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Research article

Niche partitioning overrides interspecific competition to determine plant species distributions along a nutrient gradient

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Changes in some combination of niche availability, niche overlap and the strength of interspecific interactions are thought to drive changes in plant composition along resource gradients. However, because these processes are difficult to measure in the field, their relative importance in driving compositional change in plant communities remains unclear. In an Australian temperate grassland, we added seeds of three native and three exotic grasses to 1875 experimental plots in a way that allowed us to simultaneously estimate niche availability, niche overlap and the strength of pairwise interspecific interactions along a gradient of nutrient availability, obtained by adding 0, 5 or 20 g m⁻² each of nitrogen, phosphorous and potassium jointly to plots. Niche availability (the proportion of microsites suitable for establishment and growth) was generally low and did not vary in response to nutrient addition. Most species co-occurred along the nutrient gradient by partitioning the available niche space. Where species interacted due to niche overlap, the abundance of one species, the native *Chloris truncata*, was usually facilitated by other species, with each of the five other species increasing the niche availability to *C. truncata* under at least one nutrient treatment. *Chloris truncata* also competitively excluded two species from some but not all sites they could otherwise have occupied. These outcomes did not clearly differ across nutrient treatments. Our results show that fine-scale spatial heterogeneity in establishment microsites can enable species to co-occur via niche partitioning, and competitive exclusion is rare. This finding contributes to an emerging picture that niche partitioning is common and frequently a stronger influence on recruitment outcomes than interspecific competition. The importance of competition in structuring plant communities may be overestimated if recruitment processes are overlooked.

Keywords: coexistence, competition, environmental heterogeneity, facilitation, intraspecific variation, invasion, seed addition

Introduction

Plant species composition typically changes along resource gradients (Callaway et al. 2002, Harpole and Tilman 2007, Mudrák et al. 2016). For example, species richness often declines at sites with elevated resources, such as those that are well-watered with high nutrient availability (Hautier et al. 2009, Harpole et al. 2016). Most models proposed to explain such compositional shifts involve some combination of changes in niche availability, niche overlap and the relative competitive performance of plant species (Chesson 1994, Chase and Leibold 2003). At heterogeneous low resource sites, multiple resources (such as soil moisture and different soil nutrients) may act to limit plant performance and allow species to co-occur either because species partition niche space, or because each species has a competitive advantage in some portion of shared niche space. At high resource sites, the niche space effectively collapses because, with most resources being abundant, species compete for just one or a few key limiting resources. However, few studies have managed to simultaneously quantify changes in niche availability, niche overlap and competitive performance along resource gradients and thus identify their relative contribution to species turnover. Instead, studies often focus solely on changes in the importance or intensity of competition along resource gradients (Kunstler et al. 2011, Maalouf et al. 2012).

There are several ways in which changes in niche availability, niche overlap and relative competitive performance along resource gradients could combine to generate compositional changes (Grime 1973, Tilman 1982). Focusing on changes in a single component could highlight the effect of that component, but underplay the importance of the other two. For example, the intensity of competition experienced by a target species could increase along a resource gradient if more individuals of a superior competitor were present at high resource sites and there was an increase in niche overlap between the target and competitor species, without any change in per capita strength of competition (Rees 2013, Wandrag et al. 2019). Studies that only measured per capita competition effects, including most glasshouse studies, would miss this. Alternatively, per capita strength of competition could increase along resource gradients and thus be detected in glasshouse competition studies. But if species partition niches and there is no change in niche overlap along the gradient, glasshouse competition studies may have little relevance to field situations where heterogeneity in establishment sites promote niche partitioning (Wandrag et al. 2019, Griffith et al. 2021).

Difficulties in isolating the drivers of compositional variation are compounded in situations where facilitation rather than competition more strongly affects species composition. Interspecific interactions are often facilitative under conditions of low resource or high stress (i.e. the stress gradient hypothesis; Bertness and Callaway 1994), with interactions shifting to more competitive at higher resource or lower stress levels. Additionally, there are examples of facilitation occurring under conditions of low stress or high resource

availability, with interactions between the same species pairs shifting from facilitative to competitive over time and across quite fine spatial scales (Liancourt et al. 2017, Klanderud et al. 2021, Wang and Callaway 2021). Most models of compositional change do not account for potential shifts in the direction as well as the strength of species interactions (Bimler et al. 2018, Wandrag et al. 2019).

Globally, the invasion of exotic pasture grasses into native grasslands exemplifies the need to understand the drivers of compositional change. Human activities such as livestock grazing and nutrient addition have altered grasslands in ways that favour dominance by exotic grass species (McIntyre and Lavorel 1994, Seabloom et al. 2015). Nevertheless, it is unclear whether exotic species dominate grasslands by competitively displacing native species at disturbed, high resource sites (O'Reilly-Nugent et al. 2020), or because those sites are better suited to exotic establishment and growth independent of competitive outcomes (Seabloom et al. 2003, HilleRisLambers et al. 2010). The potential for native species to facilitate the establishment of exotic species is only recently gaining attention (Lucero et al. 2019, Cavieres 2021, Lortie et al. 2021).

Wandrag et al. (2019) outlined a conceptual model aimed at quantifying niche availability, niche overlap and the relative competitive performance of plant species. By conceptualising the niche in terms of establishment microsites that are either safe or not for seedling recruitment, they showed how data obtained from seed addition experiments can be used to estimate safe-site availability with or without competitors, and how the parameters of models fitted to the data can be interpreted in terms of niche availability, niche overlap and species' relative competitive performance, as well as the strength of facilitation. Here, we use this model to understand the role of niche availability, niche overlap and interspecific interactions in driving compositional change in Australian temperate grasslands that have undergone a shift towards exotic dominance, particularly in locations with high nutrient availability (Morgan 1999, O'Reilly-Nugent et al. 2020). As with other grasslands globally, the role of interspecific interactions relative to differences in niche requirements in driving patterns of exotic dominance remains unclear, such that models that more clearly distinguish between niche requirements and interspecific interactions are needed. Using a combination of three common native grass species and three exotic grass species that vary in dominance, we carried out a seed addition experiment to test three predictions made by current conceptual models regarding how niche availability, niche overlap and the strength and direction of interspecific interactions vary along a nutrient gradient to determine patterns of compositional change, focusing on the recruitment of species from seed:

- 1) Niche availability will increase with increasing nutrient addition for all species because species should encounter more microsites that are suitable for recruitment at high relative to low nutrient sites.
- 2) Niche overlap between co-occurring species will increase with increasing nutrient addition because more microsites

will satisfy the nutrient requirements for a greater range of species at high relative to low nutrient sites.

