1   **Quantifying niche availability, niche overlap and competition for recruitment sites in**

2   **plant populations without explicit knowledge of niche axes.**

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14   **ABSTRACT**

15   1. Niche availability, niche overlap and competitive ability are key determinants of the

16   distribution and abundance of species. However, quantifying each of these components is

17   difficult because it is not always possible to identify or measure relevant environmental

18   gradients (niche axes) along which species might partition or compete for niche space.

19   2. We describe a method that uses seed addition experiments to quantify the number of 'safe-

20   sites' (microsites suitable for a species to recruit from seed) at a location and show how

21   this method can be used to quantify niche availability, niche overlap and competitive

22   ability. We illustrate our approach using two seed addition experiments in grassland.

23 3. In the first experiment, we added seeds of one native and two exotic grass species, alone

24   and in mixture, to plots that were arrayed along a gradient of soil moisture availability. We

25   show that the three species partitioned safe-sites, implying that all three species could

26   locally co-occur through niche partitioning, in part due to different responses to moisture

27   availability.

28 4. In the second experiment, we added seeds of three commonly co-occurring native grass

29   species, alone and in mixture, to plots with no obvious environmental gradients. One

30   species outcompeted two others for site occupancy, allowing us to quantify both the degree

31   of niche overlap and the relative ability of each species to compete for safe-site occupancy

32   without *a priori* knowledge of the niche axes. Results from both experiments demonstrate

33   the fine-scales at which species can partition niches to facilitate co-occurrence.

34 5. *Synthesis.* By conceptualising a plot of ground as containing a limited number of microsites

35   that are safe for the recruitment of a given species, and using seed addition experiments to

36   measure both the number of safe-sites and degree of safe-site overlap among species, we

37   show how niche availability, niche overlap and competitive ability can be quantified at

38   fine-scales without *a priori* knowledge of niche axes. Our approach allows questions about

39   niche availability and competition for shared niche space to be empirically tested, and to

40   examine how these processes vary along environmental gradients to shape species

41   distributions and patterns of co-occurrence.

42 **Keywords:** biotic interactions, coexistence, competition, environmental heterogeneity,

43 facilitation, grasslands, niche partitioning, recruitment function, seed limitation, fundamental

44 niche.

INTRODUCTION

The distribution and local abundance of plant species is determined, in part, by the match between species' requirements for recruitment and local environmental conditions. However, where species have similar requirements for recruitment, such that their fundamental niches overlap, competition among species may exclude some from sites they could otherwise occupy (Esch, Ashbacher, Kopp, & Cleland, 2018; Levine & HilleRisLambers, 2009; MacArthur & Levins, 1967). Consequently, if a species is not seed or dispersal limited, its distribution and abundance should depend on: 1) the availability of fundamental niche space (niche availability); 2) the degree to which species' fundamental niches overlap (niche overlap); and 3) the ability of species to compete with other species for overlapping niche space (competitive ability). The potential for species to co-occur at a location depends on the interplay among these components. Species could co-occur if they partition niche space, or if each species has a competitive advantage over other species in at least some portion of shared niche space (Gause, 1934; MacArthur & Levins, 1964). While these concepts are fundamental to understanding how plant communities are structured, it has proven difficult to devise methods that allow us to simultaneously measure niche availability, niche overlap and competitive ability in the field.

Current approaches to assess the degree to which species partition or compete for niche space, and how this influences co-occurrence, stem from co-existence models (Letten, Ke, & Fukami, 2016). Two main approaches are recognised. First, models of interacting species can be used to quantify the relative strength of intra- to inter-specific density dependence and resulting niche and fitness differences, which then determine whether two species can coexist (modern coexistence theory; Chesson, 2000). Second, mechanistic consumer-resource models (contemporary niche theory; Chase & Leibold, 2003) aim to quantify how species use particular resources, and how differences in resource use then influence the potential to coexist

(MacArthur & Levins, 1964; Tilman, 1982). However, neither approach provides a straightforward way to quantify niche availability, which is necessary to understand first how local environmental conditions determine where individual plant species could potentially occur, and subsequently how interactions among plant species determine realised patterns of distribution and abundance. Specifically, modern coexistence theory identifies only niche differences, which are defined in terms of the relative strength of interactions among and within species, while in consumer-resource models niches are defined in terms of specific limiting resources, which may not always be obvious.

A key difficulty with measuring both niche availability for single species and niche partitioning among species is that the measurements often rely on identifying the relevant axes along which species might differ in their niche requirements (Silvertown & Law, 1987; Tilman, 1982). While there is strong evidence that niche partitioning along environmental gradients allows species to co-occur (García-Baquero, Silvertown, Gowing, & Valle, 2016; Pickett & Bazzaz, 1978; Rees, 2013; Tilman, 1987), co-occurring species often also show substantial niche overlap (Berdugo et al., 2018; Mahdi, Law, & Willis, 1989). Species with niches that appear to overlap along a specific gradient may co-occur because one or both species is dispersal limited (Soberon, 2007), but might also co-occur because they partition niches along other, unidentified niches axes (Silvertown, 2004). The difficulty in identifying relevant axes along which species might partition niches is exacerbated by the very fine spatial scale at which plant species can respond to environmental variation (Harper, Williams, & Sagar, 1965; Stowe & Wade, 1979). For example, up to 89 species have been recorded within 1 m^2 of temperate grassland (Cantero, Partel, & Zobel, 1999), but it is difficult to measure environmental variation, and thus quantify niche availability and niche differentiation, at such fine-scales (Blonder et al., 2018; Snaydon, 1962).

Our aim in this paper is to overcome some of the difficulties in measuring niche availability, niche overlap and competitive ability by describing a relatively straightforward way to quantify each component in the field without knowing the specific axes along which niches may vary. We do this by conceptualising a plot of ground as comprising an array of microsites, each large enough to support a single plant (c.f. the regeneration niche of Grubb, 1977). Species-specific requirements for germination and seedling establishment mean that even small differences among microsites can alter conditions to favour the recruitment of one species over another (Fowler & Antonovics, 1981; Harper et al., 1965). Because the number of microsites suitable for a given species will vary among habitats and along environmental gradients (Duncan, Diez, Sullivan, Wangen, & Miller, 2009; Miller et al., 2014; Spotswood, Mariotte, Farrer, Nichols, & Suding, 2016), locations with greater numbers of microsites suitable for a given species coincide with areas of greater fundamental niche availability. Measuring the number of suitable microsites at different locations thus allows us to quantify niche availability without knowing precisely what underpins recruitment outcomes. By extension, species with similar requirements for germination and growth will share microsites suitable for recruitment (Aicher, Larios, & Suding, 2011). Consequently, the degree to which two species share suitable microsites reflects their degree of niche overlap, while the ability of one species to occupy shared microsites at the expense of a second species reflects their relative competitive abilities.

Using this approach, we outline a model that can be parameterised with data from seed addition experiments to simultaneously quantify: 1) the availability of microsites that are suitable for recruitment (i.e. "safe" sensu Harper, Clatworthy, McNaughton, & Sagar, 1961) as a proxy for niche availability; 2) the degree to which microsites that are suitable for one species are shared by another (niche overlap); and 3) relative competitive ability when species compete for occupancy of shared microsites (competitive ability). We use data from two grassland

118   experiments to illustrate this approach, highlighting the potential for fine-scale niche

119   differentiation to allow multiple species to co-occur in plant communities.

