increased competitive size-asymmetry does not equate to the loss of small species (Fig. 4-3), likely because species have differential vulnerabilities to competitive size-asymmetry (Chapter 2). These differential vulnerabilities suggest we must consider variations in tolerance and suppression between species during size-dependent plant-plant interactions, which may promote species coexistence as all small species may not be negatively impacted during size-dependent competition.

The removal of vegetation, through small-scale disturbances, leads to distinct seedbank communities

After a disturbance, seedbank composition becomes increasingly dissimilar to that of the previous or surrounding standing vegetation over time, likely due to altered seed inputs and outputs rates (Chapter 5). This suggests that differences in seedbank dynamics between disturbed and non-disturbed local communities may be a mechanism for increased beta-diversity in a landscape. The removal of vegetation through small-scale disturbances may not only promote the persistence of ruderal species through competitive release (Levins & Culver 1971; Tilman 1994) but also by enabling novel seeds to reach the community through increased seed rain (Fig. 5-5). The presence or density of vegetation is typically associated with and used to measure competitive processes (Aarssen & Epp 1990; Weigelt & Jolliffe 2003), but it is important to additionally consider the non-competition-based processes that may differ with vegetation removal as they could have important implications for community assembly and stability.

Implications and future directions

Overall, the results of this thesis promote new understanding of how competition structures communities, the mechanisms of competitive size-asymmetry, and the mechanisms that support beta-diversity. It is clear that the different facets of competition have independent and differential impacts on community assembly (Chapter 4, Laird & Schamp 2006; Allesina & Levine 2011; DeMalach *et al.* 2016). Better incorporation of these different facets of competition into future competition-diversity or species coexistence models may clarify the importance of competition for community structure. It has been recognized that we need to distinguish between the intensity and importance of competition (Welden & Slauson 1986; Brooker *et al.* 2005). However, before we can adequately judge the importance of competition for community structure relative to other assembly factors, we first need to understand the relative importance of each facet of competition to understand under which conditions each may be most important.

Unfortunately, however, the conditions under which each competitive facet is most important for community assembly is likely more complicated than originally thought. This thesis has challenged the idea that belowground competition is size-symmetric and that pre-emption is required for competitive size-asymmetry to occur (Chapter 2). This suggests that future work examining the mechanisms of competitive interactions should incorporate species-specific strategies or behaviours as well as the interaction between aboveground and belowground processes. Further, this thesis has demonstrated that there can be important non-competition-based mechanisms by which neighbor presence can alter ecological processes (Chapter 5), that ultimately can impact diversity patterns. Overall, these results add to understanding of the mechanisms of community assembly and provide some insight into how we may be able to manage species diversity. For example, through manipulating size structures in communities (Chapter 3) and maintaining small-scale disturbances in a landscape (Chapter 5).

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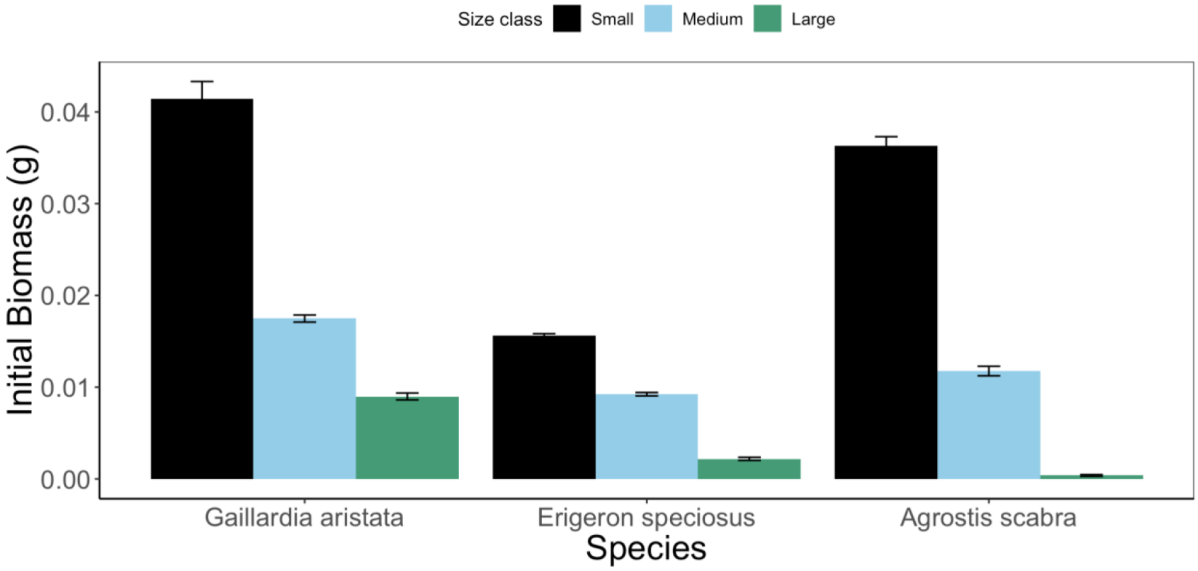
Appendices

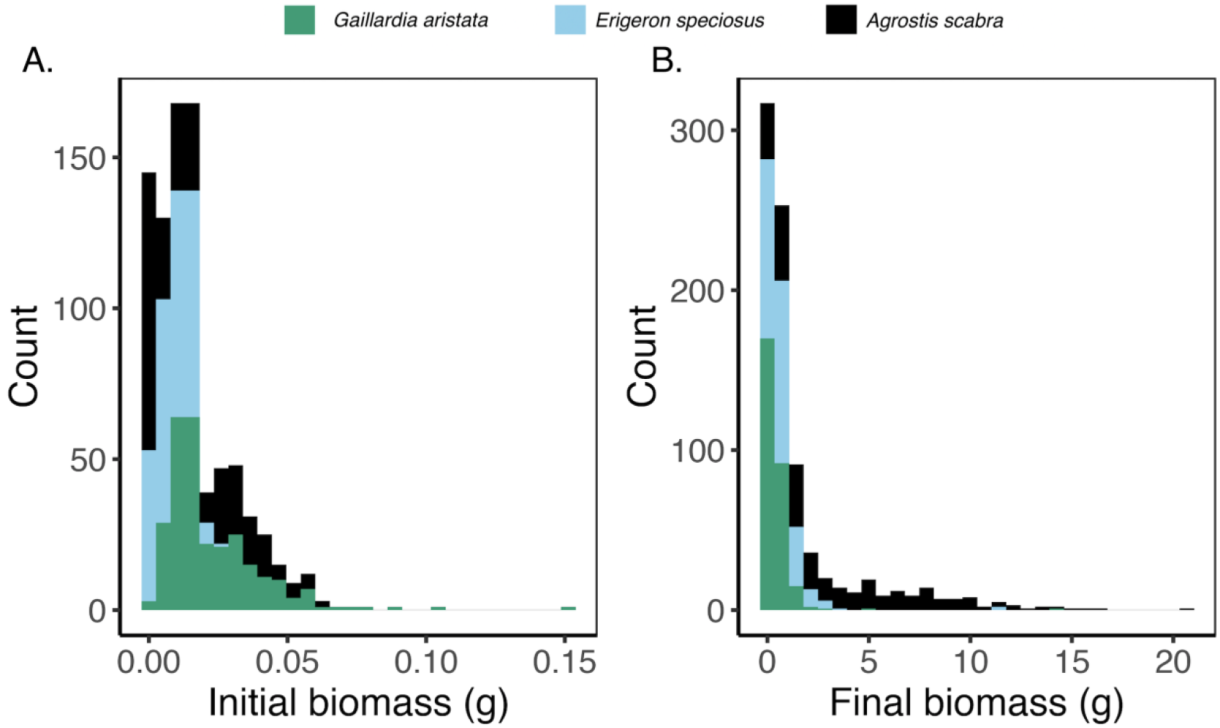
Appendix 2-S1. Measured traits and the results of linear regressions for species used in the study. Models were selected using backward stepwise regressions; AIC was used to select the most parsimonious model. Forcing all variables had a trivial effect on R^2 so the most parsimonious model was used.

Species	**Measured Traits**					**No. individuals**	$\mathbf{R^2}$
	Height	**Breadth (widest)**	**Breadth (perpendicular to widest)**	**No. leaves**	**Length of longest leaf**		
Erigeron speciosus	-	-	0.0051	0.0023	-	11	0.817
Gaillardia aristata	-	-0.0038	0.0161	0.0116	-	12	0.875
Agrostis scabra	-	-	0.0065	-	-	17	0.635

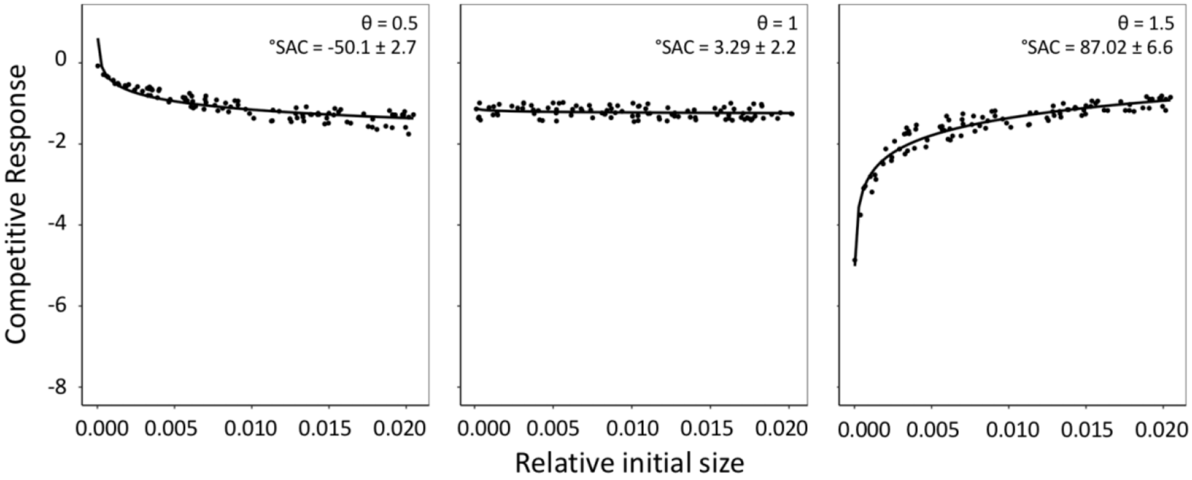
Appendix 2-S2. Average biomass (mean ± standard error) for each size class per species at the beginning of the experiment. Biomass values were estimated using the species-specific biomass regressions outlined in Table S1. Size classes were created by geminating plants 10, 8, 6 and 4 weeks before transplantation into the experiment.



Appendix 2-S3. Histogram of initial and final biomass per species. Initial biomass estimates were estimated using species-specific biomass regressions outlined in Appendix 2-S1.