- 3) The nature of interspecific interactions will shift along the nutrient gradient. Specifically, facilitation will be more common at low nutrient levels with competition becoming more important as nutrient levels increase.

Methods

We carried out a seed addition experiment in an area of grassland on the Univ. of Canberra campus, Australian Capital Territory during Austral summer 2016/2017. The site is characterised by generally dry, shallow and nutrient poor soils (Wandrag et al. 2019).

Species selection

We selected three native (*Bothriochloa macra*, *Chloris truncata* and *Rytidosperma caespitosum*) and three exotic (*Dactylis glomerata*, *Eragrostis curvula*, *Phalaris aquatica*) species that are common in grasslands around our study site. The species comprised a mix of C3 and C4 grasses, with C3 and C4 grasses thought to show differences in their ability to compete for shared resources at high and low levels of nutrient availability, respectively (Badgery et al. 2005). The three native species (the C4 *B. macra* and *C. truncata* and the C3 *R. caespitosum*) all co-occur at our site and more generally in temperate grasslands in Australia. Of the exotic grass species, *E. curvula* (a C4 grass) is often associated with disturbed ground and was common around the study site, while *D. glomerata* and *P. aquatica*, both common (C3) pasture grasses, were not present at our site but are locally common in the grassland around our study site. Where present, *D. glomerata* and *P. aquatica* are generally associated with high moisture and nutrient availability and hence represent the C3 pasture grasses typically associated with shifts towards exotic dominance as nutrient availability increases.

Experimental design

Before the start of the experiments, we fenced a 41 × 21 m area of grassland to prevent human disturbance and kangaroo grazing. We removed existing vegetation by applying glyphosate weedkiller and raking to remove dead material. We repeated this procedure several times before the start of the experiment to deplete the seedbank as much as possible. This ensured that light was not initially limiting for establishing seedlings and any competition for light arose only due to the competitive effects of the focal species. Within the fenced area we marked out 2160 plots, each of 0.3 × 0.3 m, with a buffer between each plot of at least 0.1 m. Plots were arranged in 30 blocks, corresponding to ten replicate rows of three blocks, with one block per replicate assigned one of each of three nutrient treatments (below; the blocked design was intended to reduce nutrient contamination among plots receiving different treatments). Blocks were separated by a 1.5 m walkway on all sides and consisted of 72 plots arranged

in six rows of 12 plots, with a 0.5 m walkway after every second row (Supporting information).

Two weeks before seed addition, we applied one of three nutrient treatments to a randomly assigned block within each replicate row: no nutrient addition (0 g m⁻²), 5 g m⁻² and 20 g m⁻² of each of nitrogen (N, applied as slow release urea), phosphorous (P, applied as triple-super-phosphate) and potassium (K, applied as 0-0-41-18 potassium sulphate). We chose these nutrient addition levels to correspond to half and double the levels added by the global NutNet experiment (<www.nutnet.org>), since this has revealed a strong influence of nutrient addition on interspecific interactions among grasses, including those in Australia (Morgan et al. 2016).

To confirm differences in soil nutrient content across each of our three treatments, we took soils samples at the time of seed addition. Using a soil corer, we sampled soil from buffer zones around plot-edges. We collected a total of nine soil cores per nutrient treatment per replicate for nine out of the ten total replicates (total of 243 soil cores), collecting samples to a depth of 5–10 cm (where possible, soils were often shallow). To reduce the cost of testing, we homogenized soil samples in groups of three (replicates 1–3, 4–6 and 7–9 were homogenised) to give one sample per nutrient treatment per replicate group of three (a total of nine soil samples). From each of the nine homogenized samples, we took three subsamples for analysis. Samples were placed in ziplocked sandwich bags and shipped on the same day to APAL Agricultural Laboratories in Adelaide where Colwell P, nitrate, ammonia and Colwell K tests were performed.

The recruitment model described in Wandrag et al. (2019) estimates safe-sites and hence niche availability for individual species by fitting Eq. 1 to data on the number of recruits arising from a given level of seed addition. To allow us to estimate niche availability for each of our target species, we added seeds of each species in monoculture to plots at one of six densities: 50, 250, 500, 750, 1250 and 2500 (corresponding to 556, 2778, 5555, 8333, 13 888 and 27 775 seeds per m², respectively). Seed densities were chosen based on an earlier experiment, which suggested that 2500 seeds were enough to saturate microsites within each plot (Wandrag et al. 2019). We replicated each species × density × nutrient combination ten times, such that each of the thirty blocks contained one of each species × density combination.

Wandrag et al. (2019) show how estimates of niche overlap and the strength and direction of interspecific interactions can be obtained by adding seeds of two species to a single plot (polyculture plots). Adding seeds of two species at densities sufficient to saturate the safe-sites for each species means that seeds must compete for occupancy of any safe-sites suitable for the recruitment of both species. It also means that safe-site availability for one species can be increased by a second species if interactions are facilitative. Consequently, we added seeds of each pairwise combination of our six species to plots at the highest seed density (2500 seeds). We replicated each species combination × nutrient treatment 20 times, such that each of the 30 blocks contained two of each pairwise species combination.

Our design resulted in a total of 66 plots per block receiving a seed addition treatment, and six empty plots within each block. For the exotic *Eragrostis curvula* we did not have enough seed for all 20 replicates of each pairwise species combination \times nutrient treatment. Thus, we randomly removed from the experiment seven of the 20 replicates of each pairwise combination involving *E. curvula*, which resulted in an additional 105 empty plots across the experiment (5 species combinations \times 3 nutrient treatments \times 7 replicates).

