

Important declarations

Please remove this info from manuscript text if it is also present there.

Associated Data

Data supplied by the author:

figshare.com/s/8458a1b5ada945e87255

Required Statements

Competing Interest statement:

The authors declare that they have no conflict of interest.

Funding statement:

This study was possible thanks to the National Sciences and Engineering Research Council of Canada (NSERC) grant awarded to C.J.L.

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

Calvin Cho¹, Christopher J Lortie^{1,2}, Jenna Braun¹, Malory Owen¹, Nargol Ghazian^{Corresp. 1}

¹ Biology, York University, Toronto, ON, Canada

² National Center for Ecological Analysis and Synthesis, Santa Barbara, California, United States

Corresponding Author: Nargol Ghazian
Email address: nargolg1@my.yorku.ca

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.

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

Calvin Cho¹, Christopher J. Lortie^{1,2}, Jenna Braun¹, Malory Owen¹, and Nargol Ghazian^{1*}.

¹Department of Biological Science, York University, 4700 Keele St, Toronto, ON M3J 1P3, Canada

²National Centre for Ecological Analysis and Synthesis (NCEAS), 735 State St #300, Santa Barbara, CA 93101, United States

*Corresponding Author: Department of Biological Science, York University, 4700 Keele St, Toronto, ON, M3J 1P3, Canada. Email: nargolg1@my.yorku.ca, CELL: (+1) 416-721-0616.

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 (Aguilar 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 $\mu\text{mol s}^{-1} \text{m}^{-2}$ 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 °C. 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. tanacetifolia* emergence and final densities (Fig 1, Table 1) with clumped patterns outperforming dispersed in both censuses (Post hoc contrast analyses, Appendix B). *Phacelia tanacetifolia* 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* exhibited intraspecific 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 facilitation 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 intraspecifics 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 *Phacelia* 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 *Phacelia* 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 (Taylor 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.

Acknowledgement

This study was possible thanks to the National Sciences and Engineering Research Council of Canada (NSERC) grant awarded to C.J.L.

Special thank you to our colleague and friend H. Ly for assisting with greenhouse trial maintenance and data collection.

Works Cited

- Abella, S. R., Craig, D. J., Chiquoine, L. P., Prengaman, K. A., Schmid, S. M., & Embrey, T. M. (2011). Relationships of Native Desert Plants with Red Brome (*Bromus rubens*): Toward Identifying Invasion-Reducing Species. *Invasive Plant Science and Management*, 4(1), 115–124. doi: 10.1614/ipsm-d-10-00013.1
- Adler, F.R. (2010). The effects of intraspecific density dependence on species richness and species abundance distributions, *Theoretical Ecology* 10.1007/s12080-010-0108-7, 4, 2, (153-162).
- Aguiar, M. R., Soriano, A., & Sala, O. E. (1992). Competition and Facilitation in the Recruitment of Seedlings in Patagonian Steppe. *Functional Ecology*, 6(1), 66. doi: 10.2307/2389772
- Amarasekare, P. (2002). Interference competition and species coexistence. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269(1509), 2541–2550. doi: 10.1098/rspb.2002.2181
- Bacq-Labreuil, A., Crawford, J., Mooney, S. J., Neal, A. L., & Ritz, K. (2019). Phacelia (*Phacelia tanacetifolia* Benth.) affects soil structure differently depending on soil texture. *Plant and Soil*, 441(1-2), 543–554. doi: 10.1007/s11104-019-04144-4
- Beatley, J. C. (1966). Ecological Status of Introduced Brome Grasses (*Bromus* Spp.) in Desert Vegetation of Southern Nevada. *Ecology*, 47(4), 548–554. doi: 10.2307/1933931