Appendix 2-S4. The degree of size-asymmetric competition for simulated data with varying levels of size-asymmetric competition. Theta values represent the size-asymmetric competition coefficient from DeMalach et al. 2016 (1=size-symmetric competition, >1=size-asymmetric competition; partially symmetric was not addressed in DeMalach et al. 2016, but here is denoted as <1). The degree of size-asymmetric competition was calculated as the slope of the logarithmic relationship between an individual's competitive response and relative initial biomass (<0 = partially symmetric, 0 = size-symmetric, >0 = size-asymmetric). Data was simulated using the model from DeMalach et al. 2016. Plant growth was simulated for 1000 timesteps. Competitive response was calculated at the final timestep. Initial size represents plant size at timestep zero. Soil resource availability was set to 150. Models were run with one alteration to the original model: initial sizes varied randomly from 0 to 1 rather than being constant among all individuals.



Appendix 2-S5. Effects of soil treatments on shoot, root, and total mesocosm-level biomass and competitive response. Plant biomass was log transformed for analysis.

	Ln(Biomass)		**Competitive response**	
Tissue	**F_{df}**	**p-value**	**F_{df}**	**p-value**
Shoot	$79.67_{4,89}$	$<2e^{-16}$	$8.87_{4,89}$	$4.52e^{-6}$
Root	$15.31_{4,89}$	$1.45e^{-9}$	$14.53_{4,89}$	$3.6e^{-9}$
Whole plant	$89.62_{4,89}$	$<2e^{-16}$	$9.971_{4,89}$	$1.03e^{-6}$

Appendix 2-S6. Effects of soil treatment on the degree of size-asymmetric competition overall and for each *a priori* comparison. Results obtained from a mixed linear model with relative initial size and treatment as fixed factors and pot and species as random factors. p-values for soil treatments represent a two-way interaction between relative initial size and soil treatment. Bold values represent significant parameters. Shoot, root, and total headings correspond to which plant tissue was used in the calculation of competitive response. See Fig.1B for more information about *a priori* comparisons.

Effects of	Total		Shoot		Root	
	Estimate ± SE		Estimate ± SE		Estimate ± SE	
	F value$_{df}$/ T ratio$_{df}$	p-value	F value$_{df}$/ T ratio$_{df}$	p-value	F value$_{df}$/ T ratio$_{df}$	p-value
Soil Treatment	2.979$_{4,806}$	**0.019**	4.588$_{4,806}$	**0.001**	3.557$_{4,806}$	**0.007**
Increased soil fertility	0.498 ± 0.468		1.068 ± 0.528		-0.773 ± 0.478	
	1.065$_{806}$	0.287	2.022$_{806}$	**0.044**	-1.618$_{806}$	0.106
Nutrient heterogeneity (high-quality patch)	-0.222 ± 0.452		-0.335 ± 0.510		-0.303 ± 0.462	
	-0.492$_{806}$	0.623	-0.656$_{806}$	0.512	-0.655$_{806}$	0.513
Nutrient heterogeneity (low-quality patch)	0.719 ± 0.465		0.497 ± 0.525		1.724 ± 0.475	
	1.549$_{806}$	0.122	0.948$_{806}$	0.343	3.630$_{806}$	**>0.001**
Initial microbial suppression	0.188 ± 0.475		0.352 ± 0.537		0.063 ± 0.486	
	0.396$_{806}$	0.692	0.655$_{806}$	0.513	0.130$_{806}$	0.897

Appendix 2-S7. Species-specific responses in the degree of size-asymmetric competition to soil treatment comparisons. Results obtained from a mixed linear model with relative initial size, treatment and species as fixed factors and pot as a random factor. p-values represent a three-way interaction between the relative initial size, soil treatment and species identity. Bold values represent significant parameters. p-values are corrected using the Bonferroni correction (α * 4). Shoot, root, and total headings correspond to what plant tissue was used in the calculation of competitive response.

Gaillardia aristata

Effects of	Total			Shoot			Root		
	Estimate ± SE	T ratio (df)	p-value	Estimate ± SE	T ratio (df)	p-value	Estimate ± SE	T ratio (df)	p-value
Increased soil fertility	7.449 ± 2.147	3.472 (786)	**0.0022**	9.300 ± 2.439	3.815 (786)	**0.0006**	5.557 ± 2.085	2.667 (725.5)	**0.0313**
Nutrient heterogeneity (high-quality patch)	7.762 ± 2.072	3.748 (786)	**0.0008**	7.752 ± 2.354	3.294 (786)	**0.0041**	7.953 ± 2.012	3.954 (719.8)	**0.0003**
Nutrient heterogeneity (low-quality patch)	-5.772 ± 2.056	-2.810 (786)	**0.0203**	-6.986 ± 2.336	-2.993 (786)	**0.0114**	-4.253 ± 1.997	-2.131 (742.1)	0.1336
Initial microbial suppression	2.680 ± 2.146	1.250 (786)	0.8474	3.480 ± 2.437	1.428 (786)	0.6151	0.878 ± 2.083	0.422 (707.5)	1.0000

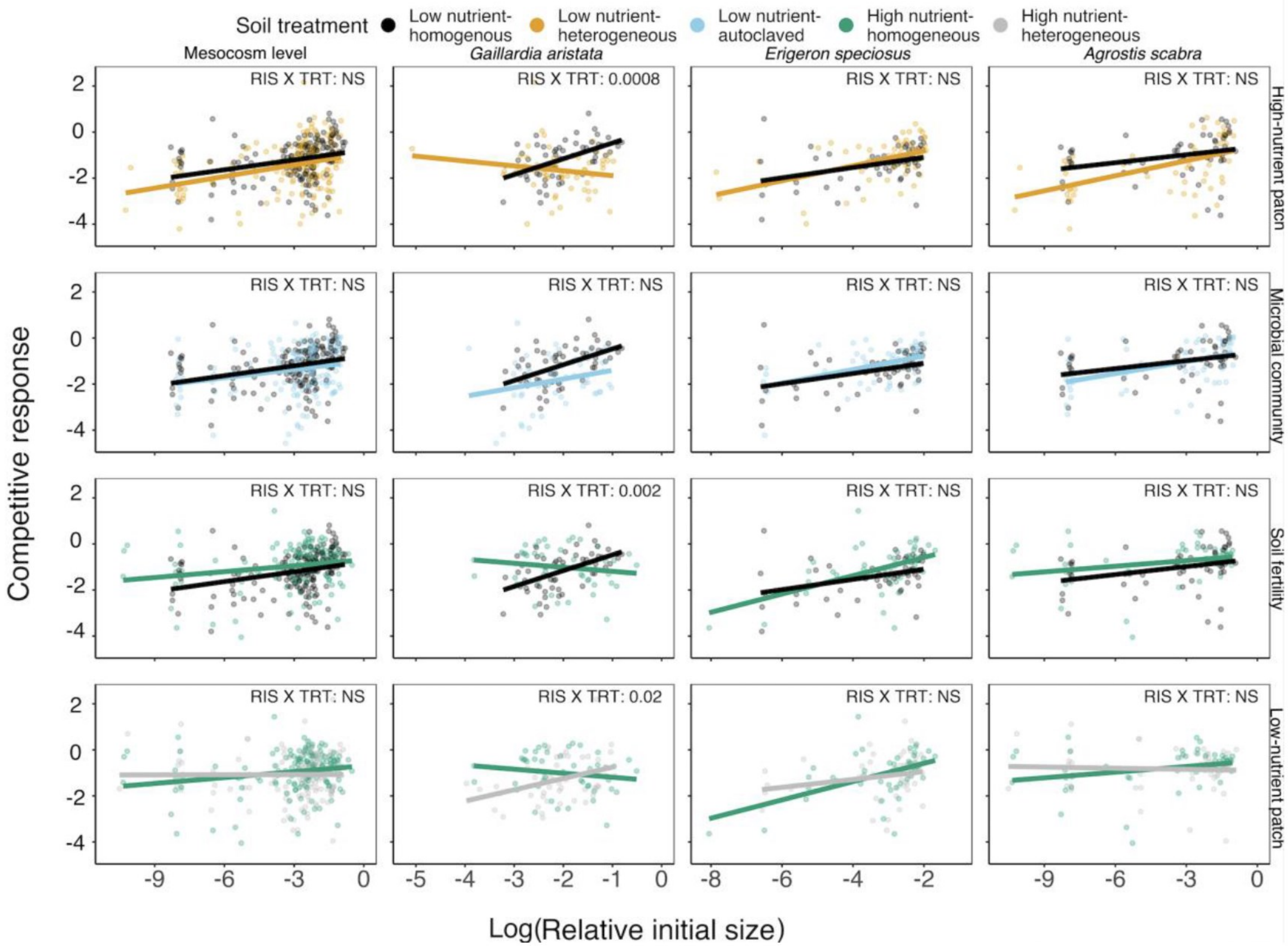
Erigeron speciosus

Effects of	Total			Shoot			Root		
	Estimate ± SE	T ratio (df)	p-value	Estimate ± SE	T ratio (df)	p-value	Estimate ± SE	T ratio (df)	p-value
Increased soil fertility	-1.512 ± 1.114	-1.358 (786)	0.6994	-1.894 ± 1.266	-1.497 (786)	0.5391	-1.415 ± 1.083	-1.309 (744.8)	0.7642
Nutrient heterogeneity (high-quality patch)	-0.880 ± 0.985	-0.894 (786)	1.0000	-2.557 ± 1.120	-2.286 (786)	0.0901	-0.372 ± 0.957	-0.389 (736.2)	1.0000
Nutrient heterogeneity (low-quality patch)	1.957 ± 1.213	1.616 (786)	0.4263	1.913 ± 1.378	1.390 (786)	0.6596	2.294 ± 1.179	1.949 (757.2)	0.2068
Initial microbial suppression	-0.637 ± 1.072	-0.595 (786)	1.000	-1.514 ± 1.218	-1.244 (786)	0.8551	-0.528 ± 1.041	-0.508 (738.2)	1.0000