To reduce the potential for moisture availability, rather than nutrient availability, to influence any variation in recruitment success, we watered the plots at the time of seed addition and regularly throughout the experiment, ensuring that plots remained moist. We added seeds in December 2016. Since our model focuses on initial recruitment from seed, we counted the number of recruits once all species had started to or were flowering (three months later).

Analysis

For a single species, i , Eq. 1 quantifies the relationship between the number of seeds (s_i) added and the number of plants that recruit (r_i) in terms of the availability of establishment microsites, assuming that seeds are randomly dispersed in a plot (Duncan et al. 2009):

$$r_i = b_i n_i (1 - e^{-s_i/n_i}) \quad (1)$$

where n_i is the number of microsites in a plot of sufficient size to support a single plant, and b_i is the proportion of those microsites that are safe-sites and provide the conditions necessary for successful recruitment. The parameter $b_i n_i$ is the asymptotic number of safe-sites available to be occupied in a plot. Both $b_i n_i$ and b_i estimate a species' fundamental niche space: $b_i n_i$ equals the asymptotic number of recruits and hence describes the maximum abundance of each species per plot, while b_i describes the proportion of all microsites that are safe for each species and thus measures the area of fundamental niche space in a given location (Wandrag et al. 2019).

For two species, i and j , we can estimate the parameter b_i by adding seeds of species i to plots in monoculture, and the parameter b_{ij} (the proportion of microsites that species i occupies in the presence of species j) by adding seeds of both species to a plot in polyculture. We can then estimate the strength and direction of interspecific interactions by calculating the ratio:

$$d_{ij} = (b_i - b_{ij}) / b_i \quad (2)$$

which is the proportion of microsites that are safe for species i but captured by species j when the seeds of two species are at saturation. The parameter d_{ij} can be interpreted as a measure of the degree to which species show niche overlap, and the potential impact of one species on another. For example, a positive value of d_{ij} would imply the competitive

exclusion of species i by species j over some of the niche space the two species share, while a negative value of d_{ij} would imply the facilitation of species i by species j (species j increases safe-site availability and hence niche space for species i). Values of d_{ij} that do not differ from zero suggest complete niche differentiation (species occupy entirely different safe-sites).

Model fitting

We fitted Eq. 1 to data on the number of recruits recorded at each seed addition density, under each of the three nutrient treatments, doing so for both monoculture (all seed densities) and polyculture (highest seed density only) plots. Following Wandrag et al. (2019), we modelled variation in the observed number of recruits, r_{ik} , of species i in plot k , using a negative binomial distribution:

$$r_{ik} \sim \text{NegBinom}(\mu_{ik}, \lambda_i)$$

$$\mu_{ik} = b_{ik} n_i (1 - e^{-s_{ik}/n_i})$$

where μ_{ik} is the mean number of recruits of species i in plot k , and λ_i is a dispersion parameter that measures the degree to which plots had more or fewer recruits than expected. Smaller values of λ_i imply greater unexplained variation among plots in the number of recruits, which would imply there is some unexplained factor(s) causing spatial aggregation of safe-sites such that some plots had more and others fewer safe-sites than expected.

Estimating b_i (the proportion of safe-sites in monoculture, a measure of fundamental niche space) and b_{ij} (the proportion of safe-sites in polyculture, a measure of the proportion of microsites that species i occupies in the presence of species j) allows us to estimate d_{ij} (the strength and direction of interspecific interactions), and how each of these parameters varied across our nutrient gradient.

To identify changes in niche availability and overlap in relation to nutrient addition, we estimated b_i by modelling the proportion of microsites that were safe-sites for species i in plot k at a given nutrient level l , b_{ikl} :

$$\text{logit}(b_{ikl}) = \alpha_{il}$$

where α_{il} is an estimate on the logit scale of b_i for a given nutrient treatment, l .

We then estimated b_{ijkl} by modelling the change in safe-site availability for species i in the presence of species j under a given nutrient treatment, l :

$$\text{logit}(b_{ijkl}) = \alpha_{il} + \gamma_{ijl}$$

where γ_{ijl} is the difference between b_{il} and b_{ijl} (an estimate of b_{ij} for a given nutrient treatment, on the logit scale).

We fitted models in a Bayesian framework using the software JAGS ver. 4.2.0 (Plummer 2003), which we ran using the package jagsUI (Kellner 2015) in R ver. 4.0.5 (<www.r-project.org>). We modelled each of the parameters describing the proportion of safe-sites (α_p , γ_{ij}), safe-site aggregation (λ) and the total number of microsites (n) hierarchically. Modelling data hierarchically allows us to use the information present in data for all species and helps regularise the estimates and prevent them from becoming unreasonably large or small on the logit (α_i and γ_{ij}) or log (λ and n) scale. To then estimate a mean value for each parameter, for each species, under each nutrient treatment, we modelled those means as coming from a normal distribution that had a different mean for each species and variance described by a non-informative uniform prior (0–10) on the standard deviation. The means of the normal distribution for each species were in turn drawn from a normal distribution that had an overall mean taken from a normal distribution with mean zero for parameters b_p , b_{ij} and λ and five for n , and variance 10, with variance described by a non-informative uniform prior (0–10) on the standard deviation. We used median values for

the point estimates of the posterior distributions of all parameter estimates to characterize central tendency.