- 354 Bennett, R. J., & Haining, R. P. (1985). Spatial Structure and Spatial Interaction: Modelling
355 Approaches to the Statistical Analysis of Geographical Data. *Journal of the Royal Statistical*
356 *Society. Series A (General)*, 148(1), 1. doi: 10.2307/2981508
- 357 Benthem, K.J.V. and Wittmann, M.J. (2019). Density dependence on multiple spatial scales
358 maintains spatial variation in both abundance and traits, *Journal of Theoretical Biology*,
359 10.1016/j.jtbi.2019.110142, (110142).
- 360 Bertness, M. D. (1989). Intraspecific Competition and Facilitation in a Northern Acorn Barnacle
361 Population. *Ecology*, 70(1), 257–268. doi: 10.2307/1938431
- 362 Boerner, R. E. J., & Harris, K. K. (1991). Effects of collembola (arthropoda) and relative
363 germination date on competition between mycorrhizal *Panicum virgatum* (Poaceae) and non-
364 mycorrhizal *Brassica nigra* (Brassicaceae). *Plant and Soil*, 136(1), 121–129. doi:
365 10.1007/bf02465227
- 366 Bolker, B.M., Pacala, S.W. and Neuhauser, C. (2003). Spatial Dynamics in Model Plant
367 Communities: What Do We Really Know? *The American Naturalist*, 162(2), 135-148.
- 368 Callaway, R. M., & Walker, L. R. (1997). Competition And Facilitation: A Synthetic Approach
369 To Interactions In Plant Communities. *Ecology*, 78(7), 1958–1965. doi: 10.1890/0012-
370 9658(1997)078[1958:cafasa]2.0.co;2
- 371 Chen, S. S. C., & Thimann, K. V. (1966). Nature of Seed Dormancy in *Phacelia*
372 *tanacetifolia*. *Science*, 153(3743), 1537–1539. doi: 10.1126/science.153.3743.1537
- 373 Cho, C. (2020). Spatial plant data. *Figshare*, figshare.com/s/8458a1b5ada945e87255

374 Cocucci, M., & Negrini, N. (1991). Calcium-calmodulin in germination of *Phacelia tanacetifolia*
 375 seeds: effects of light, temperature, fusicoccin and calcium-calmodulin antagonists. *Physiologia*
 376 *Plantarum*, 82(2), 143–149. doi: 10.1034/j.1399-3054.1991.820201.x

377 Cocucci, S., Ranieri, A. M., Morgiutti, S., & Cirotti, F. (1981). The role of darkness, GA and
 378 fusicoccin (FC) in breaking photodormancy in *Phacelia tanacetifolia* seeds. *Physiologia*
 379 *Plantarum*, 52(2), 177–180. doi: 10.1111/j.1399-3054.1981.tb08489.x

380 Colautti, R.I., Grigorovich, I.A. and MacIsaac, H.J. (2006). Propagule Pressure: A Null Model
 381 for Biological Invasions. *Biological Invasions*, 8, 1023-1037.

382 Cousens, R.D., Wiegand, T. and Taghizadeh, M.S. (2008). Small-scale spatial structure within
 383 patterns of seed dispersal. *Oecologia* 10.1007/s00442-008-1150-7, 158, 3, (437-448).

384 Craine, J. M., & Dybzinski, R. (2013). Mechanisms of plant competition for nutrients, water and
 385 light. *Functional Ecology*, 27(4), 833–840. doi: 10.1111/1365-2435.12081

386 Crawley, M., & May, R. (1987). Population dynamics and plant community structure:
 387 Competition between annuals and perennials. *Journal of Theoretical Biology*, 125(4), 475–489.
 388 doi: 10.1016/s0022-5193(87)80215-1

389 De Luis, M., Raventos, J., Wiegand, T. and Gonzalez-Hidalgo, J. C. (2008). Temporal and
 390 spatial differentiation in seedling emergence may promote species coexistence in Mediterranean
 391 fire-prone ecosystems. *Ecography*, 31(5), 620-629.

392 Dong, K., Hao, G., Yang, N., Zhang, J.-L., Ding, X.-F., Ren, H.-Q, Gao, Y.-B. (2019).
 393 Community assembly mechanisms and succession processes significantly differ among

394 treatments during the restoration of *Stipa grandis* – *Leymus chinensis* communities. *Scientific*
 395 *Reports*, 9(1). doi: 10.1038/s41598-019-52734-0

396 Dray, S., Péliissier, R., Couteron, P., Fortin, M.-J., Legendre, P., Peres-Neto, P. R., ... Wagner,
 397 H. H. (2012). Community ecology in the age of multivariate multiscale spatial
 398 analysis. *Ecological Monographs*, 82(3), 257–275. doi: 10.1890/11-1183.1

399 Garcia, D. and Houle, G. (2016). Fine-scale spatial patterns of recruitment in red oak (*Quercus*
 400 *rubra*): What matters most, abiotic or biotic factors? *Ecoscience*, 12(2), 223-235.

401 Griffith, D. A., & Peres-Neto, P. R. (2006). Spatial Modeling In Ecology: The Flexibility Of
 402 Eigenfunction Spatial Analyses. *Ecology*, 87(10), 2603–2613. doi: 10.1890/0012-
 403 9658(2006)87[2603:smietf]2.0.co;2

404 Harper, J.L., Clatworthy, J.N., McNaughton, I.H. and Sagar, G.R. (1961). The evolution and
 405 ecology of closely related species living in the same area. *Evolution*, 15, 209-227.