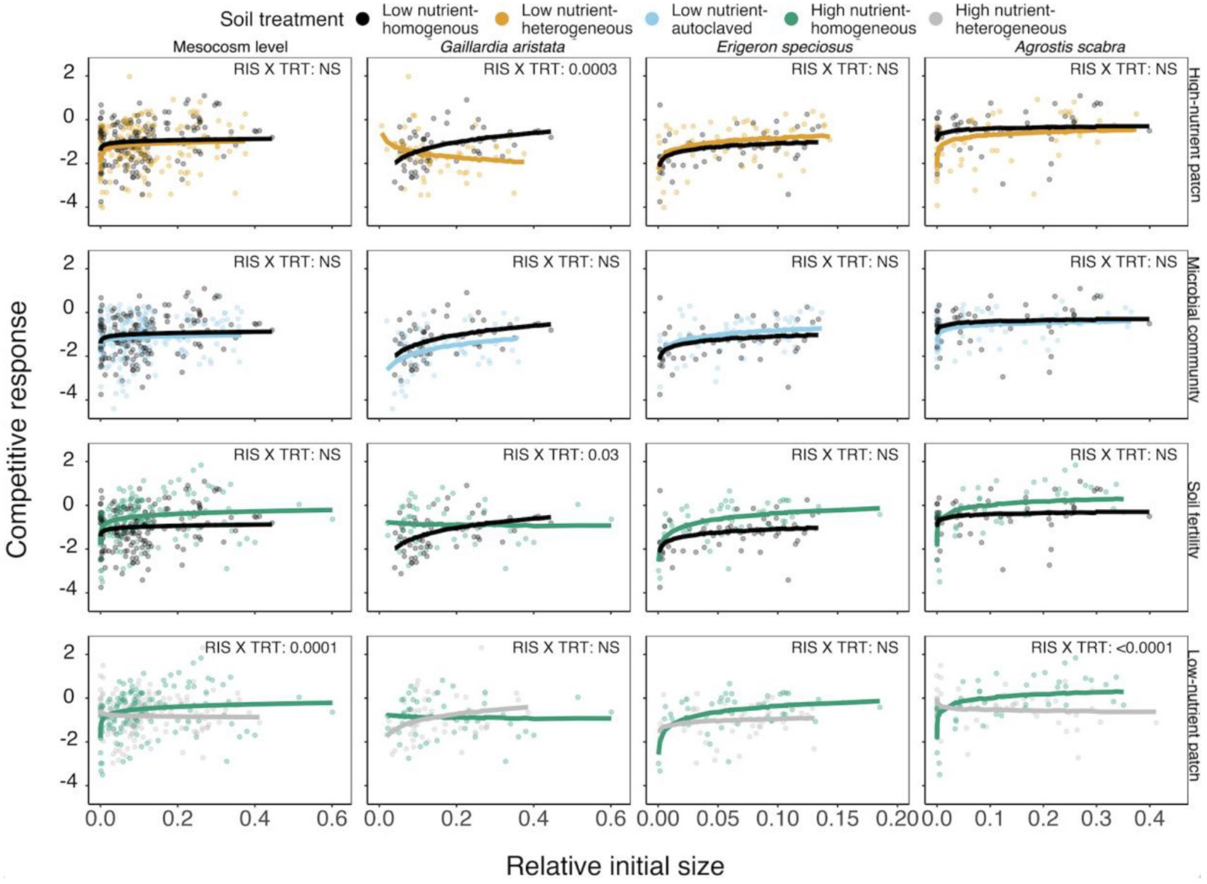
Agrostis scabra

Effects of	Total			Shoot			Root		
	Estimate ± SE	T ratio (df)	p-value	Estimate ± SE	T ratio (df)	p-value	Estimate ± SE	T ratio (df)	p-value
Increased soil fertility	0.296 ± 0.545	0.543 (786)	1.0000	0.784 ± 0.619	1.267 (786)	0.8226	-1.217 ± 0.529	-2.300 (718.7)	0.0869
Nutrient heterogeneity (high-quality patch)	-0.883 ± 0.533	-1.654 (786)	0.3939	-0.829 ± 0.607	-1.367 (786)	0.6877	-0.874 ± 0.518	-1.687 (716.7)	0.3680
Nutrient heterogeneity (low-quality patch)	0.850 ± 0.523	1.626 (786)	0.4177	0.440 ± 0.594	0.740 (786)	1.0000	2.467 ±0.508	4.861 (719.9)	**<0.0001**
Initial microbial suppression	-0.497 ± 0.557	-0.893 (786)	1.0000	-0.412 ± 0.633	-0.651 (786)	1.0000	-0.321 ± 0.541	-0.594 (713.4)	1.0000

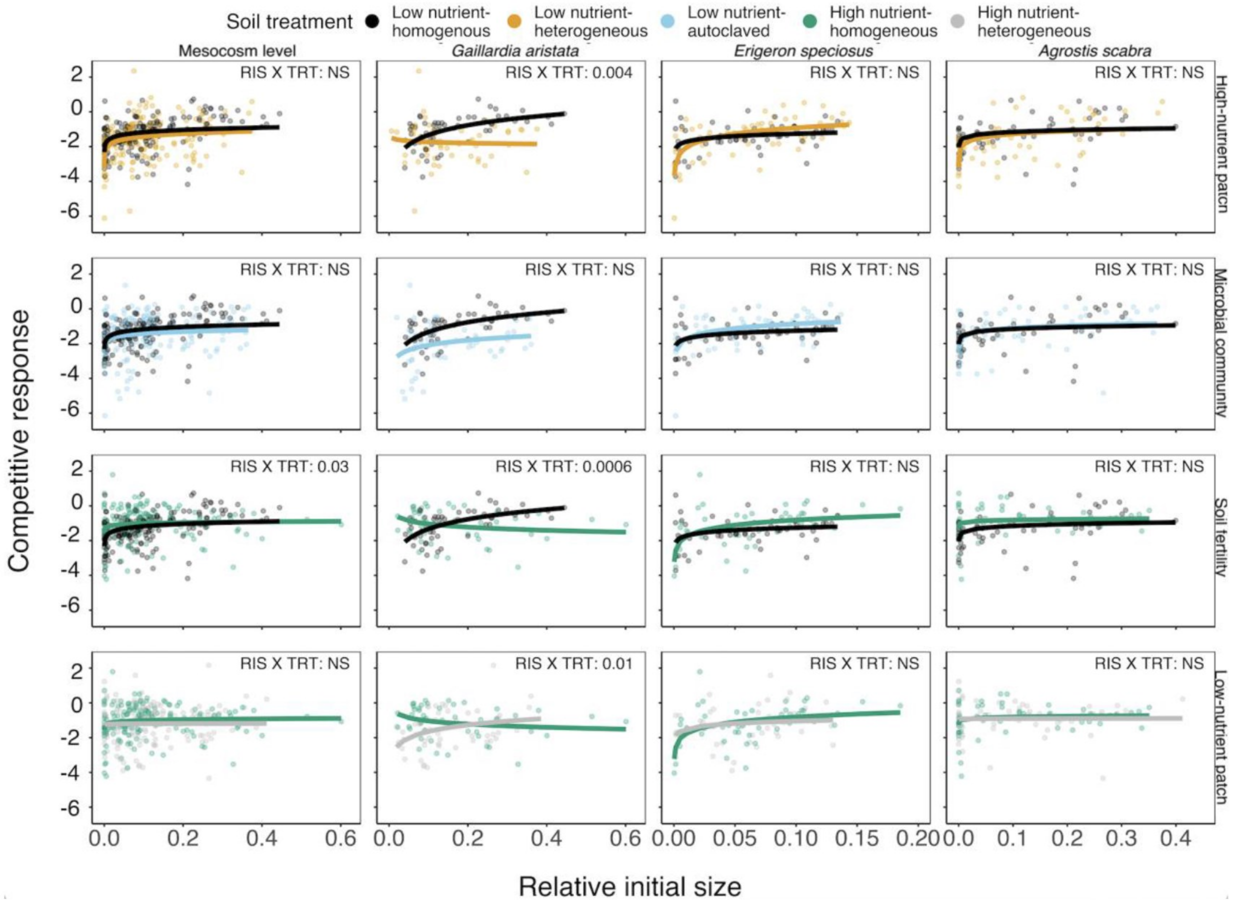
Appendix 2-S8. The relationship between relative initial size and competitive response for each soil treatment in log space at the mesocosm-level and for each species measured with total biomass. Each row represents one of the four *a priori* soil treatment comparisons (see Fig. 1B). Going from top to bottom the rows depict effects of 1) nutrient heterogeneity (low-nutrient patch), 2) initial microbial community suppression, 3) soil fertility, and 4) nutrient heterogeneity (high-nutrient patch). RIS X TRT corresponds to the significance values for the relative initial size by soil treatment interaction from the overall soil treatment and species-specific mixed linear models (NS= nonsignificant). Species-level p-value estimates were corrected using a bonferroni correction (α _* 4). To facilitate comparison within species, the relative initial size axis has been adjusted to better represent the ranges of each species.



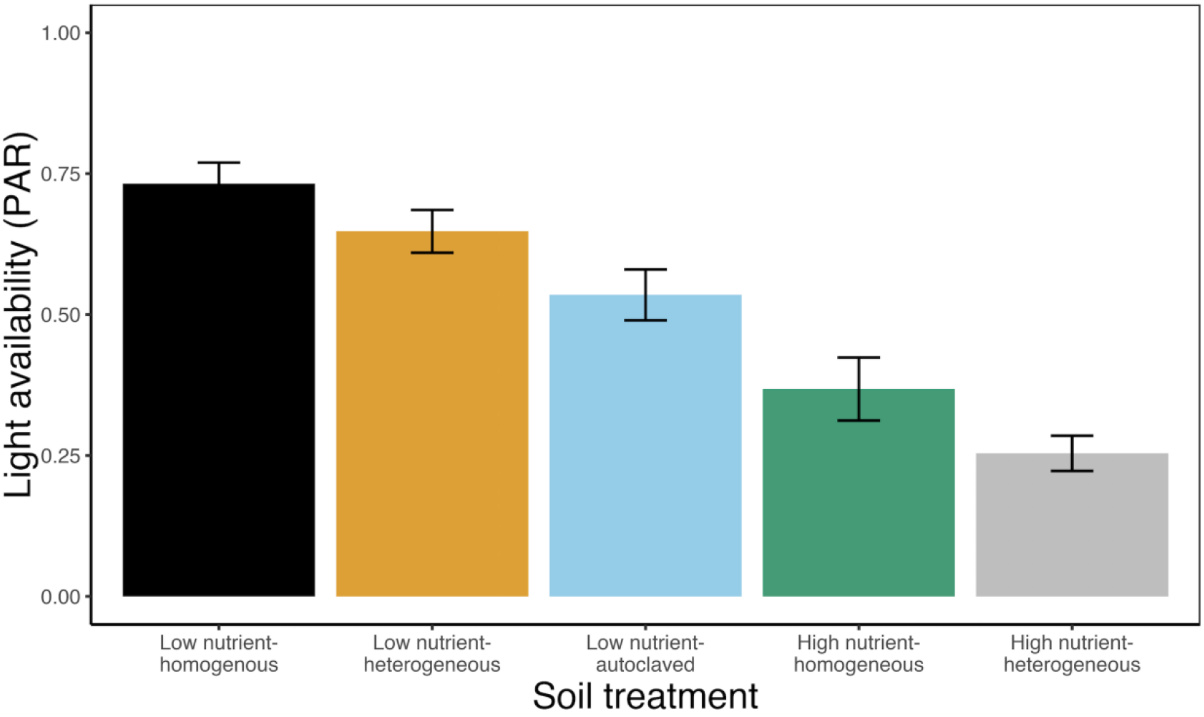
Appendix 2-S9. The relationship between relative initial size and competitive response for each soil treatment at the mesocosm-level and for each species measured with root biomass. Each row represents one of the four *a priori* soil treatment comparisons (see Fig. 1B). Going from top to bottom the rows depict effects of 1) nutrient heterogeneity (low-nutrient patch), 2) initial microbial community suppression, 3) soil fertility, and 4) nutrient heterogeneity (high-nutrient patch). Regression lines are the logarithmic relationship between relative initial size and competitive response. RIS X TRT corresponds to the significance values for the relative initial size by soil treatment interaction from the overall soil treatment and species-specific mixed linear models (NS= nonsignificant). Species-level p-value estimates were corrected using a bonferroni correction (*α* _* 4). To facilitate comparison within species, the relative initial size axis has been adjusted to better represent the ranges of each species.