Results

For all six species, the number of individuals recruiting into plots reached an asymptote at high seed densities under each of three nutrient treatments (Fig. 1). This indicated that seed supply exceeded the availability of safe-sites so that individuals of the same species must compete for occupation of safe-sites. Although we frequently recorded three species in plots other than those to which they were added as seed (the native *C. truncata* and the two exotic species *D. glomerata* and *P. aquatica*; Supporting information), this did not appear to influence overall recruitment outcomes for any species (Supporting information) and we did not consider these contaminant species further. For *C. truncata*, between-plot movement was largely due to stoloniferous spread into empty plots and areas of bare ground. In contrast, the movement of *D. glomerata* and *P. aquatica* was most likely due to the

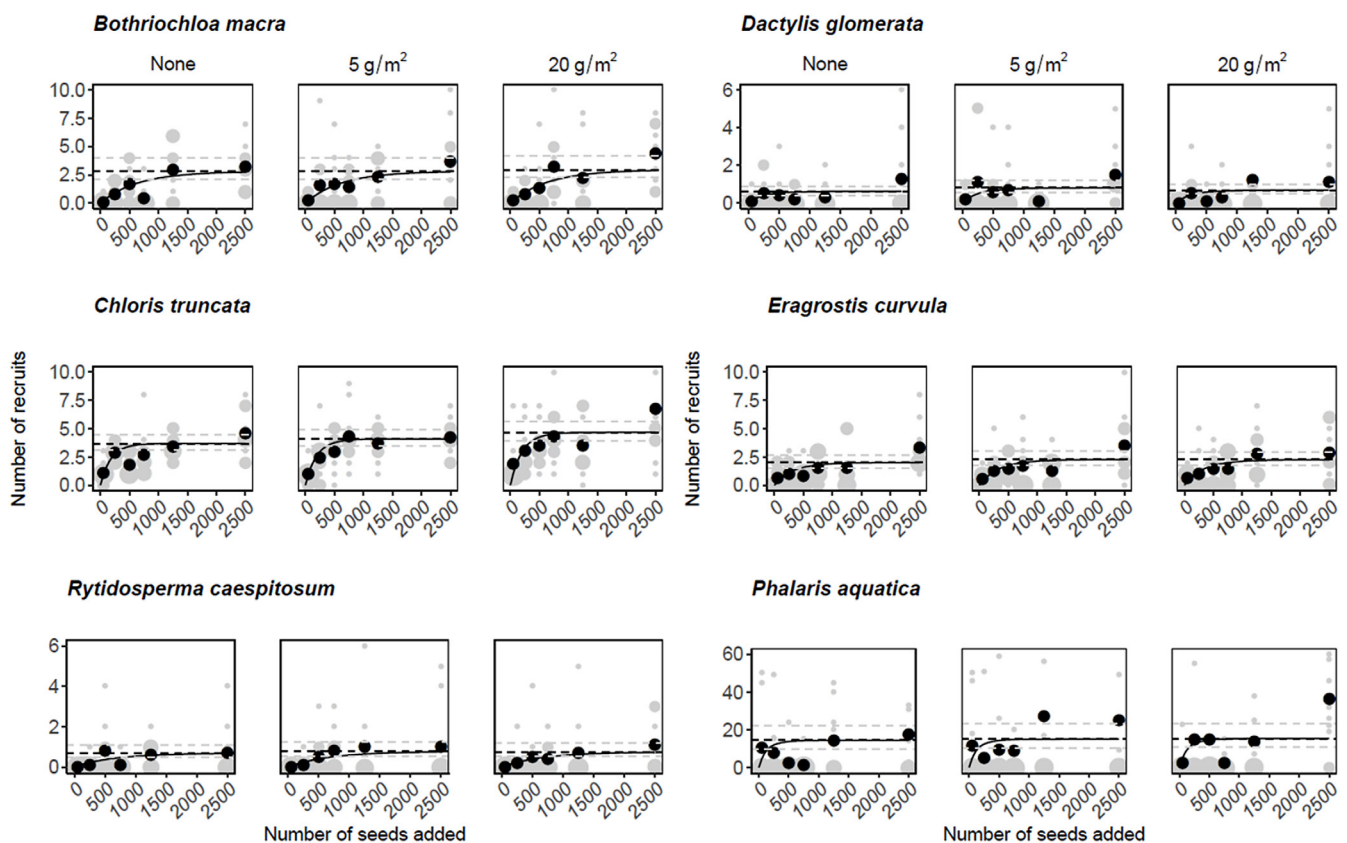


Figure 1. Fitted recruitment curves (black solid lines) for each of six species under each of three nutrient treatments (no nutrient addition and either 5 or 20 g m⁻² of each of nitrogen, phosphorous and potassium; note the y-axes vary among species). Dashed horizontal lines indicate safe-site saturation (bn ; a measure of fundamental niche availability) when species were added in monoculture (black dashed lines show median, grey dashed lines show the 95% credible intervals). Black circles show the mean number of (observed) recruits for each level of seed addition, grey circles show the raw data for the number of recruits per plot, with circle size proportional to the number of plots represented. Outliers in the raw data (grey points) have been omitted for *Chloris truncata*, *Dactylis glomerata* and *Phalaris aquatica* (though not from the analysis).

selective removal by ants of seeds of these species and subsequent seed germination in ant nests, which we observed following seed addition.

Prediction 1. Fundamental niche space will increase across the gradient

The method provides two estimates of fundamental niche availability. The parameter b_i (Fig. 2) is the proportion of microsites that are safe for each species and equates to the area of fundamental niche space for each species, while the parameter $b_i n_i$ (Fig. 1) estimates the total number of safe-sites and equates to the asymptotic number of recruits for each species.

Despite strong differences among our treatment blocks in soil nutrient content (Table 1), niche availability did not clearly change across the nutrient treatments for any species (Fig. 1, 2). Nonetheless, there were differences among species in both overall niche availability and the extent to which niche availability varied across our experimental plots. Although overall niche availability was highest for the exotic *Phalaris aquatica* at around 10% (Fig. 2), the wide credible intervals and low value of the dispersion parameter (λ ; Fig. 3) indicated high spatial variation in niche availability for this species, consistent with the observation that it failed to recruit in many plots to which it was added as seed

(Fig. 1: large number of raw data points on zero). In contrast, although overall niche availability was lower for the native *Chloris truncata* at around 2% (Fig. 2), the high dispersion parameter (Fig. 3) indicated low spatial variation in niche availability, such that this species showed more consistent levels of recruitment across experimental plots. Between 0.1 and 0.7% of microsites were safe for the other species.