120   **MATERIALS AND METHODS**

121   **Conceptual model**

122   Our model builds on the approach outlined in Duncan et al. (2009), which uses data from seed

123   addition experiments to estimate the availability of microsites suitable for the recruitment of a

124   single species. We first describe the single species model and how it can be used to estimate

125   niche availability for a given species; we then introduce an extension that estimates niche

126   overlap among species, and species' relative competitive abilities for shared niche space.

127   *Quantifying niche availability*

128   The underlying single-species recruitment model conceptualises a plot of ground as comprising

129   an array of n_i microsites. Each microsite is an area large enough to supply the resources needed

130   to support a single individual of species i. Values of n_i could vary among species if some require

131   a larger or smaller area to support a single individual and, for a given species, could vary

132   through time if a larger area is required to support individuals as they increase in size (Duncan

133   et al., 2009). Of n_i microsites that could support a single individual of species i, only a

134   proportion, b_i, have conditions suitable for successful recruitment of that species. From here

135   on we refer to microsites that are suitable for the recruitment of a species as "safe-sites" (sensu

136   Harper et al., 1961).

137   Given n_i and b_i, two processes determine the number of individuals, r_i, that recruit given the

138   arrival of s_i seeds. First, seeds landing in unsafe-sites will fail to recruit because they encounter

139   conditions unsuitable for germination or survival. Failure to recruit due to landing in an unsafe-

140   site is a density-independent process: each arriving seed has probability 1 - b_i of failing to land

141 in a safe-site regardless of the number of arriving seeds. Second, because safe-sites can support

142 only one individual, seeds of species *i* landing in the same safe-site must compete for safe-site

143 occupancy, with only a single individual recruiting regardless of how many seeds arrive. This

144 is a density-dependent process: with greater numbers of arriving seeds, more seeds will fail to

145 recruit due to competition for safe-site occupancy.

146 If seeds are randomly dispersed in a plot, such that each seed has the same probability of

147 landing in any microsite (given that the experimenter controls the distribution of seeds across

148 plots; for an alternative see Brannstrom & Sumpter, 2005), the expected number of individuals

149 recruiting from s_i seeds is (see Duncan et al., 2009):

150 $$r_i = b_i n_i \left(1 - e^{s_i/n_i}\right)$$ Equation 1

151 Parameters b_i and n_i can be estimated by fitting Equation 1 to data from a seed addition

152 experiment where different numbers of seeds are added to different plots and the resulting

153 number of recruits are recorded. Equation 1 describes a recruitment curve with an asymptote

154 at $b_i n_i$, which is the total number of safe-sites per plot and hence the number of individuals that

155 would recruit if seeds landed in all safe-sites (i.e., the plot was saturated with seeds) (Aicher et

156 al., 2011; Duncan et al., 2009; Miller et al., 2014; Spotswood et al., 2016).

157 The parameters b_i and $b_i n_i$ both measure fundamental niche availability. Parameter b_i is the

158 proportion of a plot comprising safe-sites, which equates to the area of fundamental niche space

159 available, while $b_i n_i$ is the total number of safe-sites, with a greater number of safe-sites

160 implying more available niche space.

161 *Quantifying niche overlap and competitive ability*

162   Current recruitment models (Duncan et al., 2009; Spotswood et al., 2016) do not consider how

163   competition between species can affect recruitment, which would occur if two or more species

164   have overlapping niches and compete for occupancy of the same safe-sites.

165   For two species, i and j, we can estimate the degree to which their niches overlap and they

166   compete for safe-site occupancy by: 1) experimentally adding seeds of each species to plots of

167   a given size in monoculture, and obtaining species-specific estimates of niche availability (e.g.,

168    $b_i n_i$ and $b_j n_j$; Fig. 1a, b); and 2) adding seeds of both species to a single plot at seed densities

169   high enough to saturate safe-sites, such that seeds of each species must compete for occupancy

170   of any shared safe-sites, and recording the numbers of each species that recruit (e.g., Fig 1c).

171   We can then estimate parameter b_{ij}, which is the proportion of microsites that species i occupies

172   when competing with species j for microsite occupancy (and vice versa for species j). While b_i

173   equates to the area of fundamental niche space available to species i in a plot, b_{ij} equates to the

174   area of species i's realised niche space when seeds of species j are present at saturating density.

175   Using the definitions described above, we can calculate niche overlap as the area of overlap in

176   the fundamental niches of each species, given by:

177    $o_{ij} = (b_i - b_{ij}) + (b_j - b_{ji})$.   Equation 2

178   The parameter o_{ij} can be expressed as a proportion of the fundamental niche space of each

179   species by dividing it by either b_i or b_j. Similarly, we can measure a species' competitive ability

180   relative to a second species as the proportion of the shared niche space captured by that species.

181   For species i this is:

182    $(b_j - b_{ji}) / o_{ij}$ Equation 3

183   (the amount of species j's niche space captured by species i at saturation as a proportion of the

184   amount of overlapping niche space).

185 The above calculations are easily interpretable when species' realised niches are smaller than

186 their fundamental niches, as expected due to competition. However, in our field experiments

187 some species had higher recruitment in the presence of other species, implying facilitative

188 rather than competitive interactions. This resulted in some realised niches being larger than the

189 fundamental niches, which made it difficult to interpret the measures of niche overlap and

190 competitive ability described above. To accommodate this, we can instead calculate the ratio:

191 $d_{ij} = (b_i - b_{ij}) / b_i$ Equation 4

192 which is the proportion of species i's safe-sites captured by species j when seeds of both species

193 are at saturation. Parameter d can be interpreted as a measure of the potential impact of one

194 species on another when both species are at saturating seed densities, and allows for both

195 competitive and facilitative interactions (see below).

196 *Interpreting the parameter d*

197 A value of $d_{ij} = 0$ would mean that species j has no impact on the recruitment of species i. This

198 could arise because: 1) the two species fundamental niches do not overlap, such that they

199 partition the niche space; or 2) the fundamental niche of species j overlaps with species i, but

200 species i always outcompetes species j for safe-site occupancy. We can distinguish between

201 these alternatives by calculating d_{ji}, the proportion of species j's safe-sites captured by species

202 i. If $d_{ij} = d_{ji} = 0$ (Fig. 2a) then neither species affects the other, implying complete niche

203 differentiation. If $d_{ij} = 0$ and $d_{ji} = 1$ (Fig. 2b) then the niche of species j must overlap completely

204 with that of species i, and species i always outcompetes species j for shared niche space.

205 Values of d_{ij} and/or d_{ji} between 0 and 1 imply some degree of niche overlap with one (or both)

206 species having a competitive impact on the other without complete exclusion. This could arise

207 if species have partially or completely overlapping niches, with each species a superior

competitor in some portion of the shared niche space (e.g. Fig. 2c, with the species with the largest d value having the greatest competitive impact), or if they have partially overlapping niches with one species always the superior competitor for shared niche space (e.g. Fig. 2d). It is worth noting that in a situation where species have overlapping niches and each species excludes the other in half of shared safe-sites (Fig. 2e), the method would be unable to determine whether the impact of each species on the other arises because they are each competitively superior in half of shared safe-sites, or because they are competitively equal and sites were won at random (i.e. neutrality; Hubbell, 2001). Finally, while values of d cannot exceed 1 they can fall below 0, which would indicate that recruitment of a species was facilitated by the presence of a second species at seed saturation (Fig. 2f). We calculated d values and used these to infer niche overlap and the resulting competitive impact of one species on another in our experiments.