Appendix 2-S10. The relationship between relative initial size and competitive response for each soil treatment at the mesocosm-level and for each species measured with shoot biomass. Each row represents one of the four *a priori* soil treatment comparisons (see Fig. 1B). Going from top to bottom the rows depict effects of 1) nutrient heterogeneity (low-nutrient patch), 2) initial microbial community suppression, 3) soil fertility, and 4) nutrient heterogeneity (high-nutrient patch). Regression lines are the logarithmic relationship between relative initial size and competitive response. RIS X TRT corresponds to the significance values for the relative initial size by soil treatment interaction from the overall soil treatment and species-specific mixed linear models (NS= nonsignificant). Species-level p-value estimates were corrected using a bonferroni correction (α _* 4). To facilitate comparison within species, the relative initial size axis has been adjusted to better represent the ranges of each species.



Appendix A2-S11. Average light availability (mean ± standard error) for each soil treatment. Light availability was measured at the center of each pot as the ratio of photosynthetic active radiation (PAR) available below the canopy compared to above the canopy.

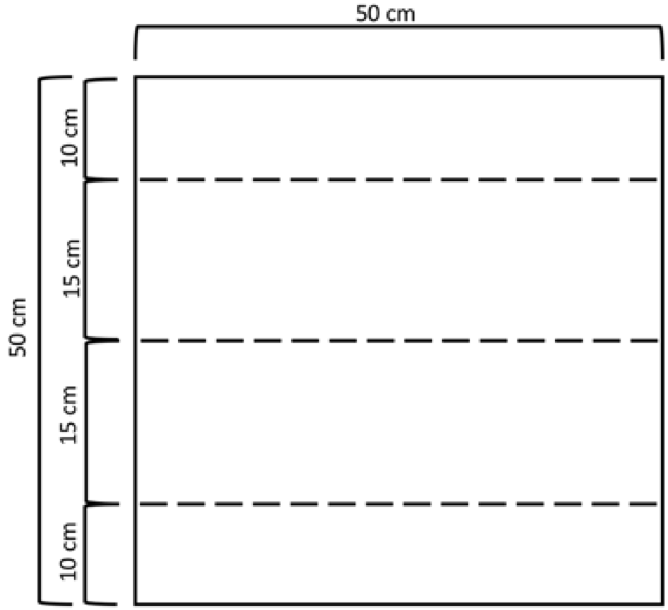


Appendix 3-S1. Frequency and average abundance of species found in study plots. Species are listed in order of most abundant to least abundant. Frequency was calculated as the proportion of plots a species was present in out of the 32 plots sampled. Average abundance was calculated by averaging the total percent cover of each species over all 32 plots sampled.

Family	**Species**	**Frequency**	**Average Abundance**
Poaceae	*Hesperostipa curtiseta* (Hitchc.) Barkworth	0.968	34.903
Poaceae	*Poa pratensis* L.	0.677	19.065
Cyperaceae	*Carex* spp.	0.839	13.161
Rosaceae	*Rosa arkansana* Porter	0.710	7.677
Scrophulariaceae	*Penstemon gracilis* Nutt.	0.194	5.774
Poaceae	*Festuca hallii* (Vasey) Piper	0.581	5.323
Asteraceae	*Artemesia ludoviciana* Nutt.	0.355	4.806
Asteraceae	*Symphyotrichum falcatum* (L.) A. Love & D. Love	0.484	3.774
Asteraceae	*Achillea millefolium* L.	0.516	3.742
Asteraceae	*Artemesia frigida* Willd.	0.355	3.677
Poaceae	*Bouteloua gracilis* Willd. Ex Kunth	0.226	2.710
Poaceae	*Elymus trachycaulus* Gould ex Shinners	0.419	2.677
Poaceae	*Elymus glaucus* Buckley	0.484	2.226
Fabaceae	*Astragalus agrestis* Douglas ex G. Don	0.452	2.194
Rosaceae	*Geum triflorum* Pursh	0.323	2.097
Poaceae	*Koeleria macarantha* (Ledeb.) Schult.	0.323	1.645
Poaceae	*Pascopyrum smithii* (Rydb.) A. Love	0.290	1.548
Asteraceae	*Solidago missouriensis* Nutt.	0.387	1.516
Rubiaceae	*Galium boreale* L.	0.323	1.484
Poaceae	*Nassella viridula* (Trin.) Barkworth	0.129	1.484
Poaceae	*Agrostis scabra* Willd.	0.065	1.452
Asteraceae	*Symphyotrichum leave* (L.) A. Love & D. Love	0.194	1.419
Campanulaceae	*Campanula rotundifolia* L.	0.194	1.387
Caryophyllaceae	*Cerastium arvense* L.	0.355	1.290
Ranunculaceae	*Pulsatilla patens* (L.) Mill.	0.161	1.258

Violaceae	*Viola adunca* Sm.	0.194	1.161
Poaceae	*Poa interior* Rybd.	0.161	0.935
Fabaceae	*Thermopsis rhombifolia* (Nutt. Ex Pursh) ex Richardson	0.226	0.903
Poaceae	*Agropyron dasystachyum* (Hook.) Scribn. & J.G. Sm.	0.194	0.839
Santalaceae	*Comandra umbellata* (L.) Nutt.	0.484	0.742
Asteraceae	*Antennaria parvifolia* Nutt.	0.194	0.677
Asteraceae	*Taraxacum officinale* F.H. Wigg	0.258	0.645
Poaceae	*Agropyron cristatum* (L.) Gaertn.	0.194	0.581
Asteraceae	*Antennaria neglecta* Greene	0.065	0.581
Fabaceae	*Vicia Americana* Muhl. Ex Willd.	0.194	0.548
Asteraceae	*Erigeron caespitosus* Nutt.	0.161	0.484
Gentianaceae	*Gentiana amarella* (L.) Borner	0.097	0.452
Fabaceae	*Oxytropis campestris* (L.) DC.	0.161	0.419
Rosaceae	*Potentilla concinna* Richardson	0.065	0.355
Iridaceae	*Sisyrinchium montanum* Greene	0.032	0.258
Fabaceae	*Astragalus drummondii* Douglas ex Hook	0.032	0.161
Fabaceae	*Astragalus flexuosus* Douglas ex Hook	0.032	0.161
Poaceae	*Avenula hookeri* (Scribn.) Holub	0.032	0.161
Rosaceae	*Potentilla arguta* Pursh	0.032	0.161
Caprifoliaceae	*Symphoricarpos occidentalis* Hook	0.032	0.161
Elaegnaceae	*Elaeagnus commutata* Bernh. Ex Rydb.	0.065	0.129
Asteraceae	*Tragopogon dubius* Scop.	0.065	0.129
Asteraceae	*Erigeron glabellus* Nutt.	0.032	0.097
Scrophulariaceae	*Orthocarpu luteus* Nutt.	0.097	0.097
Caryophyllaceae	*Stellaria longipes* Goldie	0.032	0.097
Chenopodiaceae	*Chenopodium album* L.	0.065	0.065
Primulaceae	*Androsace septentrionalis* Pursh	0.032	0.032

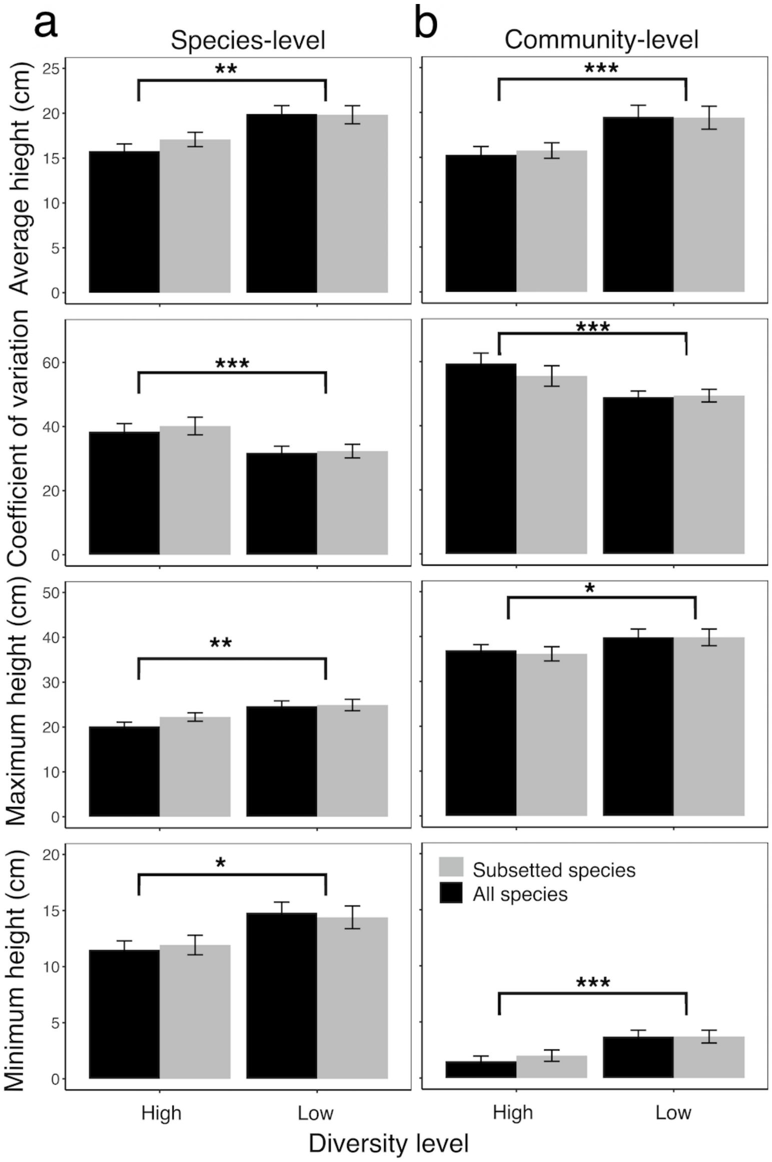
Appendix 3-S2. Diagram of the study plot used to estimate size structure. Dashed lines represent transects. Species identity and height was recorded for all ramets that touched the transects. Vertical size structure parameters were calculated from height data from all three transects combined.



Appendix 3-S3. Correlation matrix of for size structure parameters.