Predictions 2 and 3. with increasing niche availability, niche overlap will increase and interspecific interactions will shift towards competitive exclusion under high nutrients

There was only limited support for our second prediction, that niche overlap would increase across the nutrient gradient. When seeds were added together at saturating seed densities, estimates of d (a measure of niche overlap) for the majority of pairwise interactions were close to zero or had credible intervals crossing zero, suggesting that strong niche differentiation among species was common across all three nutrient levels (Fig. 3).

Support for our third prediction – that increasing niche overlap will lead to increased competitive exclusion of some species under high nutrients – was also limited. Where we did find evidence of increasing niche overlap and competitive exclusion, the native *Chloris truncata* was always the dominant

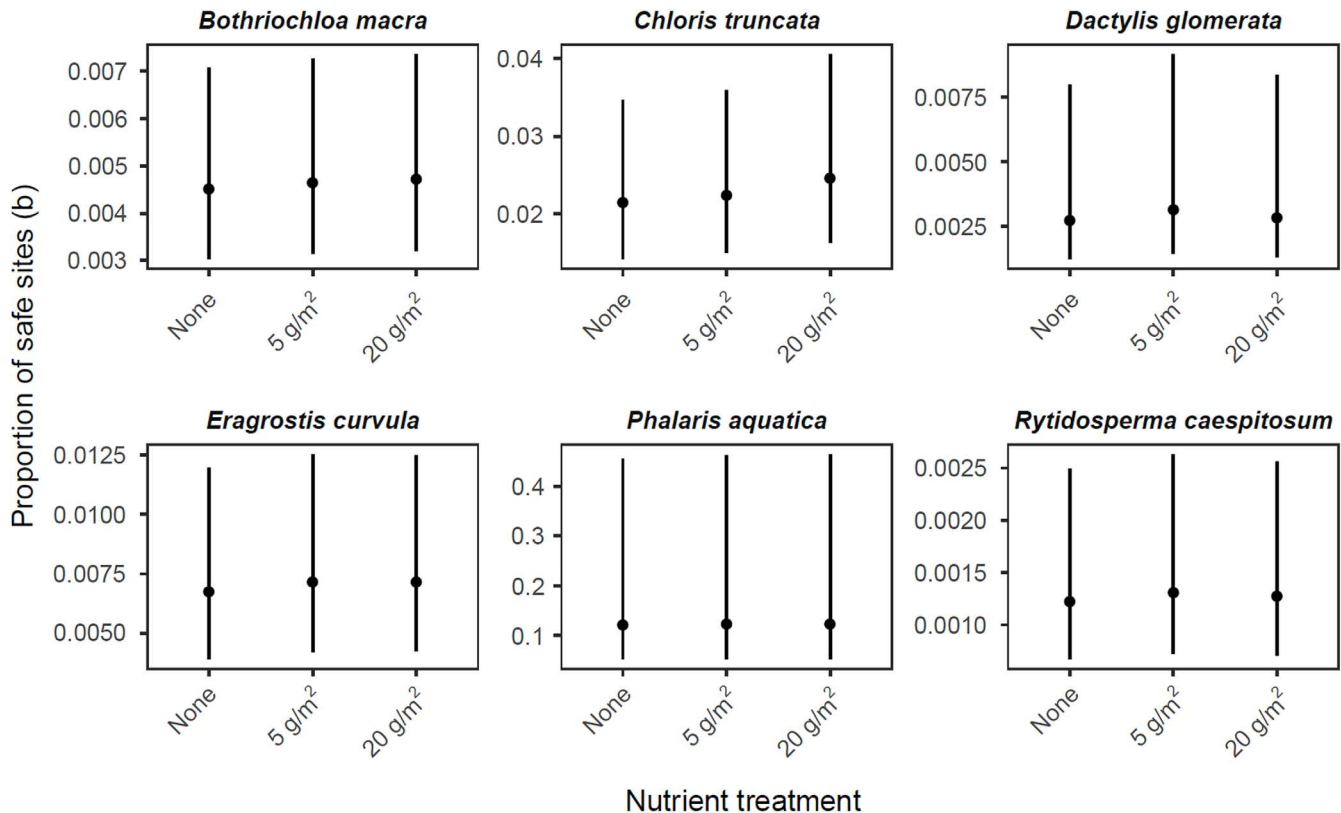


Figure 2. The proportion of microsites that are safe for the recruitment for each of the six target species (b_i ; a measure of fundamental niche availability) at each of three levels of addition of N, P and K. Points represent medians and bars represent 95% credible intervals. Note the different scales on the y axes.

Table 1. Soil nutrient status of treatment blocks after experimental nutrient addition but before seed addition. Errors represent 95% confidence intervals.

Treatment	Ammonium (mg kg ⁻¹)	Nitrate (mg kg ⁻¹)	Phosphorous (mg kg ⁻¹)	Potassium (mg kg ⁻¹)
No addition	17.10 ± 2.89	155.36 ± 9.94	41.33 ± 8.51	387.44 ± 13.60
5 g m ⁻²	70.51 ± 8.48	173.23 ± 21.00	101.11 ± 16.70	429.78 ± 9.96
20 g m ⁻²	215.70 ± 41.6	236.47 ± 21.40	256.11 ± 50.4	680.00 ± 81.8

competitor. *Chloris truncata* showed clear niche overlap with two of the five other species: the native *Bothriochloa macra* and exotic *Eragrostis curvula*.

Interactions between *C. truncata* and *B. macra* matched our prediction that niche overlap and hence competitive exclusion should increase with increasing nutrient availability. Estimates of d under the no nutrient addition treatment were around zero, suggesting no niche overlap, but increased with increasing nutrient addition so that *C. truncata* occupied around 50 and 70% of fundamental niche space available to *B. macra* at low and high nutrient addition, respectively. The decrease in niche space available to *B. macra* corresponded to a reduction from a mean of 2.7 recruits per plot to around 1.3 under the low nutrient treatment, and from 2.9 recruits per plot to around 0.8 under the high nutrient treatment. For the exotic *Eragrostis curvula*, there was no clear pattern in relation to nutrient treatment. *Chloris truncata* occupied nearly 50% of fundamental niche space available to *E. curvula* under the no and high nutrient addition treatment, corresponding to a reduction from around two recruits per plot to one recruit in both no and high addition treatments.