Field experiments

To illustrate our approach, we carried out two seed addition experiments in grassland on the University of Canberra campus, Australian Capital Territory. The grassland site resulted from historical land clearing (formerly grassy-woodland) and was dominated by a mixture of native and introduced species. Before the start of the experiment, the area was grazed by kangaroos and mowed regularly.

Experiment 1

In the first experiment, we aimed to measure niche overlap and the relative competitive ability of three grass species along a gradient of soil moisture availability. One species, *Rytidosperma caespitosum*, is native to the Australian Capital Territory and is common on dry, shallow soils, while the other two species (*Dactylis glomerata* and *Phalaris aquatica*) are non-native pasture grasses commonly found in areas with higher soil moisture. We were interested in why these

232 species varied in abundance along the gradient: was it because they had different fundamental

233 niches and partitioned safe-sites accordingly, or did their fundamental niches overlap such that

234 any differences in their relative abundances were due to interspecific competition for shared

235 safe-sites?

236 We carried out the first experiment during austral summer 2015/2016. The study site was on

237 an east-facing slope that had generally shallow soils with a pronounced gradient in soil

238 moisture availability (Appendix S1) associated with soil depth. We fenced the site to prevent

239 mowing and kangaroo grazing. A pilot study revealed very low rates of recruitment when seeds

240 were added to established vegetation. Therefore, to enable recruitment of our target species,

241 we removed the resident vegetation before adding seed. We cleared vegetation by applying

242 glyphosate weedkiller and removing dead material by raking, repeating this procedure several

243 times in the weeks prior to seed addition to deplete the soil seedbank as much as possible. After

244 seed addition, species that had not been experimentally added to plots were removed as they

245 appeared through careful spot application of glyphosate until our experimental plants had

246 established and weeding of non-target plants was no longer possible without damaging our

247 experiment. Because our study site is very dry, with mostly shallow soils and frequent periods

248 without rain during summer, we watered soils at the time of seed sowing and during dry

249 weather. Watering ensured that seeds germinated and survived, and maintained the moisture

250 gradient throughout the experiment. Without watering, soil across the whole site would have

251 dried out completely during periods without rain. Watering ensured that moist sites retained

252 some moisture, while dry sites became dry again soon after watering.

253 We added seeds of each of the three species in monoculture to 0.3×0.3 m plots at each of six

254 densities: 25, 75, 150, 500, 1250 and 2500 (corresponding to 278, 833, 1,667, 5,555, 13,888

255 and 27,775 seeds per m^2, respectively). Seed densities were chosen to span a range up to a

256 maximum we thought would saturate microsites with seeds, and each species $\times$ density

257 treatment was replicated 10 times. Adding seeds of each species at different densities in

258 monoculture and counting the resulting number of recruits allowed us to fit recruitment curves

259 using Equation 1 and estimate b_i and n_i for each species.

260 For each pairwise combination of species, we added 2500 seeds of both species to the same

261 plot (polyculture), with each pairwise combination replicated 20 times. The aim was to ensure

262 that all microsites in these plots were saturated with seeds of both species such that they would

263 compete for any shared safe-sites, allowing us to calculate b_{ij} and b_{ji} and hence d_{ij} and d_{ji}

264 (Equation 4). The monoculture and polyculture plots were randomly distributed within two

265 blocks that were arranged such that one block was located at the drier end of the moisture

266 gradient and the other at the wetter end (Appendix S1). Each block comprised 156 plots of 0.4

267 × 0.4 m (each 0.3 × 0.3 m seed addition plot with a 0.05 m buffer around the edge of each plot

268 so they were at least 0.1 m apart) arrayed in 26 columns and 6 rows, with a 0.5 m walkway

269 every second row. Within each block, each monoculture treatment was replicated five times,

270 and each polyculture treatment replicated ten times (with 36 plots per block left over and having

271 no seed addition).

272 We added seeds to plots in December 2015 and counted the number of recruits in each plot

273 four months later (April 2016) when all species were beginning to flower. In February 2016

274 we measured relative soil moisture at the centre of each plot using a handheld soil moisture

275 sensor (Delta-T Devices, ML3 Sensor). We timed this measurement to occur 24 hours after

276 rain to ensure the rainwater had enough time to enter the soil but before the soil had completely

277 dried out, which was common during periods of low rainfall.

278 *Experiment 2*

279 The second experiment involved three native species (*Bothriochloa macra*, *Chloris truncata*

280 and *Rytidosperma caespitosum*) that commonly co-occur in grasslands around our field site

281   (e.g. Driscoll, 2017). Our aim was to understand the roles of niche availability, niche overlap

282   and competition in influencing the co-occurrence of these species in a relatively homogenous

283   habitat, particularly the extent to which they partitioned microsites at a fine-scale.

284   We carried out the second experiment during austral summer 2016/2017. We selected an area

285   close to our first experiment, but on flat ground with no obvious moisture gradient. As with the

286   first experiment, we removed established vegetation before the start of the experiment through

287   herbicide application and raking, fenced the plots, carried out spot applications of glyphosate

288   to kill non-target species until experimental plants had established, and watered the plots

289   regularly. We added seeds in monoculture at the following densities: 50, 250, 500, 750, 1250

290   and 2500 (corresponding to 556, 2778, 5555, 8333, 13,888 and 27,775 seeds per m^2,

291   respectively), and seeds in two-species polycultures at the highest density (27,775 seeds per m^2

292   for both species). The monoculture seed densities differed slightly from Experiment 1 because

293   we wanted to better measure recruitment at intermediate seed densities. We replicated each

294   monoculture treatment 10 times and each polyculture treatment 20 times. Plots were arranged

295   in ten blocks that were each 6.3×4.9 m in size (including space for walkways). Each block

296   contained one of each monoculture treatment and two of each polyculture treatment (with six

297   empty plots per block). There were a total of 72 plots per block (720 overall). We added seeds

298   in December 2016, and counted the number of recruits four months later, which corresponded

299   with the onset of flowering for all species.

300   **Analysis**

301   For each experiment, we fitted Equation 1 to data on the number of recruits recorded at each

302   level of seed addition, for both the monoculture (all seed densities) and polyculture (high seed

303   density only) plots. We modelled variation in the observed number of recruits, r_{ik} of species i

304   in plot k, using a negative binomial distribution:

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

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

307   where μ_{ik} is the mean number of recruits of species i in plot k, and λ_i is a dispersion parameter

308   that captures unexplained differences among plots in the number of recruits. Smaller values of

309   λ_i indicate greater variability among plots in the number of recruits, implying there is some

310   unexplained factor(s) causing spatial aggregation of safe-sites, such that some plots have more

311   and others fewer safe-sites than expected.

312   The value for b_{ik} for each plot varied depending on whether species were sown in monoculture

313   or polyculture, and therefore whether we were estimating b_i or b_{ij}, respectively. Specifically,

314   we modelled b_{ik} as follows:

315    $\text{logit}(b_{ik}) = \alpha_i + \gamma_{ij}$

316   Where α_i is the estimate of b_i on the logit scale, and γ_{ij} is the difference between b_i and b_{ij} (on

317   the logit scale), which was set to zero for monoculture plots and estimated from the data for

318   polyculture plots. We used the resulting estimates to calculate d_{ij} and d_{ji} using Equation 4.

319   To examine how safe-site availability varied along the moisture gradient in Experiment 1, we

320   included an additional term in the model for each species:

321    $\text{logit}(b_{ik}) = \alpha_i + \gamma_{ij} + \beta_i * \text{moisture}_k$

322   where moisture_k is the measure of soil moisture for plot k (centred on the mean) and β_i is a

323   species-specific parameter estimated from the data that describes how safe-site availability

324   changes with soil moisture (on the logit scale).