Parameters	Average height	Gini coefficient	Scale	Shape
Average height	1			
Gini coefficient	-0.666	1		
Scale	0.999	-0.680	1	
Shape	0.720	-0.968	0.732	1

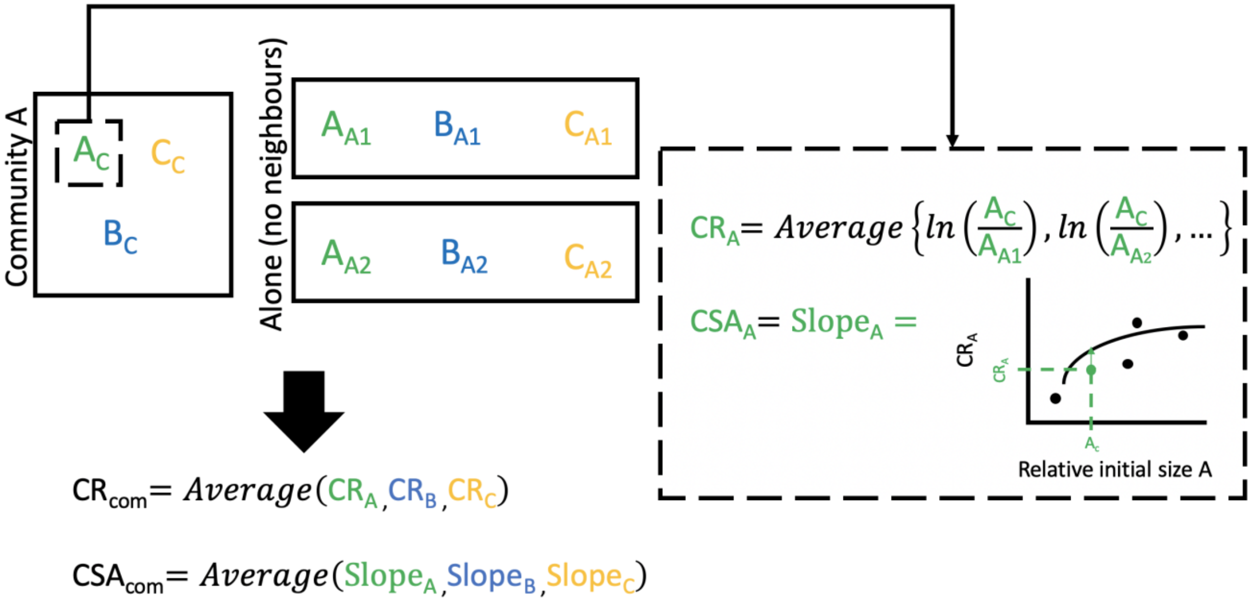
Appendix 3-S4. Average species- (a) and community-level (b) height characteristics per richness level for all species found in a plot (black bars) and only species found in both high and low richness plots (grey bars). Height characteristics were either summarized by species (species-level) or by plot irrespective of species identity (community-level). To assess high and low richness sites, we separated height data into two diversity levels: low diversity and high diversity based on the 1st and 3rd quantiles (Low richness ≤ 11 species, high richness ≥14 species). Asterix represents significance (*<0.05, **<0.01, ***<0.001) of diversity level (high or low) from eight separate linear mixed models. Species grouping (all or subset) nor the diversity level by species grouping interaction were significant for any model. In each linear mixed model, diversity level and species grouping were fixed factors, block was a random factor, and each of the four height characteristics were response variables. For species-level analysis, species identity was additionally fit as a random factor.



Appendix 4-S1. The number of replicates of focal species per thinning treatment at the start and end of the experiment found within all blocks.

	Species															
	Artemisia frigida		*Artemisia ludoviciana*		*Festuca hallii*		*Galium boreale*		*Geum triflorum*		*Hesperostipa curtiseta*		*Poa pratensis*		*Rosa arkansana*	
Thinning treatment	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End	Start	End
No removal	8	7	5	3	6	5	5	3	6	5	9	9	5	5	8	7
Large-sized neighbours	8	7	5	3	6	5	6	4	6	6	9	9	5	5	7	6
Medium-sized neighbours	8	8	6	5	6	6	6	5	6	6	8	8	4	4	8	7
Small-sized neighbours	7	7	3	3	6	5	6	5	6	5	9	9	5	5	7	6
Total removal	6	3	5	3	6	2	6	5	6	5	9	8	5	4	7	5
Total number	37	32	24	17	30	23	29	22	30	27	44	43	24	23	37	31

Appendix 4-S2. Schematic of how community-level competitive intensity (CR_{com}) and competitive size-asymmetry (CSA_{com}) were calculated. Letters (A, B, and C) correspond to different species. Subscript “C” = grown in community, subscript “A1” = grown alone (replicate 1), subscript “A2” = grown alone (replicate 2). Community-level competitive intensity was calculated by averaging the competitive responses of species found within the plot. A species’ competitive response was calculated by averaging each competitive response for all alone treatment replicates(Lamb & Cahill 2008). Community-level competitive size-asymmetry was calculated by averaging the degree of size-asymmetric competition experienced by each individual in the community. An individual’s degree of size-asymmetric competition was calculated by taking the derivative of the logarithmic relationship between an individual’s competitive response and initial size for each species. The initial size of each focal individual was estimated using species-specific biomass regressions created from destructive harvests of individuals found outside of the experimental treatments.

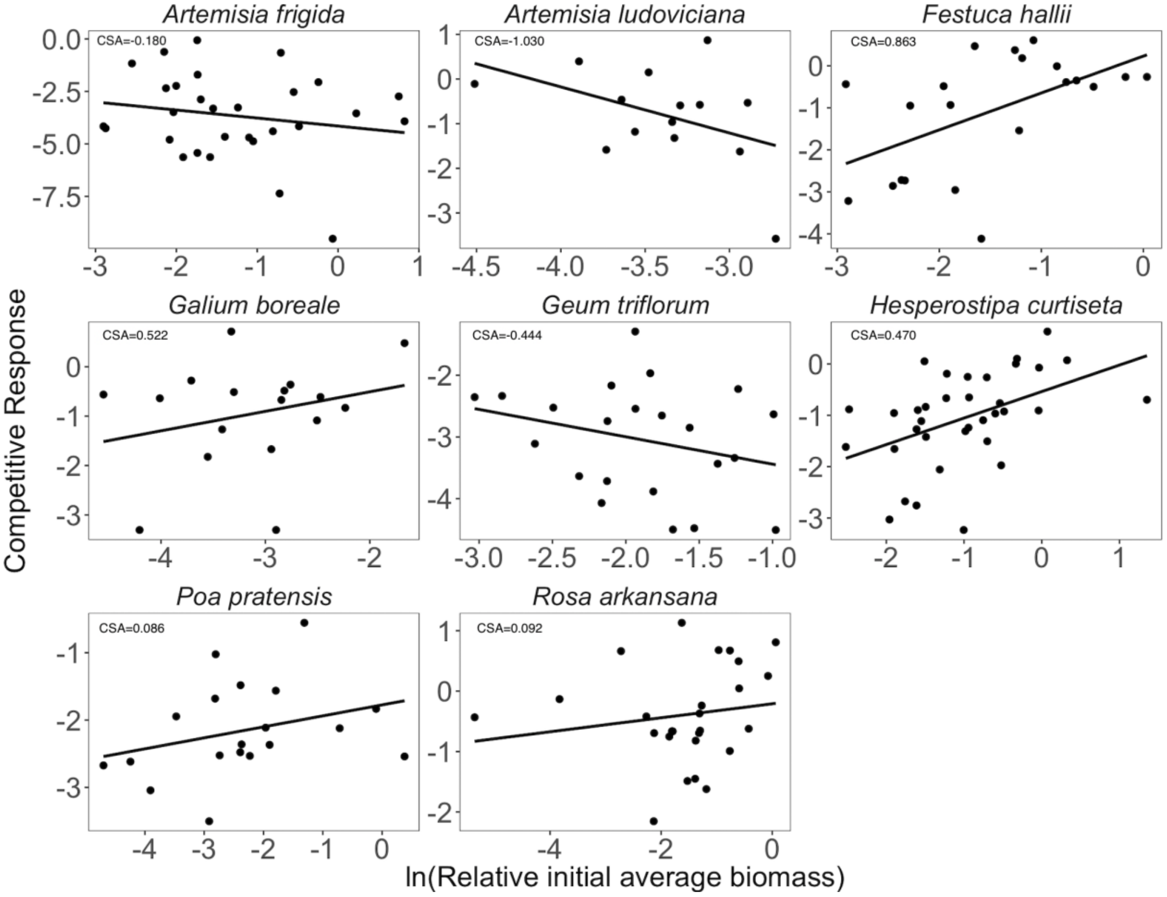


Appendix 4-S3. Focal plants in each plot used for community-level analyses. 'X' means it was found within the plot. "-"means that the plot was excluded from the analysis.

Block	Subplot	*Artemisia frigida*	*Artemisia ludoviciana*	*Festuca hallii*	*Galium boreale*	*Geum triflorum*	*Hesperostipa curtiseta*	*Poa pratensis*	*Rosa arkansana*
1	No removal			X			X		X
1	Large-sized neighbours			X		X	X		X
1	Medium-sized neighbours			X		X	X		X
1	Small-sized neighbours			X			X		X
2	No removal	X					X		X
2	Large-sized neighbours						X		X
2	Medium-sized neighbours	X					X		X
2	Small-sized neighbours	X					X		X
3	No removal	X					X		X
3	Large-sized neighbours	X					X		X
3	Medium-sized neighbours	X							X
3	Small-sized neighbours	X					X		X
4	No removal	X	X		X		X		
4	Large-sized neighbours	X			X		X		
4	Medium-sized neighbours	X	X		X		X		
4	Small-sized neighbours	X	X		X		X		
5	No removal	X					X		X
5	Large-sized neighbours	X					X		X
5	Medium-sized neighbours	X					X		X
5	Small-sized neighbours	X					X		X
6	No removal		X					X	X
6	Large-sized neighbours		X					X	
6	Medium-sized neighbours	-	-	-	-	-	-	-	-
6	Small-sized neighbours	-	-	-	-	-	-	-	-
7	No removal	X					X		
7	Large-sized neighbours	X					X		
7	Medium-sized neighbours	X					X		
7	Small-sized neighbours	X					X		
8	No removal	-	-	-	-	-	-	-	-
8	Large-sized neighbours	X					X		
8	Medium-sized neighbours	X					X		X
8	Small-sized neighbours						X		X
9	No removal	X					X	X	X

9	Large-sized neighbours	X					X	X	X
9	Medium-sized neighbours	X					X	X	X
9	Small-sized neighbours	X					X	X	
10	No removal					X		X	
10	Large-sized neighbours				X	X		X	
10	Medium-sized neighbours		X		X	X		X	
10	Small-sized neighbours				X	X		X	
11	No removal		X	X		X			
11	Large-sized neighbours		X	X	X	X			
11	Medium-sized neighbours		X	X	X	X			
11	Small-sized neighbours		X	X	X	X			
12	No removal			X	X	X	X		
12	Large-sized neighbours			X		X	X		
12	Medium-sized neighbours			X	X	X	X		
12	Small-sized neighbours			X	X	X	X		
13	No removal			X	X	X			
13	Large-sized neighbours			X		X			
13	Medium-sized neighbours			X	X	X			
13	Small-sized neighbours			X	X	X			
14	No removal		X	X		X		X	
14	Large-sized neighbours		X			X		X	
14	Medium-sized neighbours		X	X		X		X	
14	Small-sized neighbours		X	X		X		X	
15	No removal							X	X
15	Large-sized neighbours			X	X			X	X
15	Medium-sized neighbours		X	X				X	
15	Small-sized neighbours							X	X

