**Seed aggregation tips the scale in plant competition: exploring heteromyopia with native, exotic, and mimic plants.**

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**Abstract**

Community assembly experiments in ecology provide a means to contrast abiotic and biotic influences that structure plant communities. Competition and facilitation are two common biotic predictors of species success in plant communities. Abiotic limitations can include but are not limited to space, light, and water. Spatial ecology of biotic and abiotic drivers is critical to the better understanding of plant invasion dynamics. Here, we test the relative importance of seed aggregation and light on the net outcome of interactions between a native desert annual and an invasive plant species *Phacelia tanacetifolia* and *Bromus madritensis ssp. rubens*, respectively. In particular, we tested the ecological heteromyopia hypothesis that competition occurs over shorter distances between seeds and plants. Monoculture and mixture seed trials were done under controlled greenhouse conditions for both species. *Phacelia tanacetifolia* and *Bromus madritensis ssp. rubens* preferred a clumped arrangement in monocultures and mixtures; and only *B. madritensis* experienced a significant negative response to *P. tanacetifolia* - even more so under clumped arrangement mixture.The native *P. tanacetifolia* did not respond to a plastic brome mimic we also tested to explore interference or space effects of this exotic species on natives. The light intensity experienced under these experimental conditions did not significantly influence the outcomes of seed trials. These findings suggest that seed aggregation is a potential key predictor of success for both the native and invasive species and that clumping in mixtures can benefit natives more than exotics. This study highlights the importance of spatial structure in predicting community assembly outcomes in invaded arid grasslands and provides insight for the better understanding of invasive species establishment.

Keywords: competition, facilitation, native plant, exotic plant, spatial ecology, desert, mimics.

**Introduction**

Plant interactions and community assembly are a major focus in ecological research and can advance restoration ecology. These dynamics depend on several environmental factors such as stress and biotic factors including inter and intra-specific interactions between plants (Lortie et al. 2004; Kraft et al. 2014). These interactions are particularly important during the initial phases of germination in influencing the relative abundances and assembly of plant communities (Dong et al. 2019). Individuals that secure the “upper hand” in terms of competition and/or facilitation will germinate and hoard space and resources from other species. This is known as interference competition (Amarasekare 2002; Vahl et al. 2005), and with respect to seed ecology is sometimes termed ‘safe sites’ (Harper et al. 1961; Harper, Williams and Sagar 1965). Plant competition and facilitation has been extensively studied in ecology (Aguiar et al. 1992; Callaway and Walker 1997; Bertness 1989). Local seed and plant density is commonly established as important in community assembly (McCallum et al. 2018; Hart and Marshall 2009), but interactions and other potential drivers of fine-scale dynamics in desert species in particular are not extensively studied (Lortie et al. 2005). It is also likely that there is significant heterogeneity at fine-scales in many systems relevant to seeds (Richardson et al. 2012; Garcia and Houle 2016) and that there is variation in the distribution of seeds at fine-scales (Richardson et al. 2012). This suggests that for many systems including those invaded by exotic annual species, examination of interactions in the context of fine-scale patterning of seeds is important.

An important consideration in plant ecology when examining competition within communities is spatial pattern of seeds and plants. Spatial ecology is a critical and growing field of ecological research since the physical structure of a community can predict species success (Miller 1989; Crawley and May 1987). Spatial aggregation and density dependence might interact and modify each other to differentially influence community level-dynamics (Lortie *et al.* 2005). Additionally, seedling emergence and plant establishment in the community is density-dependent, but are also influenced by resource limitation such as those resulting from spatial aggregation (Lortie and Turkington 2002a). Spatial aggregation may also promote species-coexistence; this however can be ecosystem-dependent (De Luis *et al.* 2008). Manipulating seed structure in the field is challenging because of the natural complexities of spatial patterns (Bolker et al. 2003). Despite this, experimental attempts for studying spatial ecology that has provided empirical results have proceeded usually with two spatial patterns: random and aggregated because these patterns seem to be the simplest, most frequently occurring patterns in some natural communities (Bolker et al. 2003; Pielou 1960). Common spatial structure hypotheses predict coexistence of plants at the population level, even in a competitive exclusion environment (Velazquez et al. 2014). This seems paradoxical since a clustered population of seeds should lead to increased intra-specific competition and therefore decreased success. However, when more than one species is involved, a lack of seed clustering may leave room for a second species to invade and possibly outcompete the first species (Velazquez et al. 2014). This phenomenon, known as ecological heteromyopia, describes where species with similar dynamics (i.e. a monoculture) will coexist more successfully than species with contrasting dynamics (Murrell and Law 2003). This trade-off is likely common in most plant communities (Murrell and Law 2003; Wilson et al. 2019). It is also highly relevant to invaded plant communities because native species may utilize this phenomenon as a counteractive measure against the nascent competitive pressure. This suggests that new species can invade communities depending on how tightly the seeds and plants are aggregated (Moore *et al.* 2003). This relates to both the propagule pressure hypothesis (Colautti *et al.* 2006) in invasion biology and the empty niche hypothesis (Pearson *et al.* 2012). The propagule pressure hypothesis posits that the success of invasive establishment is dependent on the initial size and frequency of introductions, and the empty niche hypothesis posits that any given ecosystem can sustain more species than the amount currently being sustained due to the presence of many opportunities/resources not being used by existing species. This empty niche hypothesis also goes hand in hand with Darwin’s naturalization hypothesis, where species with less relatedness are more likely to colonize and coexist with native species due to differing needs such as pH and temperature resulting in relatively low competition (Pearson *et al.* 2012). Considering these natural phenomena, it seems that seed aggregation plays a major role in influencing whether an exotic species will coexist well or poorly with a native species, and understanding this predictor can advance restorative and preventative measures against ecosystem invasiveness.