The native *C. truncata* was the only species that experienced facilitation. Although there were no clear patterns relating to nutrient availability, the addition of each of the five other species increased niche availability in at least one of the nutrient treatments, with *B. macra* increasing safe-site availability for *C. truncata* by up to 50% in the low nutrient addition treatment.

Discussion

Although most models of compositional change along resource gradients invoke inter-specific competition as a key driver of change, difficulties obtaining separate estimates of niche availability, niche overlap and the relative competitive performance of plant species mean that explicit tests of the full set of drivers are rare. We used a modelling approach that provided separate estimates of niche availability, niche overlap and the relative competitive performance of plant species using data from a seed addition experiment and tested three predictions regarding how these factors should vary in importance along a nutrient gradient. We found that both niche availability and interspecific interactions were highly idiosyncratic among species and across treatments in our study grassland. While niche overlap and subsequent competitive displacement of inferior competitors is predicted to increase with increasing nutrient addition, this was the case for only one of the fifteen pairwise interactions we examined: the native *Chloris truncata* increasingly excluded the native *Bothriochloa macra* from shared niche space as nutrients increased. Instead, our results are consistent with recent experimental work that has failed to find any consistent patterns regarding shifts in niche availability and interspecific interactions across resource gradients (Bimler et al. 2018, Wainwright et al. 2019, O'Reilly-Nugent et al. 2020). This finding supports increasing evidence that fine-scale heterogeneity can allow most species to co-occur (Mudrák et al. 2016, Tamme et al. 2016, Griffith et al. 2021), and that the

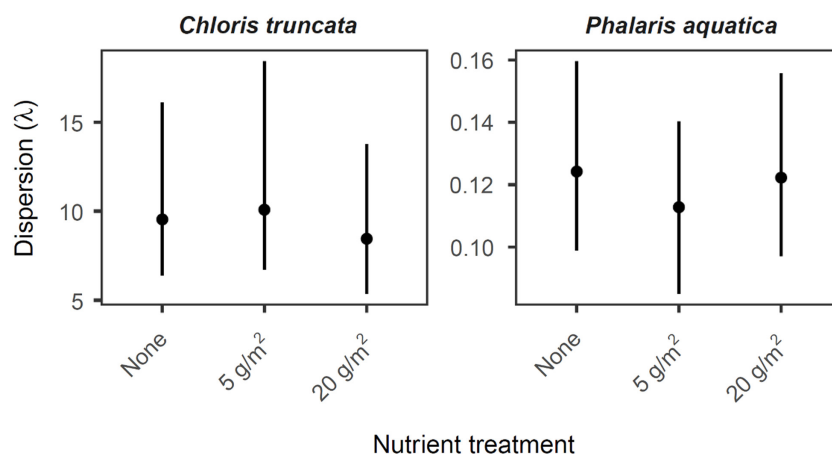


Figure 3. The dispersion parameter (λ , a measure of the spatial aggregation of safe sites) at each of three levels of addition of N, P and K for two species that show contrasting distribution patterns across experimental plots. Lower values indicate higher aggregation of safe sites. Points represent median values and bars the 95% credible intervals. Note the different scales on the y-axes.

importance of competition in structuring plant communities may have been overestimated (Simha et al. 2022).

Prediction 1. Fundamental niche space will increase across the gradient

In contrast to the prediction that niche availability in the absence of competition would increase with increasing nutrient addition, niche availability was constant for all six species across our soil nutrient gradient. Our data suggest that niche availability was low for four out of our six species (*Bothriochloa macra*, *Dactylis glomerata*, *Eragrostis curvula* and *Rytidosperma caespitosum*) relative to the remaining two species (*Chloris truncata* and *Phalaris aquatica*). Estimates of b , a measure of fundamental niche space, for those four species were only between 1 and 30% of estimates for *C. truncata* and *P. aquatica*. For two species, niche estimates were also lower relative to a similar experiment the previous year (Wandrag et al. 2019). Niche availability in 2017 was only around 20 and 25% of that recorded in 2016 for *D. glomerata* and *R. caespitosum*, respectively, a difference which could arise due either to spatial or temporal variation in biotic and abiotic constraints on recruitment (Bakker et al. 2003, Groves and Brudvig 2019). That recruitment of all species reached an asymptote indicates that all safe-sites were occupied, and individuals of the same species must compete for occupation of the same safe-sites. Intraspecific competition for limited niche space was hence the main determinant of species abundance across our gradient.

It is unlikely that the limited niche space across our gradient was due to low soil nutrient content, especially under our high nutrient addition treatment. The levels of nitrogen, phosphorous and potassium we recorded pre-treatment (Table 1) were low relative to many grasslands worldwide. For example, phosphorus values as high as 227.6 mg kg⁻¹ and potassium levels in the range 30–748 mg kg⁻¹ have been recorded in North America (Fay et al. 2015). However, nutrient addition significantly increased as nutrients were added (Table 1) and reached levels comparable to and beyond those recorded globally, and beyond those usually encountered in Australian soils. Nitrate values of around 19 mg kg⁻¹ (Gibson-Roy et al. 2009) and phosphorus and potassium values in the range 9.3–44.0 mg kg⁻¹ and 76–456 mg kg⁻¹, respectively (Fay et al. 2015), have been recorded in other Australian grasslands. Nutrient differences across our treatments were still evident at the time of data collection (Supporting information). Further, increased nutrients led to increased niche overlap and competitive interactions for two out of our six species (*Chloris truncata* and *Bothriochloa macra*), as well as increases in the height of those species (Supporting information), suggesting that our treatments were effective in altering nutrient availability and promoting plant growth across plots. Instead, the consistently low niche space suggests that other factors overrode nutrients to constrain niche availability across our gradient.