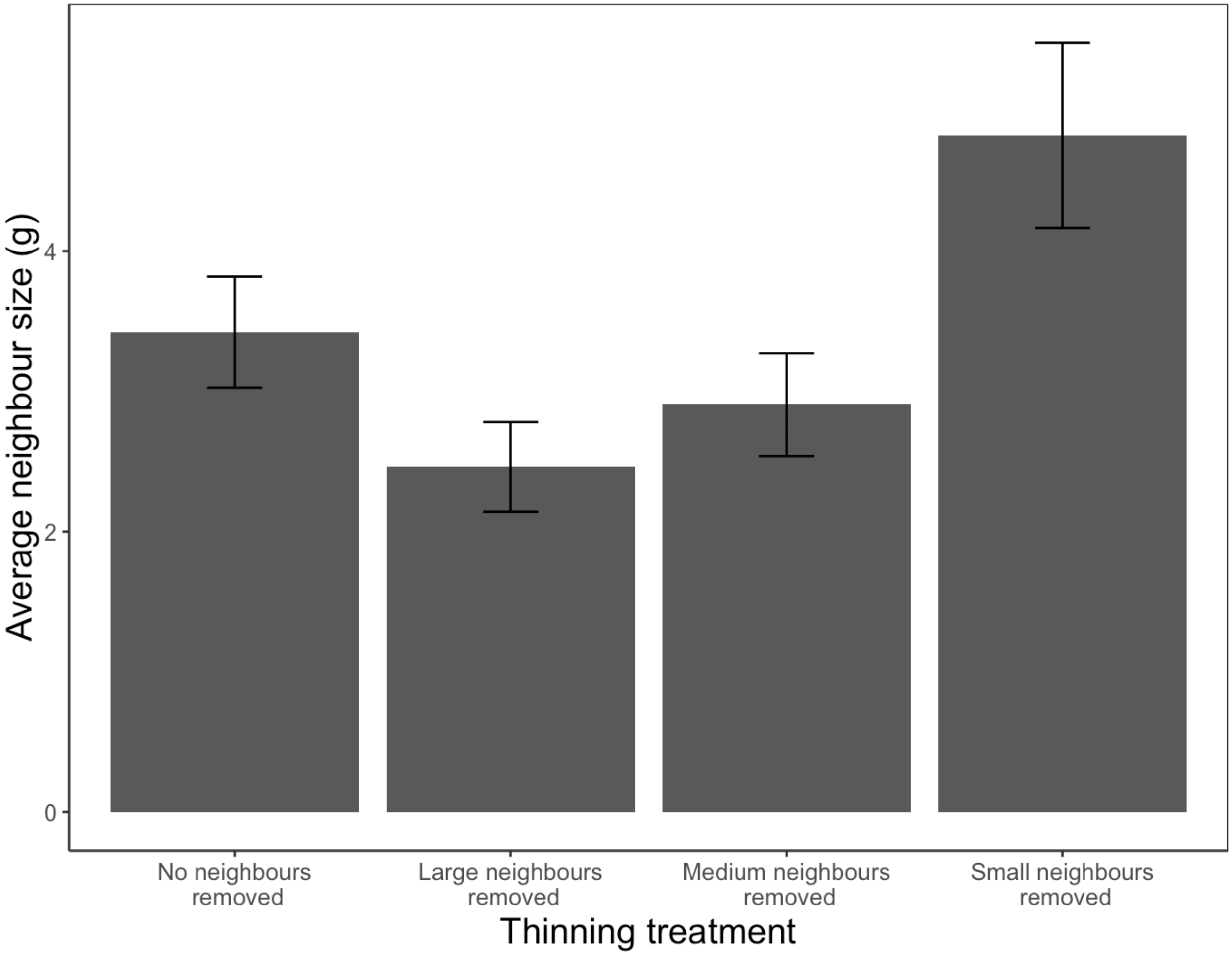
Appendix 4-S4. Species-level competitive size-asymmetries for each focal species. Plotted using natural-log-transformed initial size to better display the degree of size-asymmetry, measured as the slope from a logarithmic regression between an individual's competitive response and its initial size. Slope values shown in upper corner and were used in the measurement of individual-level competitive size-asymmetry. A positive slope represents size-asymmetric competition; a negative slope represents partially symmetric competition; a horizontal line represents size-symmetric competition. Relative initial average biomass was calculated as the absolute initial biomass of a focal individual divided by the average initial biomass of neighbouring plants, which was calculated by dividing the total biomass of the plot by the ramet density in the plot.



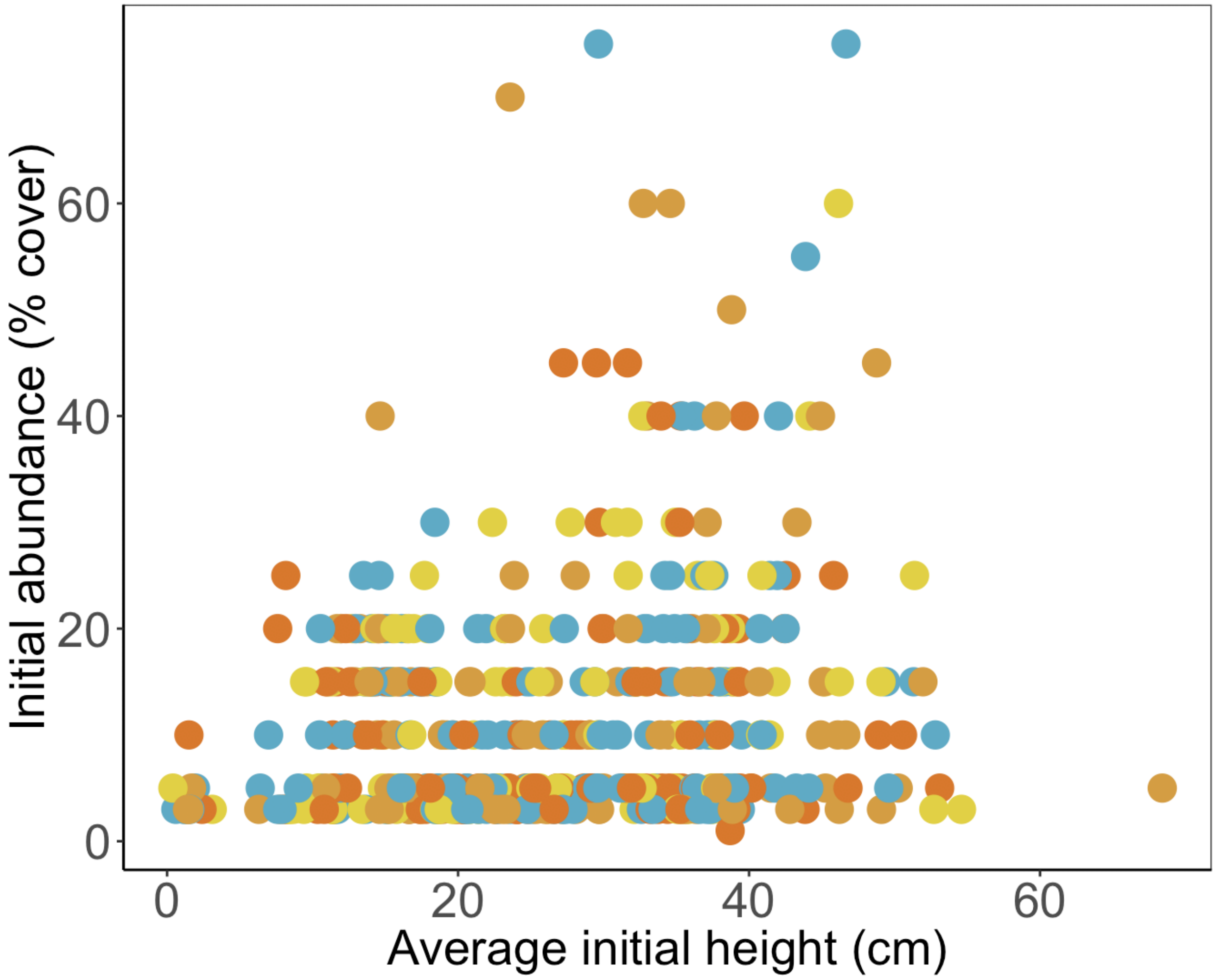
Appendix 4-S5. Measured traits and the results of linear regressions for species used to estimate initial biomass. Area is a measure of the total area taken up by the plant; calculated as an ellipse using the longest width and the width perpendicular to the longest width. Biomass was square-root transformed prior to analysis. The coefficient for the y-intercept was set to 0 as plants cannot have negative weights.

	Predictors			
Species	Height	Area	Flowering	R^2
Artemisia frigida	0.058	0.003	0.764	0.945
Artemisia ludoviciana	0.031	-0.001	-	0.989
Festuca hallii	0.015	0.191	0.007	0.952
Galium boreale	0.017	0.017	-	0.971
Geum triflorum	0.038	0.002	0.321	0.968
Hesperostipa curtiseta	0.031	0.073	0.024	0.971
Poa pratensis	0.012	0.551	0.078	0.962
Rosa arkansana	0.032	0.010	-	0.951

Appendix 4-S6. Mean average neighbor size (± SE) for each of the thinning treatments. Average neighbor size was calculated by dividing plot biomass by plot ramet density.