Here, we apply this model on controlled populations of two Southern Californian species. We tested the highly invasive species *Bromus madritensis ssp. rubens*, or Red Brome (Salo 2004; Salo 2005), and the native annual *Phacelia tanacetifolia* (Calflora 2020). *B. rubens* has been known to outcompete several native species including members of the Phacelia genus (Abella 2017). The hypothesis tested is that the spatial aggregation of seeds shifts the net outcome of native-exotic interactions at early life-stages. The following three predictions were examined: (i) increased seed aggregation increases competitive interactions intra and inter-specifically for each species, (ii) native seeds can outcompete an invasive species at some seed aggregations, and (iii) one of the key effects of the invasive species brome is physical interference with natives. A mimic for brome was used to explore physical interference directly aboveground.

**Materials and Methods**

***Study Species & Location***

*Bromus rubens*, or red brome- a herbaceous, grass/sedge annual that can grow up to 40 cm tall and propagate an average of 76 seeds per plant in the wild (USDA Plants Database 2018). Introduced unintentionally as an invasive species from southern Europe to America, *B. rubens* finds success even in the presence of drought at low to medium elevations (i.e. under 1500 meters) (Beatley 1966). *Phacelia tanacetifolia*, known commonly as the California bluebell, is a herbaceous annual native to the southwestern United States that can grow up to a height of 100 cm. Seeds of *P. tanacetifolia* and are photodormant (or negatively photoblastic) (Serrato-Valenti et al. 1998). This means that they can only germinate in the absence of light and, comparably to *B. rubens*, at elevations below 5000 feet (Chen and Thimann 1966). With both species sharing similar habitats and elevations, interspecies competition between the two annuals commonly occurs. Seeds of annuals *Bromus rubens L*. and *Phacelia tanacetifolia* were purchased from Outsidepride.

This study was conducted at the York University Department of Biology greenhouse in Toronto, Canada (43° 46’ 13.81” N, -79° 30’ 7.83” W). High pressure sodium lamps provided relatively even light levels throughout the greenhouse during the day, which was measured using a LI-COR Biosciences LI-250A light intensity meter with a LI-190R quantum sensor. The experimental trial was done from October 29 to December 16, 2019. Seeds of both species were planted in 15 cm diameter pots. Pots were filled with a mix of 50% organic material, 25% vermiculite, and 25% sand. Soil was also enhanced with a standard NPK mix prior to experiment. Seeds were sown in the top 1 cm of soil and lightly covered and then immediately watered to ensure they remained intact and in place.

***Experimental Design***

There were a total of four treatments at each spatial pattern for 20 replicates per level. For the two monoculture treatments, one native and one exotic, we planted 10 seeds of either *P. tanacetifolia* or *B. rubens* per pot. The mixed treatment had a total of 10 seeds, two seeds of *B. rubens* and eight seeds of *P. tanacetifolia.* To test for space and interference effects, we conducted additional mixture treatments replacing *B. rubens* with 3D printed mimics (See Appendix A for description and photos of mimics). Spatial patterns were either clumped (seeds centered on the middle of the pot with a minimum distance of 3 to 3.5 cm) or dispersed (seeds distributed along the edges of the pot with a minimum distances of 0.5 to 1 cm). Pots were watered on a weekly basis for eight weeks with each pot receiving 6 mL of water per seed per pot.