325   We fitted models and did the resulting calculations in a Bayesian framework using the software

326   JAGS v4.2.0 (Plummer, 2003), which we ran using the package jagsUI (Kellner, 2015) in R

327   v3.4.2 (R Development Core Team, 2017). The parameters describing the proportion of safe-

328   sites (α_i, γ_{ij} and β_i) were constrained to reasonable values on the logit scale by specifying a

329   Cauchy prior distribution with a median of 0 and scale of 2.5, following Gelman (2008). For

330   each species, the parameter n_i was given a weakly informative prior, specified as coming from

331   a normal distribution with mean 1000 and large variance, and the dispersion parameter λ_i was

332   given a broad uniform prior (0-500). We used median values of the posterior distributions of

333   all parameters to characterize central tendency and 95% credible intervals to capture

334   uncertainty in our parameter estimates.

335   **RESULTS**

336   *Experiment 1*

337   When seeds of each species were sown at varying densities in monoculture, the recruitment

338   curves fitted using Equation 1 all approached an asymptote at high seed densities (Fig. 3). The

339   estimated asymptotic number of recruits is the estimated number of safe-sites per plot ($b_i n_i$; a

340   measure of fundamental niche availability). That all species approached an asymptote implies

341   that seed supply exceeded the number of safe-sites available for recruitment, such that seeds

342   competed for safe-site occupancy at high seed densities. The number of safe-sites per plot was

343   greatest for the native *R. caespitosum* (18.9, 95% credible intervals 10.6 – 39.1) and lower for

344   the non-native species, *P. aquatica* (9.4, 95% credible intervals 3.8 – 27.1) and *D. glomerata*

345   (8.2, 95% credible intervals 3.6 – 19.6).

346   Values of n_i (the number of microsites that could theoretically support one individual) were

347   similar for all three species (Fig. 4a). However, *R. caespitosum* had more safe-sites per plot

348   (more fundamental niche space) because a greater proportion of microsites were suitable for

349   its recruitment (b_i, Fig. 4b). Approximately 2% of microsites were safe for *R. caespitosum*

350   compared to less than 1% for *D. glomerata* and *P. aquatica*. The dispersion parameters (λ_i)

351   revealed more spatially variable recruitment for *D. glomerata* and *P. aquatica* relative to *R.*

352   *caespitosum* (0.95 for *R. caespitosum* versus 0.40 and 0.14 for *D. glomerata* and *P. aquatica*,

353   respectively, with lower values indicating greater spatial aggregation of safe-sites; Fig. 4c).

354   The finding that, for *R. caespitosum*, there were more safe-sites per plot and recruitment was

355   less variable among plots appeared due to its tolerance of a wider range of soil moisture

356   conditions relative to the two non-native species. While *R. caespitosum* had a relatively even

357   rate of recruitment across the moisture gradient, the two non-native species had low rates of

358   recruitment at low soil moisture with increasing recruitment at higher soil moisture, particularly

359   *P. aquatica* (Fig. 5).

360   When seeds were at saturation, the presence of a second species in the polyculture plots did not

361   substantially alter the number of recruits relative to the monoculture plots for any species (Fig.

362   3). For all pairwise combinations, estimates of d_{ij} and d_{ji} had values close to zero, albeit with

363   wide 95% credible intervals (Fig. 4d-f). As such, there was no clear evidence that the

364   fundamental niches of the three study species overlapped and that they competed for safe-site

365   occupancy.

366   *Experiment 2*

367   In Experiment 2, recruitment curves for all species again reached an asymptote at high seed

368   densities, indicating that safe-sites rather than seed supply limited further recruitment (Fig. 6).

369   In monoculture plots, *R. caespitosum* had the lowest asymptotic number of recruits, with an

370   estimated 0.8 individuals recruiting at seed saturation (95% credible intervals 0.4 – 1.4),

371   compared with 3.3 individuals (95% credible intervals 2.2 – 4.9) for *B. macra* and 3.5

372   individuals (95% credible intervals 2.8 – 4.9) for *C. truncata*.

373   Differences in the number of safe-sites per plot for each species (b_in_i) resulted from both

374   differences in the total number of microsites available (n_i; Fig. 7a) and the proportion of

375   microsites that were safe for recruitment (b_i; Fig. 7b). The estimated number of microsites per

376   plot was around five times higher for *B. macra* and *R. caespitosum* than for *C. truncata* (around

377   1000 compared to just over 200) suggesting that, after four months, the area required to support

378   a single *C. truncata* individual was greater than for the other two species. In contrast, the

379   proportion of microsites that were safe-sites was higher for *C. truncata* (around 1.5%) than *B.*

380   *macra* (less than 0.01%) and *R. caespitosum* (less than 0.001%), suggesting greater niche

381   availability for *C. truncata*. The dispersion parameter (λ_i; Fig. 7c) indicated high spatial

382   variation in safe-site availability for *B. macra* and *R. caespitosum* among plots ($\lambda_i = 2.4$ and

383   3.4, respectively), and a more even distribution of safe-sites among plots for *C. truncata* ($\lambda_i =$

384   271.7).

385   Neither the recruitment of *B. macra* (Fig. 6a) nor *R. caespitosum* (Fig. 6c) declined when seeds

386   of these species were added in polyculture relative to monoculture plots. Values of *d* for both

387   species (Fig. 7d) were close to zero, suggesting these species occupied distinct niches and did

388   not compete for safe-site occupancy. In contrast, recruitment of *B. macra* declined when seeds

389   were added together with those of *C. truncata* (Fig. 6a) but there was no concurrent decrease

390   in recruitment of *C. truncata* (Fig. 6b). Values of *d* indicated the two species had overlapping

391   niches, with *C. truncata* the superior competitor for shared niche space: *C. truncata* occupied

392   around 45% of microsites that would otherwise have been safe-sites for *B. macra*. There was

393   evidence that *B. macra* facilitated *C. truncata* such that recruitment of *C. truncata* increased in

394   plots where *B. macra* was present (Fig. 6c). A *d* value for *B. macra* of -0.43 (Fig., 7e) suggests

395   a 43% increase in the number of safe-sites (and hence niche space) available to *C. truncata*,

396   albeit with wide credible intervals.

397 The recruitment of *R. caespitosum* also declined when added together with seeds of *C. truncata*,

398 with no concurrent decline in *C. truncata* recruitment. Values of *d* again suggest this was due

399 to niche overlap with *C. truncata* the superior competitor for shared niche space. In polyculture,

400 *Chloris truncata* occupied more than 80% of safe-sites that *R. caespitosum* could otherwise

401 have occupied (Fig. 7f), with some indication of facilitation of *C. truncata* by *R. caespitosum*

402 (value of *d* less than 1), though credible intervals were wide and overlapped zero.

403 **DISCUSSION**

404 Testing ideas about how niche and competitive processes determine the distribution and

405 abundance of species is challenged by the lack of a single framework to empirically quantify

406 niche availability, niche overlap and competitive ability in the field. Niche availability is

407 particularly difficult to measure since most approaches rely on identifying the specific resource

408 or environmental factors that limit species performance, and these factors can vary at quite fine

409 spatial scales (Silvertown, Dodd, Gowing, & Mountford, 1999; Vivian-Smith, 1997). We have

410 addressed this challenge by developing a model that conceptualizes the niche in terms of

411 microsites that are safe for seedling recruitment. We applied our model to two field experiments

412 to show how this allows us to: 1) quantify variation in species fundamental niche availability;

413 and 2) estimate the degree to which two species fundamental niches overlap and their relative

414 competitive ability in competition for shared niche space. One advantage of our approach is

415 that it can be applied without knowing the specific niche axes controlling species distributions.