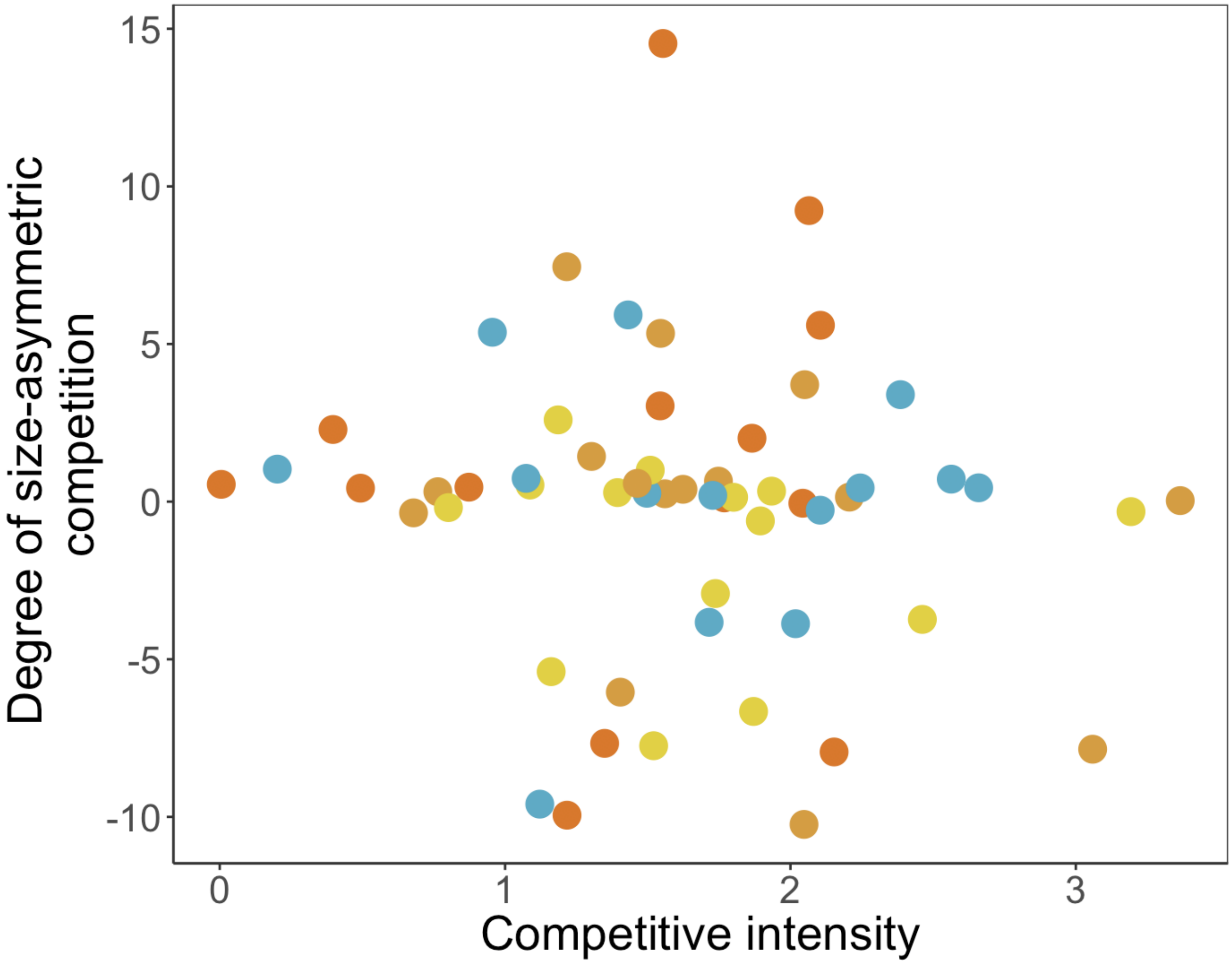
Appendix 4-S7. The relationship between a species' average initial height and initial abundance. There is no significant relationship (Regression coefficient: 0.067 ± 0.050, $t_{394.54}$=1.359, p=0.175) based on a linear mixed model with initial abundance as the response, average initial height as a fixed factor, and block and species identity as random factors.



Appendix 4-S8. Regression coefficients and significance values for the relationship between competitive intensity and the degree of size-asymmetric competition and species turnover for each metric of size-asymmetric competition. Results from two separate linear mixed models with degree of size-asymmetric competition measured using either relative total biomass (individual focal /total plot biomass) and absolute biomass (focal individual biomass). Significant values are represented in bold (at α=0.05) and underlined (at α=0.01).

	Explanatory variable							
	Degree of size-asymmetric competition				**Competitive intensity**			
Response variable	**Regression coefficient (±SE)**	**F**	**df**	**p-value**	**Regression coefficient (±SE)**	**F**	**df**	**p-value**
Calculated with relative total size								
TBI	0.085 ± 0.144	0.348	1, 50.04	0.558	- 0.082 ± 0.139	0.357	1, 53.98	0.553
Gains	-0.243 ± 0.136	3.205	1, 53.87	0.079	- 0.133 ± 0.124	1.154	1, 52.24	0.288
Losses	0.320 ± 0.135	5.616	1, 36.88	**0.023**	0.014 ± 0.133	0.011	1, 48.07	0.918
Calculated with absolute size								
TBI	0.185 ± 0.145	1.614	1, 47.21	0.210	- 0.067 ± 0.135	0.237	1, 53.98	0.629
Gains	-0.134 ± 0.143	0.882	1, 53.45	0.352	-0.131 ± 0.127	1.067	1, 51.88	0.307
Losses	0.340 ± 0.136	6.279	1, 34.57	**0.017**	0.032 ± 0.1328	0.057	1, 47.87	0.812

Appendix 4-S9. The relationship between competitive intensity and the degree of size-asymmetric competition. The color of the points represents different neighbor treatments. There is no significant relationship (Regression coefficient: -0.620 ± 0.894; $F_{1,54.67}$=0.482, p=0.491) based on a linear mixed model with degree of size-asymmetric competition as the response, competitive intensity as a fixed factor, and block as a random factor



Appendix 4-S10. Community and environmental predictors of competitive intensity and the degree of competitive size-asymmetry within the local plant communities. Variables were standardized to have a mean of 0 and a standard deviation of 1 prior to analysis. Bolded values represent significance at the 0.05 level.

	Response variable							
	Degree of size-asymmetric competition				**Competitive intensity**			
Explanatory variable	**Regression coefficient (±SE)**	**F**	**df**	**p-value**	**Regression coefficient (±SE)**	**F**	**df**	**p-value**
Focal species MDS1	-0.539 ± 0.240	5.014	1, 24.91	**0.034**	-0.071 ± 0.172	0.170	1, 15.84	0.686
Focal species MDS2	0.050 ± 0.228	0.049	1, 17.35	0.828	0.102 ± 0.146	0.493	1, 10.80	0.498
Shoot biomass	-0.053 ± 0.135	0.158	1, 41.68	0.693	0.084 ± 0.133	0.400	1, 35.91	0.531
Litter biomass	-0.309 ± 0.148	4.354	1, 42.34	**0.043**	-0.372 ± 0.141	6.972	1, 27.63	**0.013**
Root biomass	0.256 ± 0.168	2.296	1, 38.35	0.138	0.154 ± 0.177	0.753	1, 41.95	0.390
Light availability	0.068 ± 0.201	0.108	1, 44.81	0.745	-0.143 ± 0.191	0.560	1, 30.59	0.459
Soil pH	-0.153 ± 0.172	0.792	1, 45.00	0.378	0.125 ± 0.162	0.595	1, 38.94	0.445
Soil inorganic nitrogen	0.269 ± 0.137	3.886	1, 37.71	**0.056**	0.017 ± 0.144	0.014	1, 41.93	0.9087
Soil moisture	0.140 ± 0.114	1.505	1, 36.75	0.228	0.031 ± 0.127	0.060	1, 44.81	0.808
Stem density	-0.257 ± 0.165	2.447	1, 43.40	0.125	0.086 ± 0.168	0.260	1, 44.47	0.612

Appendix 4-S11. Summary of observed variables included in the linear models.

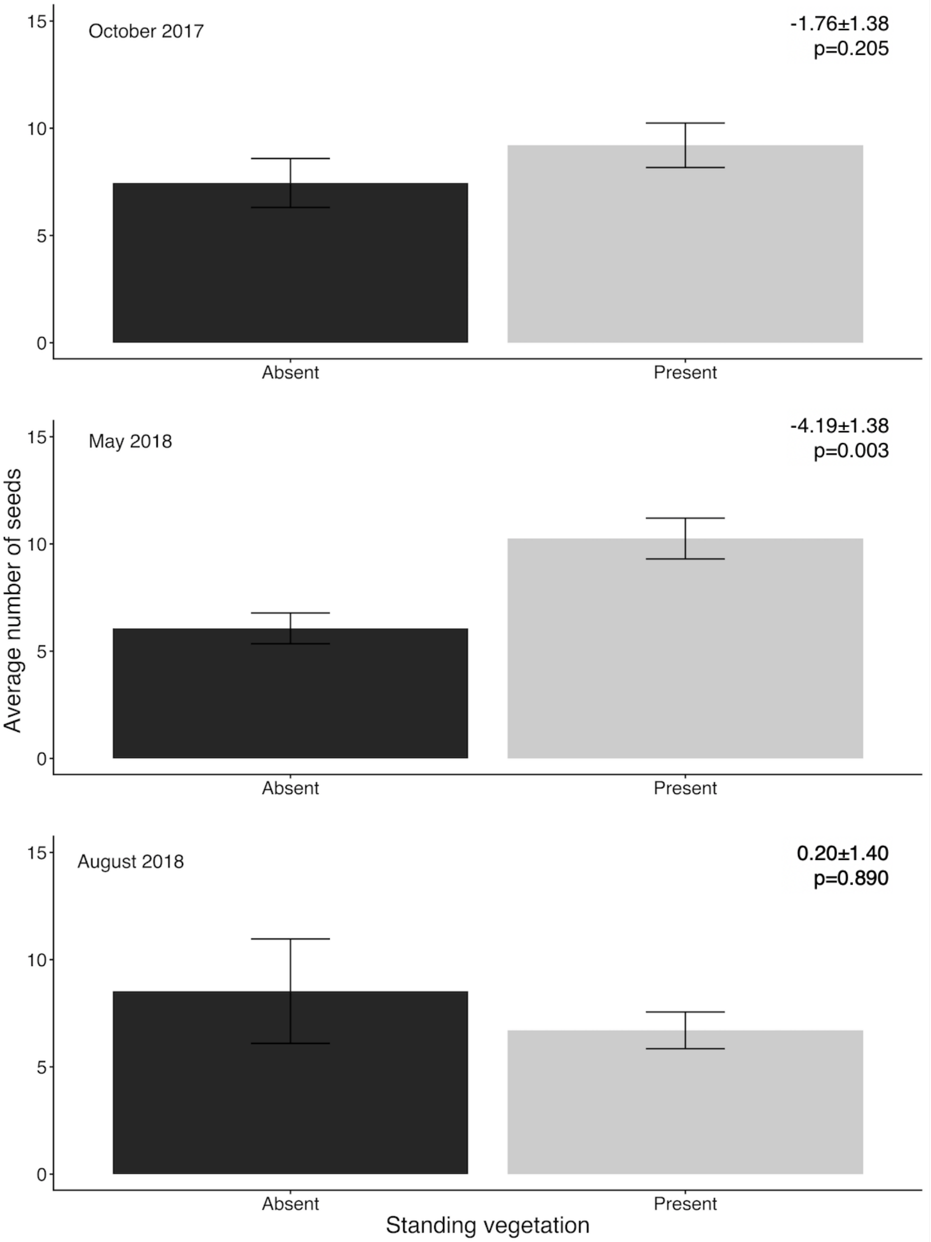
Variable	Mean ± SE	Range
Degree of size-asymmetric competition	-0.233 ± 0.622	-10.239-14.533
Competitive intensity	1.626 ± 0.090	0.005-3.366
Relative contribution of gains	0.255 ± 0.020	0.000-0.500
Relative contribution of losses	0.138 ± 0.130	0.000-0.333
Temporal beta diversity	0.393 ± 0.022	0.000-0.692
Focal species MDS1	0.041 ± 0.132	-1.116-1.560
Focal species MDS2	-0.049 ± 0.079	-0.952-1.253
Shoot biomass (g•m^{-2})	313.0 ± 11.1	176.4-586.7
Litter biomass (g•m^{-2})	176.5 ± 10.3	11.02-419.62
Root biomass (g•m^{-2})	1366.8 ± 67.8	420.2-2826.6
Light availability	0.200 ± 0.017	0.039-0.512
Soil pH	6.234 ± 0.050	5.580-7.380
Soil inorganic nitrogen (μg/g)	8.250 ± 0.332	3.108-16.981
Soil moisture (%)	13.99 ± 0.381	7.90-20.35
Stem density (stems•m^{-2})	3549 ± 119	1600-5533

Appendix 5-S1. Average abundance, frequency, and trait values associated with the species found within the standing vegetation at the study site. Average abundance is measured as the mean percent cover. Frequency is measured as the ratio of study plots each species was found in (out of 16).