***Responses***

Light intensity was measured in μmol s-1 m-2 using a LI-COR LI-250A light meter with a LI-190R quantum sensor in the same house described above. Plant height, density, aboveground cover, and total above and belowground pooled biomass were recorded. Plant height was measured by recording the tallest plant of each species in each pot was measured from soil to tip in centimeters and was measured on week 4 (establishment phase) and week 8 (final phase) of experimental trials. The density of plants in each pot was counted on a bi-weekly basis for the duration of experiment. Cover was measured visually by estimating the total percent of soil surface comprised by plant material from directly over each pot. The above non-destructive measures were recorded three times but collapsed for analyses to establishment and final censuses. Establishment was defined as the point in time after which no new seedlings emerged i.e. after 4 weeks of initiation. Lastly, biomass was measured at the final census after 8 weeks by collecting all plant material including the roots of each pot which were separated and dried for 48 hours in a Yamato Scientific America DKN912 constant temperature ovens at 65 oC. The plants were subsequently weighed in grams on a Mettler Toledo XS204 analytical balance.

***Statistical Analyses***

All statistical analyses were done in R version 4.0.0 (R Core Team 2020). Workflow and code are published on Zenodo (Lortie *et al*. 2020), and data are published on Figshare (Cho *et al.* 2020). Generalized Linear Models (GLM) were used to compare spatial pattern and treatment in both native and exotic species with light serving as a covariate (Nelder and Wedderburn 1972). Biomass and cover were modeled as Gaussian and density with a quasi-poisson distribution. Post-hoc pairwise comparisons were done using the function ‘emmeans’ from the *emmeans library* (Lenth and Herve 2019).

**Results**

Seed aggregation significantly influenced *P. tanacetfolia* emergence and final densities (Fig 1, Table 1) with clumped patterns outperforming dispersed in both censuses (Post hoc contrast analyses, Appendix B). *Phacelia tanacetfolia* biomass and cover did not significantly vary between other treatments including mixture versus monoculture or sown with a mimic (Table 1). *Bromus rubens* emergence density and cover responded to seed aggregation and mixtures (Fig 2, Table 2). *Bromus rubens* established best in monocultures and sown in clumped patterns at both censuses (Figure 2, Post hoc contrast analyses, Appendix B). Final biomass for *B. rubens* was also greatest in monocultures at clumped aggregations (Table 2, Appendix B). There was also a significant interaction term between seed pattern and mixtures for *B. rubens* with the lowest performance under clumped mixture conditions (Figure 2, Appendix B). Lastly, light was shown to be not significant in any of the models.

**Discussion**

Our findings supported the hypothesis that spatial aggregation of seeds shifts the net outcome of interactions in arid and semi-arid species, though the direction of these interactions were more complex than initially expected. In contrast, seed aggregation with a low proportion of *B. rubens* and a high proportion of *P. tanacetifolia* resulted in significant non-success of the invasive species. These results followed patterns of intraspecific tolerance/facilitation and interspecific competition of *P. tanacetifolia* and *B. rubens*, as predicted. This is to say that in mixed, interspecific circumstances, competition decreases as space increases.

Our first prediction (increased seed aggregation increases competitive interactions both intra- & inter-specifically) was not true for native plants and was only true for *B. rubens* in interspecific mixtures. This is to say that high seed aggregation of *P. tanacetifolia* resulting in higher success than a lower seed aggregation. In our greenhouse, low stress environment, *P. tanacetifolia* exhibitedintraspecific tolerance/facilitation. Despite focusing on intraspecific interactions of annuals, this result is congruent with some previous work highlighting the frequency of interspecific facilitation along the low end of a stress gradient of larger, woody plants (Longland and Dimitri 2016). *Bromus rubens*, however, did not exhibit increased faciltation or any tolerance among members of its own species despite the low stress, controlled environment. However, *B. ruben’s* results do reflect some other work that suggests that as stress decreases, intraspecific competition increases and interspecific facilitation decreases (Garcia-Cervigon et al 2013). We suggest that this difference is due, at least in part, to the difference in dispersion strategies for native annuals versus invasive grasses. Invasive plants have been shown to have consistently higher growth when paired only with members of their own species and can fill out more space (Holmes et al 2010). This is all to say that facilitative effects of seeds is specific, even in monocultural situations and that density of intrsapecifics can be influenced strongly by resource availability (Lortie & Turkington 2002a; Lortie & Turkington 2002b).

Our second prediction (native seeds can outcompete an invasive species at some seed aggregations) was true at any level of spatial aggregation, however, we also saw that natives had greater germination and growth in clumped aggregations relative to dispersed aggregations. These results are somewhat contrary to the heteromyopia hypothesis, which states that interspecific competition occurs over shorter distances than intraspecific competition (Weiner and Conte 1981; Murrell & Law 2002), which was not exhibited by our native seeds. We believe this may be due to the idea that heteromyopia is largely impacted by nutrient availability (Milkereit 2016), and in our experiments, nutrient availability was high (low stress environment). Heteromyopia, however, was consistent in certain situations. Aggregated individuals that share similar growth dynamics should coexist with greater success collectively (Murrell and Law 2003); such is the case in the clumped *Phacelia* monoculture, though not among clumped *Bromus.* Additionally, these improved germination rates among clumped *Phacelia* can be explained by the effects of intraspecific facilitation leading to increased success of all parties involved and is consistent with finding from other monoculture experiments that manipulated the frequency of intraspecific contacts (Turnbull *et al*. 2007).