416 *Niche partitioning along environmental gradients*

417 Experiment 1 shows how our approach can help identify the relative importance of niche

418 partitioning and competition for shared niche space in explaining species distributions along

419 known environmental gradients (Chase, 2007; Chesson, 1994; Kneitel & Chase, 2004) or

420 among habitats (Harrison, Cornell, & Moore, 2010). Our results were consistent with strong

421   niche partitioning ($d_{ij} = d_{ji} = 0$ for pairwise combinations of all three species), suggesting that

422   variation in recruitment along the gradient likely reflects species independent responses to

423   moisture availability rather than being the outcome of competitive interactions. Relative to the

424   two non-native species, the native species *R. caespitosum* had a wider fundamental niche in the

425   sense of having generally higher and more even recruitment along the moisture gradient (Fig.

426   5), with higher values of the dispersion parameter indicating less among-plot variation in

427   recruitment. The two non-native species had low recruitment at low soil moisture with safe-

428   site availability being more patchy (low values of the dispersion parameter, λ) and concentrated

429   in areas with high soil moisture availability. Despite both non-native species preferring sites

430   with higher moisture, there was no evidence that they competed for safe-site occupancy.

431   Rather, they appeared to partition safe-sites within plots.

432   *Niche and competitive differentiation along unidentified axes*

433   With no obvious environmental gradient, the results from Experiment 2 demonstrate how

434   quantifying safe-site availability can reveal how species partition or compete for niche space

435   in the absence of any clearly defined niche axes (Harper et al., 1965). The fundamental niche

436   of *C. truncata* overlapped with both *B. macra* and *R. caespitosum*, with *C. truncata* being the

437   dominant competitor, while *B. macra* and *R. caespitosum* showed niche differentiation.

438   The faster growth and larger size of *C. truncata* individuals likely explains their competitive

439   superiority and this, coupled with high niche availability, explains why they dominated cover

440   in plots (Appendix S2). *Chloris truncata* had a high value for *b* and a low value for the

441   dispersion parameter λ, suggesting that a large proportion of microsites were safe and these

442   were relatively evenly distributed across plots. Conversely, a low value for *n* indicated fewer

443   microsites per plot for *C. truncata* relative to other species, implying *C. truncata* individuals

444   took up more space at four months of age. This was consistent with observations of species

445   growth rates (Appendix S2): at low density, as few as five individuals of *C. truncata* could

446 achieve 100% vegetation cover in a plot, while the same number of *B. macra* reached a

447 maximum cover of only around 50% and *R. caespitosum* never recruited as many as five

448 individuals in a plot, attaining a maximum cover of 10%.

Fine-scale niche partitioning

450 Our results highlight the fine-scales over which microsite conditions can vary to allow species

451 to co-occur. This was particularly evident in Experiment 2. Although *C. truncata* had a large

452 competitive impact on both *B. macra* and *R. caespitosum*, leading to their competitive

453 exclusion at the microsite level, niche differentiation at the plot level allowed both species to

454 persist even when *C. truncata* was present. Indeed, around half of the safe-sites for *B. macra*

455 remained safe when *C. truncata* seeds were present at saturating density. Thus, although

456 competitive exclusion can occur at the microsite scale, differences among microsites results in

457 opportunities for niche differentiation and potentially neutral processes to occur within small,

458 apparently homogenous plots. This highlights a role of competitive refugia in allowing species

459 persistence at fine-scales as well as across environmental gradients (Pickett & Bazzaz, 1978).

460 Moreover, the sensitivity of species to fine-scale variation in microsite conditions could explain

461 how species can partition niches to locally co-occur within apparently homogenous

462 environments (Blonder et al., 2018; Harper et al., 1965; Vivian-Smith, 1997), and why some

463 studies have failed to detect competitive exclusion in systems with no obvious axes of niche

464 differentiation (Silvertown, 2004).

Facilitation

466 Facilitation can be as important as competition in shaping species distributions (Callaway &

467 Walker, 1997). There was strong evidence for facilitation in Experiment 2 with *C. truncata*

468 having higher recruitment in the presence of other species, especially *B. macra*. Facilitation is

469 often associated with stressful environments where the presence of one species can benefit

470   others by providing shelter or enabling resource uptake (Bertness & Callaway, 1994). Although

471   it was not clear what the mechanism for facilitation in Experiment 2 might be, the results are

472   consistent with a situation in which *C. truncata* outcompeted *B. macra* for occupancy of shared

473   safe-sites where their fundamental niches overlapped, but the presence of *B. macra* increased

474   the number of safe-sites for *C. truncata* and led to a larger realised than fundamental niche in

475   places where the two species otherwise occupied distinct niches.

476   Although our findings in Experiment 1 suggest little overlap in species fundamental niches,

477   resulting in niche differentiation, the credible intervals associated with the *d* parameter were

478   wide. Thus, it is possible that a more complex outcome, involving shifts in the relative

479   importance of competition and facilitation along the moisture gradient, may have occurred, as

480   has previously been demonstrated for species interactions along moisture gradients (Eckstein,

481   2005). Detecting such shifts would require greater experimental replication to untangle how

482   niche availability and competitive outcomes varied at points along the gradient.

483   *Beyond recruitment*

484   Our approach focuses on recruitment as an important determinant of species presence and

485   abundance in a community (Chu & Adler, 2015; Grubb, 1977). Nonetheless, niche

486   requirements and competitive interactions among species can change across life-stages

487   (Freckleton, Watkinson, & Rees, 2009; Grubb, 1977). Consequently, patterns that emerge from

488   experiments focused on early recruitment may not reflect the range of potential outcomes as

489   individuals age. Adults generally have broader fundamental niches and are more tolerant of

490   competition than seedlings, while perennial plant species may gain a competitive advantage as

491   they grow by pre-empting space that would otherwise be lost to a competitor (Corbin &

492   D'Antonio, 2004; Seabloom et al., 2013). Our approach makes no predictions as to how

493   patterns of niche versus competitive differentiation during recruitment might translate to long-

494   term demographic outcomes in successive generations. Nevertheless, tracking changes in the

495   model parameters through time can provide insight into how niche availability and competitive

496   interactions change as individuals age (Duncan et al., 2009; Miller et al., 2014), meaning our

497   method could yield insights into aspects other than the recruitment niche. Integrating model

498   parameters at different life-stages into demographic models is a potential avenue for future

499   research, and would help place some of the findings revealed by our method in a wider context

500   to understand their longer-term implications.

501   *Conclusions*

502   We have used two field experiments to demonstrate how the parameters obtained from a

503   recruitment model can be interpreted in terms of niche availability, niche overlap and

504   competitive ability, and explored general patterns that emerge from this. Our experiments

505   highlight the potential for fine-scale niche differentiation to allow multiple species to locally

506   co-occur. While this is a well-known mechanism to explain species coexistence (Stowe &

507   Wade, 1979), our approach provides a way to quantify the degree to which species partition or

508   compete for niche space at fine-scales without *a priori* knowledge of their specific niche

509   requirements. In this way, our approach is a step towards understanding the processes that

510   determine species distribution and abundance using relatively straightforward experiments.