Other factors that could have constrained niche availability at our site include generally shallow soils and additional

biotic constraints, such as predation or contamination due to the spreading into experimental plots of species from neighbouring plots. Shallow soils can affect species recruitment by, for example, limiting soil water retention and plant rooting depth (MacDougall and Turkington 2005). Nonetheless, while shallow, soils at our site are characteristic of the local area and soil depth was within the range recorded in other Australian grasslands in which these species are known to occur (Morgan 1999, Griffin and Hoffmann 2012). However, both plot contamination from neighbouring plots and the removal of seeds by seed predators was common, particularly for two of the three exotic species. We found no evidence that plot contamination affected recruitment outcomes (Supporting information), possibly due to strong niche differentiation among our species. We did observe ants removing seeds during our experiment, and a separate experiment in the same grassland confirmed the preferential removal of exotic grass seeds by ant seed predators (Wandrag et al. 2021). High rates of seed predation will strongly limit plant recruitment (Hulme 1994) and are common in grasslands globally (Turnbull et al. 2000). The generally low recruitment across our gradient may reflect biotic constraints due to seed predation, limiting our ability to detect species' responses to our nutrient gradient, but reflecting constraints on recruitment in real systems.

Overall seed recruitment was low relative to the numbers of seeds added, supporting work in other systems that micro-site limitation, not only seed limitation, is major constraint on seedling recruitment (Turnbull et al. 2000, Graae et al. 2011). Expressing the recruitment rates we recorded per m² equates to nearly 8 individuals per m² under no nutrient addition for *Rytidosperma caespitosum*, the species with the lowest recruitment rates, and nearly 200 individuals per m² for *P. aquatica*, the species with the highest recruitment rates. Such low rates of recruitment are comparable with or even higher than grass recruitment in other locations. For example, Dybzinski and Tilman (2012) recorded less than 0.001 individuals of C4 grasses per m² under ambient conditions in a North American grassland, while Edwards and Crawley (1999) recorded between 18.1 and 118.1 grass seedlings per m² recruited into grassland in the UK. That adding nutrients did not increase niche availability and hence recruitment for our six species highlights the difficulty in a priori identifying the relevant niche axes along which species may be competing for resources (Wandrag et al. 2019). Fine-scale heterogeneity appears to be crucial in driving patterns of recruitment and co-occurrence under even apparently homogenous conditions.

Predictions 2 and 3. With increasing niche availability, niche overlap will increase and interspecific interactions will shift towards competitive exclusion under high nutrients

Out of fifteen pairwise interactions, only one pair supported the prediction that niche overlap and competitive exclusion would increase with increasing nutrient availability. While

niche availability in monoculture remained constant for both *Bothriochloa macra* and *Chloris truncata* across the nutrient gradient, in polyculture the two species showed increasing niche overlap with increasing nutrients. At high nutrient addition, *B. macra* was excluded from 70% of niche space it could otherwise have occupied, which led to a mean recruitment rate of less than one individual per plot. Two aspects of our results explain this outcome. First, early facilitation of *C. truncata* by *B. macra* under all nutrient treatments (Fig. 4) expanded the niche space available to *C. truncata* leading to niche overlap. Second, in this expanded niche space, the per capita strength of interspecific competition increased with increasing nutrient addition. An increase in the per capita strength of interspecific competition could have arisen through an increase in the size of individuals. Larger individuals are better able to pre-empt light or space, thereby increasing their competitive impact on co-occurring individuals. In our experiment, both species, especially *C. truncata*, increased in height with increasing nutrients (Supporting information), potentially allowing *C. truncata* to pre-empt light or space that would otherwise be available to *B. macra*. Priority effects and temporal variation in the performance of competitors have been invoked as mechanisms promoting coexistence (Simha et al. 2022), but our results indicate that increasing niche overlap through time can shift the balance of competition in favour of a dominant competitor even in situations where a competitive subordinate has established.

The overwhelming outcome was that plant species co-occurred by partitioning niche space. Across all combinations of species and nutrient levels (45 in total), we found only four instances of interspecific competition limiting plant recruitment, with the exotic *Eragrostis curvula* also excluded by *Chloris truncata* under two of three nutrient treatments. Many examples of the competitive displacement of plant species involve just one or a few competitively dominant species that disproportionately influence the composition of plant communities. For example, in a nearby temperate grassland, joint-species modelling revealed that most plant species had little or no effect on each other, with only three of the 72 species analysed appearing to competitively displace co-occurring species (O'Reilly-Nugent et al. 2020). Even where there is a clear competitive dominant, species can often persist in a portion of their niche space unoccupied by the competitor, with the niche space often partitioned at a fine spatial scale (Wandrag et al. 2019, O'Reilly-Nugent et al. 2020). Since species need only differ in their ecological requirements over some portion of niche space to coexist (Simha et al. 2022), fine-scale heterogeneity in niche availability may be more important in influencing plant community composition than currently recognised.

The role of interspecific interactions in invasions

Exotic C3 pasture grass species often respond positively to the addition of nutrients and water, which is thought to give them