Our third and final prediction (one of the key effects of the invasive species brome is physical interference with natives) was not supported, though this result is in line with the results of our other predictions. Replicates with mimic brome (creating no nutrient competition with *Phaecelia* but maintaining aboveground space) again did not exhibit heteromyopia: we believe this is because no nutrient competition occurred. Physical space aboveground therefore should not be considered as influential in competition between native *Phaecelia* and invasive *Bromus*.

It is important to note that out of the 40 replicates of this treatment, not one pot replicate had co-germination of both species. An interesting result, this clarity may stem from a lack of replicates used; it may, however, be due to strong interspecific competitive forces driving the success of a single species. Specifically, 6 *B. rubens* seeds successfully germinated out of 80 *B. rubens* seeds planted, with 1 in 6 germinated seeds occurring in the clumped spatial pattern. This is contrasted with 7 *P. tanacetifolia* seeds germinating out of 320 seeds planted, with 4 out of the 7 germinated seeds occurring in the clumped spatial pattern. This suggests that, in the presence of interspecies competition between *P. tanacetifolia* and *B. rubens*, *P. tanacetifolia* tends to outcompete *B. rubens* when local density is high (i.e. a clumped spatial pattern), whereas *P. tanacetifolia* tends to be outcompeted by *B. rubens* when local density is low (i.e. a dispersed spatial pattern). This is in line with previous work suggesting that competition may be so strong that no germination occurs at all (Boerner and Harris 1991; Rice and Dyer 2001).

In desert ecosystems where the sun’s light is particularly strong, light intensity is an important selective pressure that has led to adaptations reliant on a lack light. The negatively photoblastic nature of *P. tanacetifolia* seeds are likely a factor in this observation (Serrato-Valenti *et al*. 1998). With there being a denser concentration of seeds to absorb light in a clumped spatial pattern, less light per cubic mm is available for each seed, which may be a significant predictor for why *P. tanacetifolia* success is greater in clumped spatial patterns when paired with *B. rubens* (Craine and Dybzinski 2013). When *P. tanacetifolia* seeds are more dispersed, individual seeds will be exposed to more light per cubic mm, decreasing the chances of germination.

This is a strong pilot study showing that albeit relatively low proportions of seed germination, a native and exotic annual species respond differently to seed aggregation under controlled conditions. There are at least three major future directions suggested by this experiment: repeating the trials in the field, repeating the trials under controlled conditions with changes in species seed density, and repeating the trials under field or controlled conditions with changes in light intensity and watering frequency.Moreover,repeating treatments with more reps (n = 50 per spatial pattern) will result in more statistical power in analyses. Both treatment 1 and 2 did not meet the assumption of normality due to a lack of germinated seeds that resulted in a lack of data points. This led to an unideal situation where low power statistical tests were performed for these treatments. Of course, the lack of germination from these two treatments could very well reflect reality, but either way an increase in reps would increase both power and certainty. Additionally, a similar study exploring the interaction of one invasive species with more than one native species may yield different results due to the increased diversity (Thébalut *et al*. 2012).

In these trials, we kept the ratio of native to exotic constant (8:2), as an attempt to replicate a natural setting where an invasive species enters and influences the community assembly of native species. In the future, changing this ratio (e.g. 5:5, 2:8) can provide greater insight into how a wider proportional scale of competitor frequency may change community assembly. With a high proportion of invasive species paired with a low proportion of native species, a highly aggregated seed clump may show success of the invasive species instead (although this may not accurately reflect nature). Furthermore, adding species exhibiting competitive strategies not already represented to the experiments will more accurately depict a natural community of plants, and may illustrate patterns of competition that cannot be analyzed with only two species.

This is all to say that we believe these results have significant implications for environmental managers struggling to combat invasive grasses where native annuals should be. Many arid ecosystems are transitioning from deserts to desert-grasslands (Hirsch 2011) due to this invasive of *Bromus*, dramatically shifting the habitat of wildlife and even the availability of unique ecosystem services of deserts which are already undervalued due to their relatively low monetary assignments by some (but not all) groups (Tayor et al 2017; Longland et al 2012; Cuni-Sanchez et al 2016). Currently, seed deposition restoration practices (and their success) varies widely, and it seems consideration for micro-level spatial distribution as we have described is less prioritized (Larson 2012). In areas seeking to return to a desert habitat from a grassland, we suggest that managers explore the feasibility of planting native annuals in clumped patterns instead. We believe this practice may improve germination success for native seeds, even among invasive *Bromus*. Overall, our results provide insight on an ideal desert annual community structure for minimizing/preventing the introduction of an exotic species and contributes to our understanding on the effectiveness and strategies of invasive species establishment.

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