511   Applying our approach to known gradients, as in the soil moisture experiment, has the potential

512   to address hypotheses about how processes such as niche partitioning and relative competitive

513   ability change along gradients to influence species distributions. Together, these approaches

514   suggest the method has wide applicability in resolving some important questions in plant

515   ecology.

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Author contributions:

Data accessibility: Data and code available from the Dryad Digital Repository: doi:10.5061/dryad.sm76ms5.

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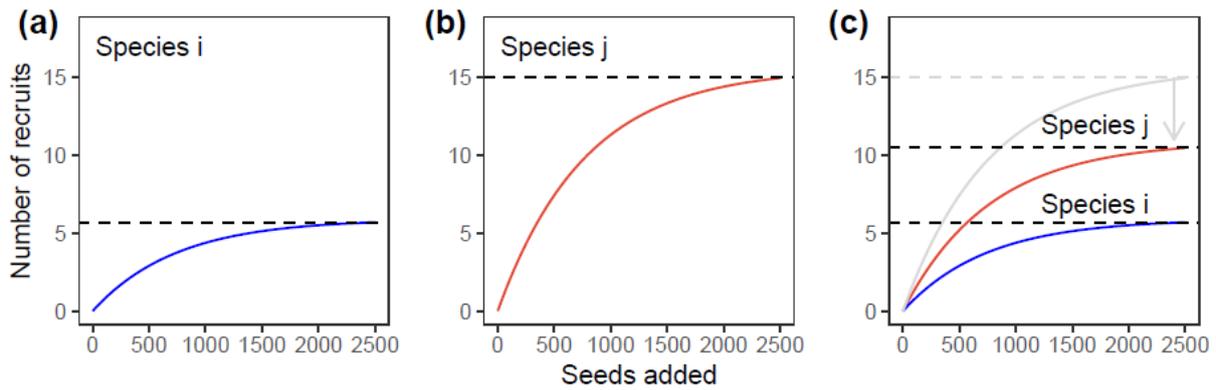
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667   **Figure 1. Conceptual diagram illustrating how recruitment curves can be used to estimate**

668   **niche availability for two species, *i* and *j*, in monoculture (fundamental niche; a, b) and**

669   **polyculture (realised niche; c).** When seeds of (a) species *i* or (b) species *j* are added at varying

670   densities to plots in monoculture, Equation 1 can be fitted to data on the resulting number of

671   recruits to estimate parameters b_i and n_i, and b_j and n_j, giving a relative measure of niche

672   availability for each species: $b_i n_i$ (dashed line in a) and $b_j n_j$ (dashed line in b). c) Adding seeds

673   of species *i* and *j* to plots in polyculture at saturating seed densities then allows estimation of

674   b_{ij} and b_{ji}, which is the proportion of microsites that are safe for species *i* in polyculture with

675   species *j*, and the proportion of microsites that are safe for species *j* in polyculture with species

676   *i*, respectively. Here, the addition of seeds of both species in polyculture lowers the recruitment

677   of species *j* (red curve; $b_{ji} n_j$ is lower than $b_j n_i$), but does not affect recruitment of species *i* (blue

678   curve; $b_{ij} n_i$, is equal to $b_i n_i$).