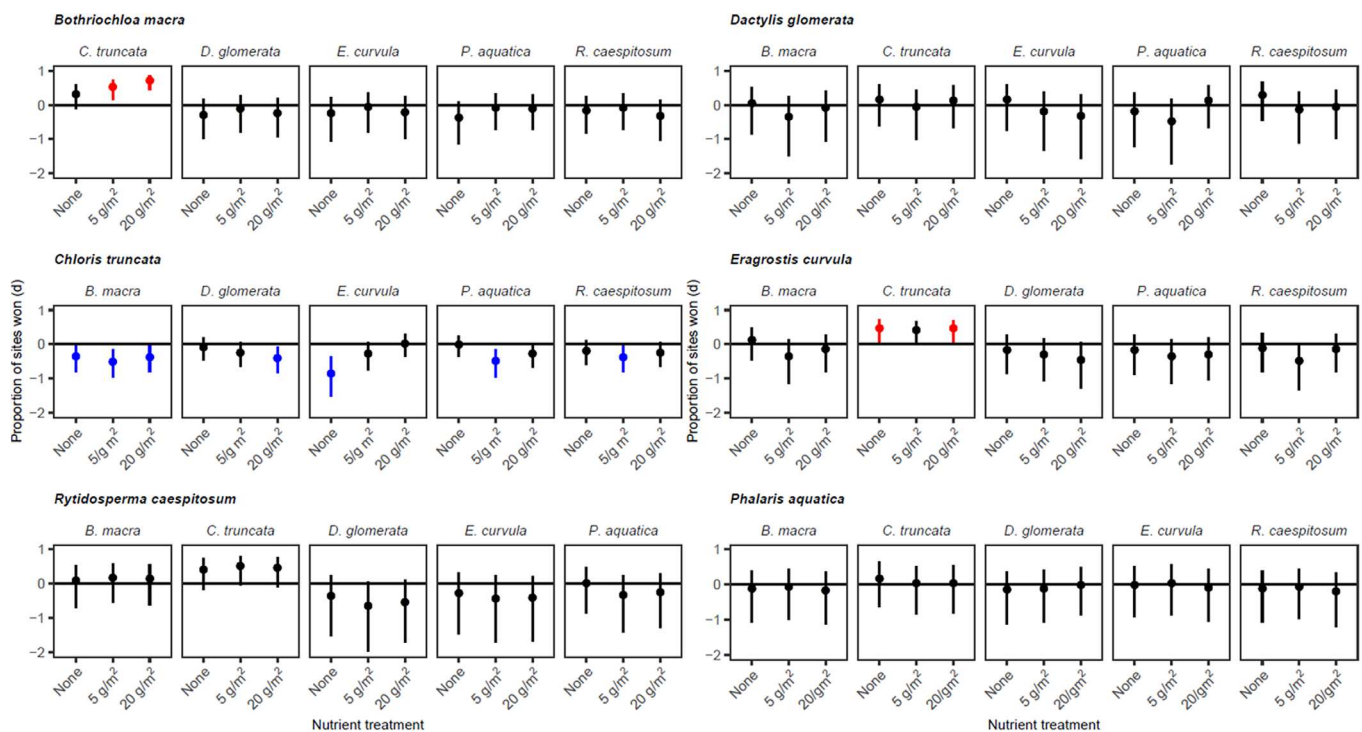


Figure 4. The proportion of safe sites lost (positive values of d , indicating competitive exclusion) or gained (negative values of d , indicating facilitation) by each of six target species (rows, species name in bold) when added to plots with each of the five other species (columns) at each of three levels of addition of N, P and K. Black circles show median and bars 95% credible intervals. Red circles highlight competitive interactions with credible intervals that do not cross zero, blue circles highlight facilitative interactions with credible intervals that do not cross zero. Black circles indicate no change in safe-site availability, consistent with niche differentiation.

an advantage over natives in grasslands globally (McIntyre and Lavorel 1994, Seabloom et al. 2015). We found no evidence of an increase in niche availability for any of the three exotics with an increase in nutrient addition, no evidence that exotics consistently outcompeted natives during recruitment, and no evidence that C3 grasses were competitively superior under our high nutrient treatment. Rather, in situations where native-exotic pairs interacted (i.e. values of d were positive or negative), those interactions involved the facilitation of a C4 native (*C. truncata*) by the exotics. Other studies have found facilitation of exotic species by natives (Lucero et al. 2019, Cavieres 2021, Lortie et al. 2021), an outcome predicted to increase as resources increase (Northfield et al. 2018), although there are fewer examples of exotic species facilitating natives (Alba et al. 2019, Wainwright et al. 2019). While our findings suggest the potential for exotic species to facilitate the establishment of a native species, they also highlight the need for caution in interpreting the outcome of species interactions in heterogeneous landscapes. Mean values for our estimates of interspecific competition/facilitation (d) for *C. truncata* were similar to those observed for other species (particularly the native *R. caespitosum* and exotic *E. curvula*), but the recruitment of *C. truncata* was more consistent across plots irrespective of competitive outcomes (high value of the dispersion parameter λ) leading to greater certainty in our estimates of the niche space available to *C. truncata* in general. The more consistent recruitment of *C. truncata* across our plots aligns with its growing status as a native weed of Australian grasslands, being one of the few native grasses to readily establish in disturbed, fertilised ground (Michael et al. 2012, Manalil et al. 2020). Overall, our findings rather highlight the complex interplay between environmental heterogeneity and species interactions (Germain et al. 2018), and the idiosyncratic outcome of both for plant species, regardless of their native/exotic status.

Implications for understanding the processes the influence the composition of plant communities

By separately estimating niche availability, niche overlap and the relative competitive performance of plant species, our results highlight the key role of spatial heterogeneity in allowing species to co-occur in these grasslands. Our finding that interactions between species may also shift from facilitative to competitive over time indicate that temporal variation in species performance could also promote co-occurrence. These results further highlight two important components of our model that generate insights into plant community dynamics. First, the dispersion parameter (λ) demonstrates that niche availability is heterogeneous even for single species in the absence of any competition. Second, the parameter (d), an estimate of niche overlap, demonstrates that facilitation is far more common under a greater range of environmental conditions than previously recognised (Liancourt et al. 2017, Wang and Callaway 2021). Both spatial variation in niche availability and facilitation should be routinely incorporated into models of plant community dynamics.

While current models of coexistence emphasize the role of competition in structuring the composition of plant communities, recent attempts to understand the drivers of compositional changes across resource gradients have failed to support the general prediction that niche and competitive exclusion increases with increasing resources. Instead, there is an emerging picture (Bimler et al. 2018, Wandrag et al. 2019) that heterogeneity in abiotic conditions and biotic interactions means that most species can co-occur under most conditions, an outcome that more closely aligns with the levels of biodiversity observed in real systems (Simha et al. 2022).

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Author contributions

Elizabeth M. Wandrag: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (lead); Methodology (lead); Project administration (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jane A. Catford:** Conceptualization (equal); Funding acquisition (equal); Methodology (supporting); Writing – review and editing (supporting). **Richard P. Duncan:** Conceptualization (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (supporting); Methodology (supporting); Resources (lead); Writing – review and editing (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.ftdz08ws>> (Wandrag et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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