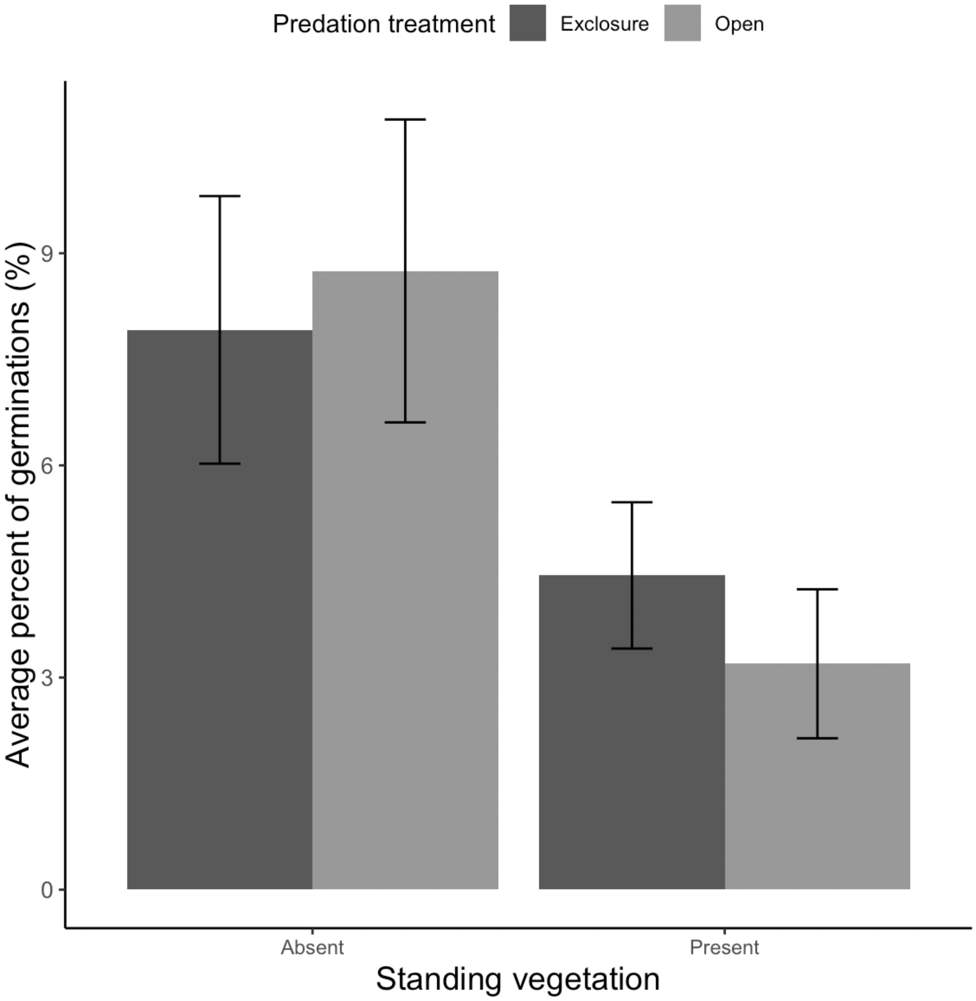
Family	**Species**	**Average Abundance**	**Frequency**	**Height**	**Width**	**SLA**	**SSD**
Poaceae	*Hesperostipa curtiseta* (Hitchc.) Barkworth	25.556	1.000	Y	Y	Y	Y
Poaceae	*Poa pratensis* L.	16.991	0.875	Y	Y	Y	Y
Cyperaceae	*Carex* spp.	13.888	1.000	N	N	N	N
Asteraceae	*Artemesia ludoviciana* Nutt.	5.389	0.625	Y	Y	Y	Y
Asteraceae	*Symphyotrichum falcatum* (L.) A. Love & D. Love	4.193	0.688	Y	Y	Y	Y
Rosaceae	*Rosa arkansana* Porter	3.577	0.688	Y	Y	Y	Y
Asteraceae	*Artemesia frigida* Willd.	2.883	0.313	Y	Y	Y	Y
Poaceae	*Koeleria macarantha* (Ledeb.) Schult.	2.506	0.438	Y	Y	Y	Y
Poaceae	*Festuca hallii* (Vasey) Piper	2.407	0.438	Y	Y	Y	Y
Poaceae	*Bouteloua gracilis* Willd. Ex Kunth	2.195	0.375	Y	Y	Y	N
Asteraceae	*Achillea millefolium* L.	1.971	0.563	Y	Y	Y	Y
Asteraceae	*Symphyotrichum leave* (L.) A. Love & D. Love	1.865	0.313	Y	Y	Y	Y
Rosaceae	*Geum triflorum* Pursh	1.566	0.250	Y	Y	Y	Y
Asteraceae	*Solidago missouriensis* Nutt.	1.401	0.500	Y	Y	Y	Y
Santalaceae	*Comandra umbellata* (L.) Nutt.	1.259	0.500	Y	Y	Y	Y
Caryophyllaceae	*Cerastium arvense* L.	1.224	0.375	Y	Y	Y	Y
Poaceae	*Elymus trachycaulus* Gould ex Shinners	1.211	0.313	Y	Y	Y	Y
Poaceae	*Agropyron dasystachyum* (Hook.) Scribn. & J.G. Sm.	1.186	0.438	Y	Y	N	N
Rubiaceae	*Galium boreale* L.	1.077	0.313	Y	Y	Y	Y
Poaceae	*Nassella viridula* (Trin.) Barkworth	0.833	0.063	Y	Y	Y	Y
Fabaceae	*Astragalus agrestis* Douglas ex G. Don	0.804	0.313	Y	Y	Y	Y
Poaceae	*Pascopyrum smithii* (Rydb.) A. Love	0.722	0.250	Y	Y	Y	N
Asteraceae	*Antennaria neglecta* Greene	0.530	0.063	Y	Y	Y	N

Rosaceae	*Potentilla hippiana* Lehm	0.458	0.125	Y	Y	N	N
Poaceae	*Agrostis scabra* Willd.	0.437	0.063	Y	Y	Y	Y
Ranunculaceae	*Pulsatilla patens* (L.) Mill.	0.437	0.063	Y	Y	Y	N
Asteraceae	*Taraxacum officinale* F.H. Wigg	0.380	0.313	Y	Y	Y	N
Asteraceae	*Antennaria parvifolia* Nutt.	0.354	0.125	Y	Y	Y	Y
Fabaceae	*Thermopsis rhombifolia* (Nutt. Ex Pursh) ex Richardson	0.333	0.063	Y	Y	Y	Y
Poaceae	*Danthonia intermedia* Vasey	0.321	0.063	Y	Y	Y	N
Scrophulariaceae	*Penstemon gracilis* Nutt.	0.263	0.125	Y	Y	Y	Y
Violaceae	*Viola adunca* Sm.	0.259	0.125	Y	Y	Y	Y
Rosaceae	*Potentilla concinna* Richardson	0.258	0.125	Y	Y	Y	Y
Poaceae	*Poa interior* Rybd.	0.250	0.125	Y	Y	Y	Y
Rosaceae	*Potentilla arguta* Pursh	0.219	0.063	Y	Y	Y	Y
Fabaceae	*Oxytropis campestris* (L.) DC.	0.131	0.063	Y	Y	Y	Y
Fabaceae	*Vicia americana* Muhl. Ex Willd.	0.131	0.063	Y	Y	Y	Y
Polygonaceae	*Fallopia convolvulus* (L.) A. lOVE	0.125	0.063	N	N	N	N
Asteraceae	*Erigeron caespitosus* Nutt.	0.123	0.063	Y	Y	Y	Y
Saxifragaceae	*Heuchera richardsonii* R. Br.	0.121	0.063	N	N	N	N
Asteraceae	*Tragopogon dubius* Scop.	0.078	0.125	Y	Y	Y	Y
Campanulaceae	*Campanula rotundifolia* L.	0.044	0.063	Y	Y	Y	Y
Brassicaceae	*Erysimum inconspicuum* (S. Watson) MacMill.	0.044	0.063	N	N	N	N

Appendix 5-S2. Effects of standing vegetation presence on seedbank seed density (left panels; mean ± SE) overtime without the outlier removed. Regression estimates and significance levels for each pairwise comparisons are shown in the upper right corner of each panel. Seedbank seed density was impacted by standing vegetation presence density ($F_{1,73.77}$= 5.754, p=0.019) but not time of year ($F_{1,73.77}$= 1.445, p=0.242); however, there was a significant interaction between standing vegetation presence and time of year ($F_{1,73.77}$= 2.504, p=0.089).



Appendix 5-S3. Effects of standing vegetation presence on germination percentage (mean ± SE) in each predation treatment. Germination based on the seeds added to the seedling establishment (open) and predation (exclosure) seed trays. Total number of seeds added was 45 seeds (5 seeds per 9 different species (see Table 1 for list of species).



Appendix 5-S4. relationships between seedbank processes and standing vegetation community and trait composition. Composition values represent the axes loadings from NMDS axis 2 (see Table 2 for relationships with loadings from NMDS axis 1). SLA is the specific leaf area. SSD is the specific stem density.

		Predictors									
Process	df	Community composition		Height composition		Plant width composition		SLA composition		SSD composition	
		X^2/F	p	X^2/F	p	X^2/F	p	X^2/F	p	X^2/F	p
Germination	1	0.495	0.482	0.538	0.463	1.107	0.293	1.445	0.229	0.821	0.365
Predation	1,14	0.003	0.956	0.200	0.662	1.625	0.223	0.532	0.478	0.566	0.464
Net inputs	1	70.042	**<0.001**	59.989	**<0.001**	14.770	**<0.001**	8.748	0.003	14.489	**<0.001**

Appendix 5-S5. Non-metric multidimensional scaling ordinations of community trait values. Points represent abundance weighted trait values. SLA is the specific leaf area. SSD is the specific stem density. Traits were measured using the methods outlined in Cornelissen et al. (2003) and Perez-Harguindeguy et al. (2013). The mean of each trait was calculated for species present in the plot and did not include absent species (i.e. zeros).