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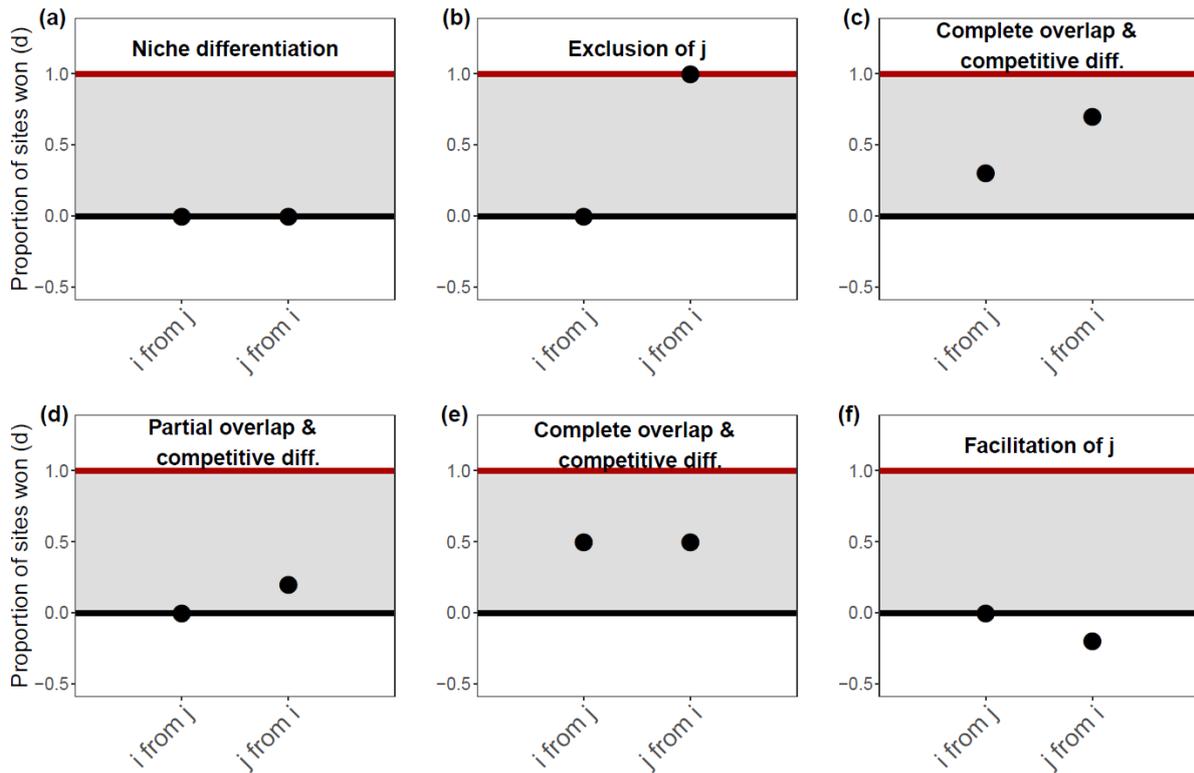
Figure 2. Interpreting the parameter *d*. The parameter *d* describes the proportion of safe-
sites won by one species from the other, with d_{ji} the proportion of safe-sites won from species
j by species *i*, and d_{ij} the proportion of safe-sites won from species *i* by species *j*. a) Two species
are completely differentiated with regard to their safe-site requirements (complete niche
differentiation) where $d_{ij} = d_{ji} = 0$; b) In contrast, where $d_{ji} = 1$, species *j* is competitively
excluded by species *i*: species *i* shares all of species *j*'s safe-sites and outcompetes species *j* for
occupation of those safe sites. Various outcomes between these two extremes are possible
depending on the degree of niche overlap and species relative competitive abilities (e.g. c-e),
including situations (e) where species have identical niches and are either competitively equal
(neutral outcome), or are each a superior competitor in half of shared niche space. Facilitation
of one species by another (an increase in the proportion of microsites that are safe) is also
possible (f). Red line indicates complete competitive exclusion of one species by another,
points in the grey shaded plot area indicate niche overlap, points in the white plot area indicate
facilitation.
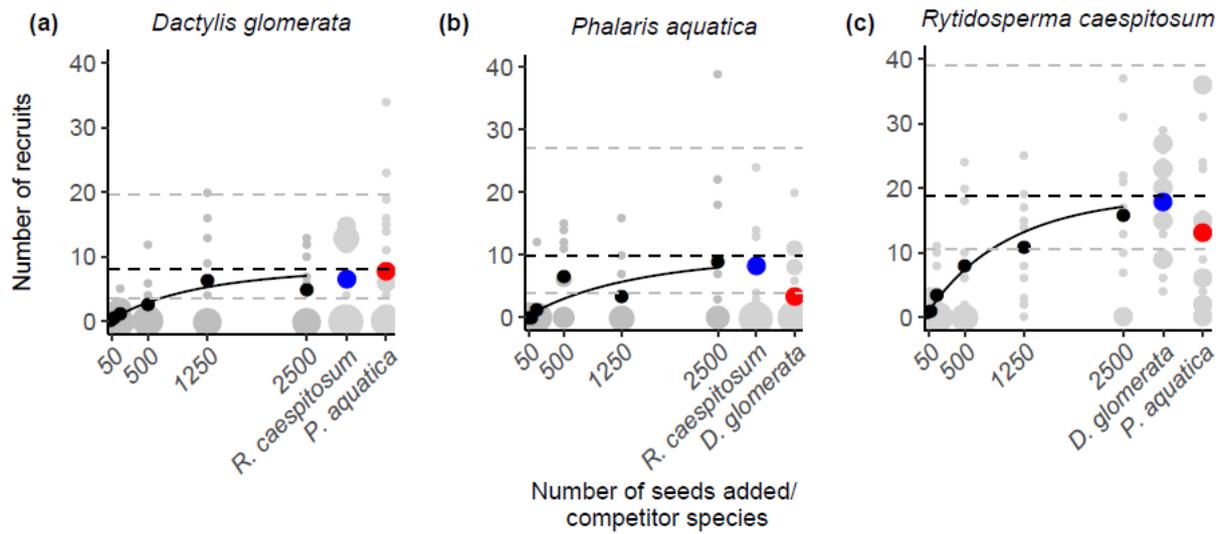
Figure 3. Fitted recruitment curves (black solid lines) for two exotic and one native species across a known moisture gradient in Experiment 1. Dashed horizontal lines show the number of safe-sites at seed saturation (i.e. $b_i n_i$: niche availability) for each species when sown in monoculture (black line shows the median and grey lines the 95% credible intervals); black points show the mean number of recruits per plot at each seed density; grey points show the raw data for the number of recruits per plot, with size proportional to the number of plots represented; coloured points show the mean recruitment per plot in polyculture (competitor species on the x axis; blue points indicate a native competitor and red an exotic).
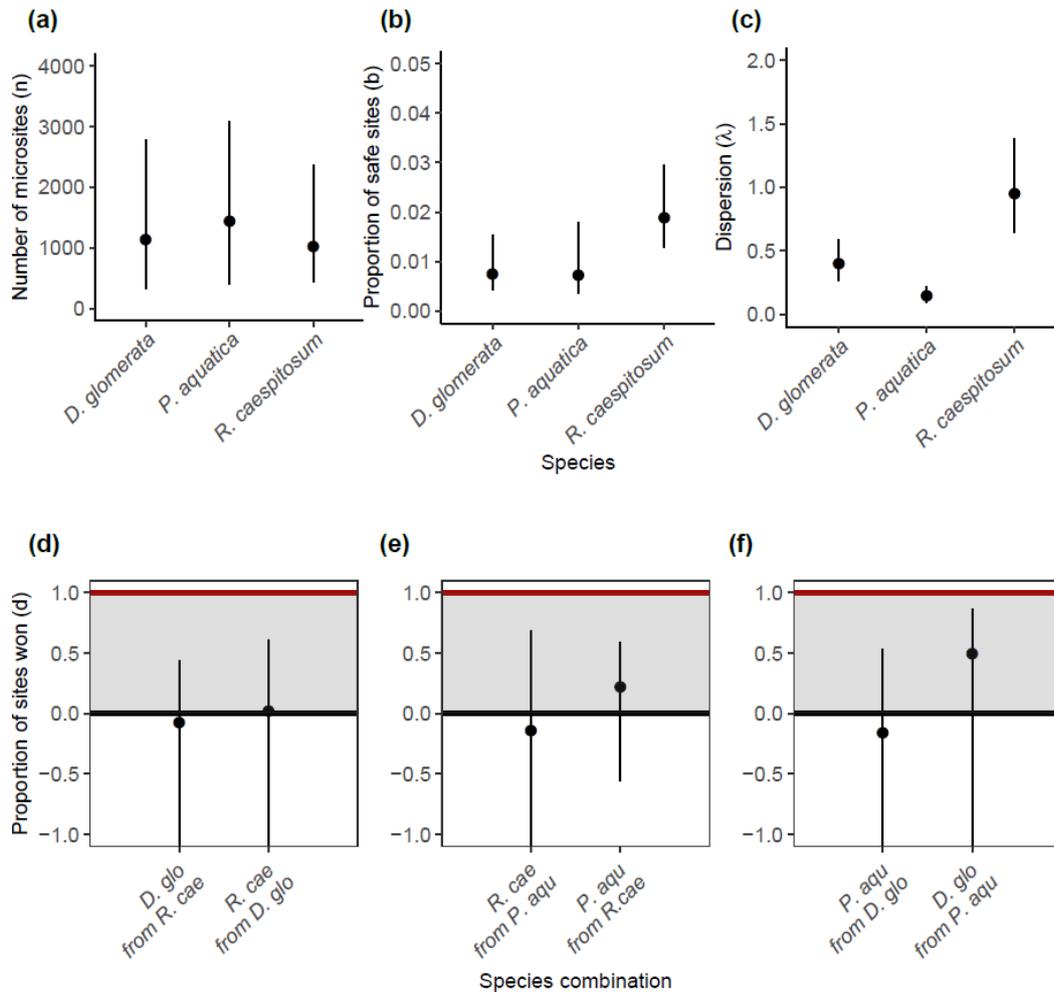
Figure 4. Model parameters for the two exotic and one native species in Experiment 1.
The parameters from the recruitment function describe: a) the median number of microsites per plot for each species; b) the proportion of microsites that are safe; and c) the dispersion of safe sites through space for each species when sown in monoculture. d-f) Values of d_{ij} and d_{ji} (the proportion of safe sites won by one species from another) for each species in each pairwise combination. Species codes in d-f: R. cae = *Rytidosperma caespitosum*; D. glo = *Dactylis glomerata*; P. aqu = *Phalaris aquatica*. Red line indicates complete competitive exclusion of one species by another, points in the grey shaded plot area indicate niche overlap, points in the white plot area indicate facilitation. Bars represent 95% credible intervals.

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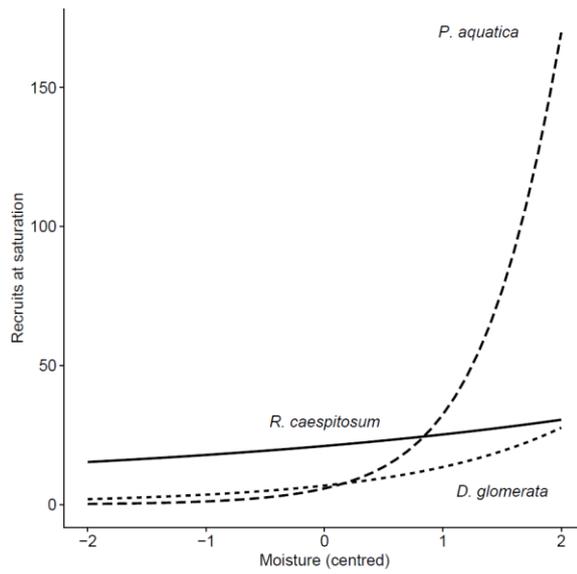
Figure 5. Modelled estimates of the mean number of recruits predicted for each species when all safe-sites are saturated across the soil moisture gradient in Experiment 1. Soil moisture values have been centred and standardised to mean = 0 and standard deviation = 1.

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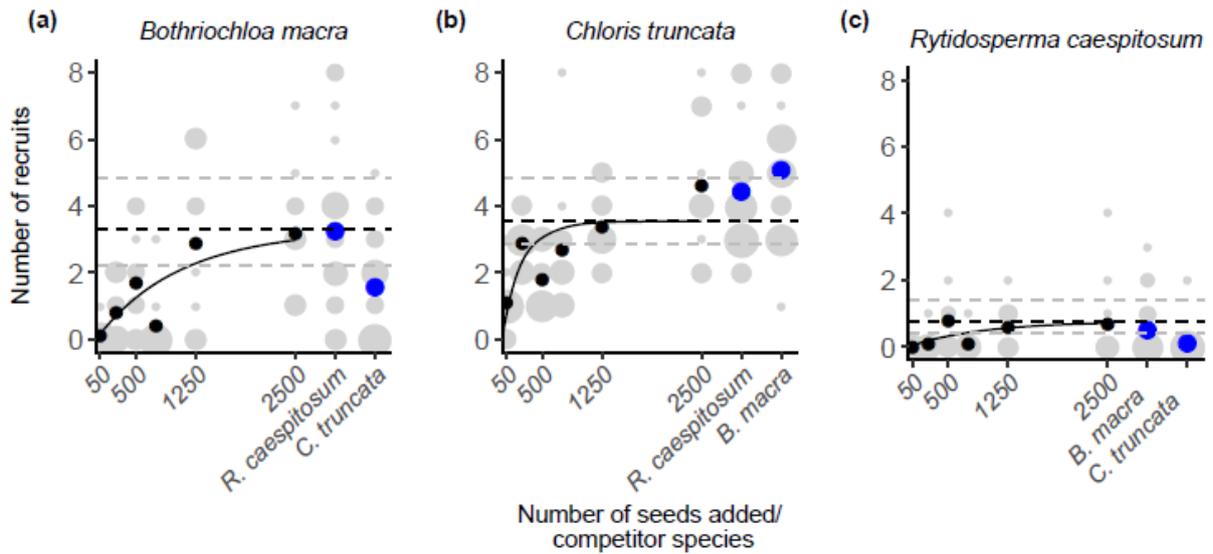
Figure 6. Fitted recruitment curves (black solid lines) for the three native species in Experiment 2. Dashed horizontal lines show the number of safe-sites at seed saturation (i.e. $b_i n_i$: niche availability) for each species when sown in monoculture (black line shows the median and grey lines the 95% credible intervals); black points show the mean number of recruits per plot at each seed density; grey points show the raw data for the number of recruits per plot, with size proportional to the number of plots represented; coloured points show the mean recruitment per plot in polyculture (competitor species on the x axis).
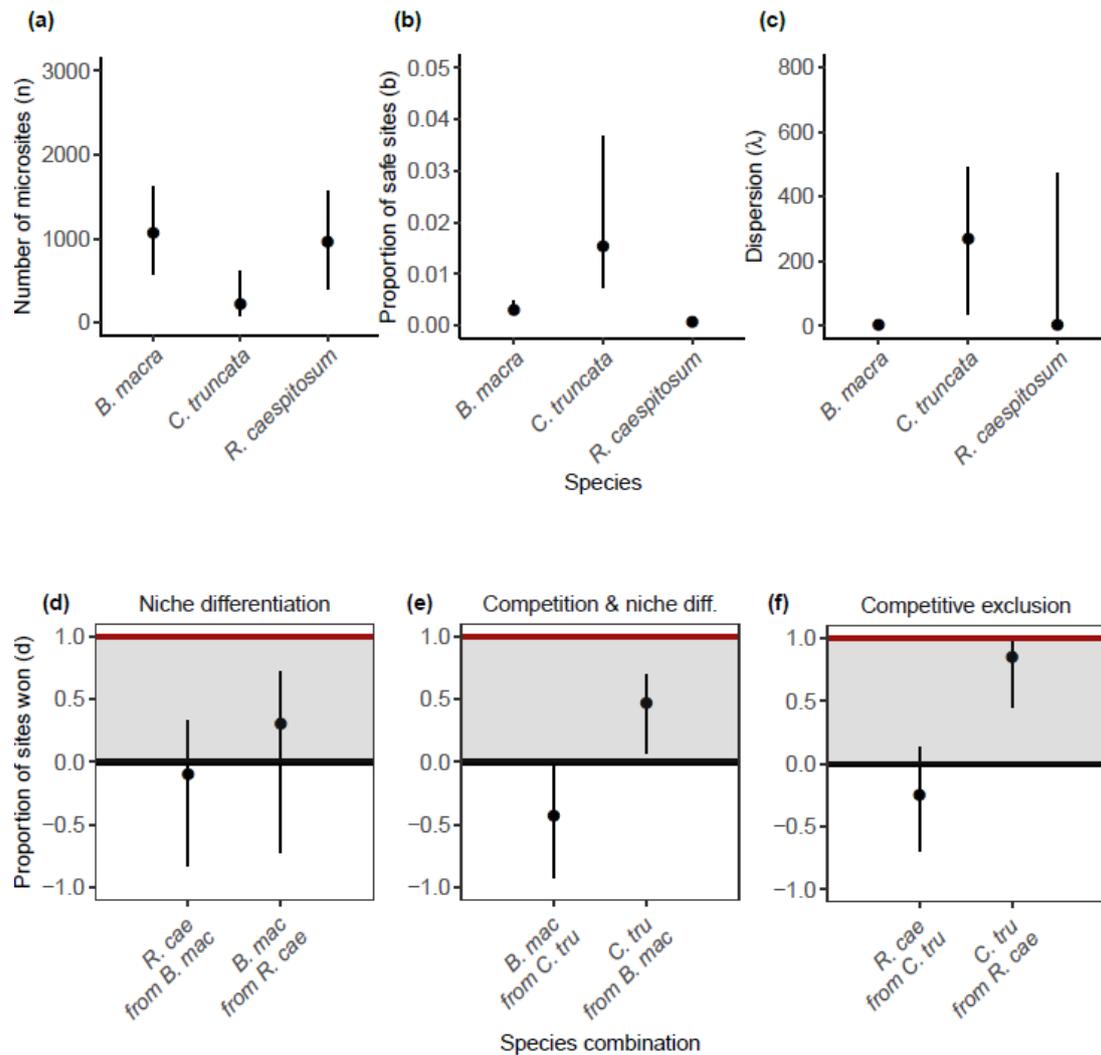
Figure 7. Model parameters for the three native species in Experiment 2. The parameters from the recruitment function describe: a) the median number of microsites per plot for each species; b) the proportion of microsites that are safe; and c) the dispersion of safe sites through space for each species when sown in monoculture. d-f) Values of d_{ij} and d_{ji} (the proportion of safe sites won by one species from another) for each species in each pairwise combination. Species codes in d-f: B. mac = *Bothriochloa macra*; C. tru = *Chloris truncata*; R. cae = *Rytidospermum caespitosum*. Red line indicates complete competitive exclusion of one species by another, points in the grey shaded plot area indicate niche overlap, points in the white plot area indicate facilitation. Bars represent 95% credible intervals.