406 Harper, J.L., Williams, J.T. and Sagar, G.R. (1965). The Behaviour of Seeds in Soil: 1. The
 407 Heterogeneity of Soil Surfaces and its Role in Determining the Establishment of Plants from
 408 Seed. *Journal of Ecology*, 53(2), 273-286.

409 Hart, S. P., & Marshall, D. J. (2009). Spatial arrangement affects population dynamics and
 410 competition independent of community composition. *Ecology*, 90(6), 1485–1491. doi:
 411 10.1890/08-1813.1

412 Herben, T. and Wildová, R. (2012). Community-level effects of plant traits in a grassland
 413 community examined by multispecies model of clonal plant growth, *Ecological Modelling*,
 414 10.1016/j.ecolmodel.2011.06.012, 234, (60-69).

415 Huston, M. A., & Deangelis, D. L. (1987). Size Bimodality in Monospecific Populations: A
 416 Critical Review of Potential Mechanisms. *The American Naturalist*, 129(5), 678–707. doi:
 417 10.1086/284666

418 Koyama, H., and T. Kira. (1956). Intraspecific competition among higher plants. VIII. Frequency
 419 distribution of individual plant weight as affected by the interaction between plants. *Journal of*
 420 *the Institute of Polytechnics*, Osaka City University 7:73–94.

421 Kraft, N.J.B., Adler, P.B., Godoy, O., James, E.C., Fuller, S. and Levine, J.M. (2014).
 422 Community assembly, coexistence and the environmental filtering metaphor. *Community*
 423 *Phylogenetics and Ecosystem Functioning*, 29(5), 592-599.

424 Laird, R. A., & Schamp, B. S. (2008). Does Local Competition Increase The Coexistence Of
 425 Species In Intransitive Networks. *Ecology*, 89(1), 237–247. doi: 10.1890/07-0117.1

426 Law, R., Dieckmann, U., & Metz, J. A. (2000). The Geometry of Ecological
 427 Interactions. *Cambridge University Press, Cambridge*, 1–6. doi:
 428 10.1017/cbo9780511525537.001

429 Length, R. and Herve, M. (2019). *Emmeans, Estimated Marginal Means, Aka Least-Squared*
 430 *Means*. (version 1.1.2).

431 Lortie, C.J. (2020). Spatial density series. *Zenodo*,
 432 *zenodo.org/account/settings/github/repository/cjlortie/Spatial_density_series*.

433 Lortie, C. J., Brooker, R. W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F. I., & Callaway,
 434 R. M. (2004). Rethinking plant community theory. *Oikos*, 107(2), 433–438. doi: 10.1111/j.0030-
 435 1299.2004.13250.x

436 Lortie, C.J., Ellis, E., Novoplansky, A. and Turkington, R. (2005). Implications of spatial pattern
437 and local density on community-level interactions. *Oikos*, 109(3), 495-502.

438 Lortie, C.J. and Turkington, R. (2002a). The effect of initial seed density on the structure of a
439 desert annual plant community. *Journal of Ecology*, 90, 435-445.

440 Lortie, C.J. and Turkington, R. (2002b). The facilitative effects by seeds and seedlings on
441 emergence from the seed bank of a desert annual plant community. *Ecoscience*, 9(1), 106-111.

442 Lortie, C.J. and Turkington, R. (2002c). The small-scale spatiotemporal pattern of a seed bank in
443 the Negev Desert, Israel. *Ecoscience*, 9(3), 407-413.

444 Lortie, C.J. and Turkington, R. (2008). Species-specific positive effects in an annual plant
445 community. *Oikos*, 117, 1511-1521.

446 Mccallum, K. P., Lowe, A. J., Breed, M. F., & Paton, D. C. (2018). Spatially designed
447 revegetation-why the spatial arrangement of plants should be as important to revegetation as they
448 are to natural systems. *Restoration Ecology*, 26(3), 446–455. doi: 10.1111/rec.12690

449 Miller, T. E., & Weiner, J. (1989). Local Density Variation may Mimic Effects of Asymmetric
450 Competition on Plant Size Variability. *Ecology*, 70(4), 1188–1191. doi: 10.2307/1941388

451 Moore, J.L., Mouquet, N., Lawton, J.H. and Loreau, M. (2003). Coexistence, saturation and
452 invasion in simulated plant assemblages. *Oikos*, 94(2), 303-314.

453 Murrell, D.J. and Law, R. (2003). Heteromyopia and the spatial coexistence of similar
454 competitors. *Ecology Letters*, 6, 48-59. doi:10.1046/j.1461-0248.2003.00397.x.

455 Nelder, J. A., & Wedderburn, R. W. M. (1972). Generalized Linear Models. *Journal of the Royal*
456 *Statistical Society. Series A (General)*, 135(3), 370. doi: 10.2307/2344614

457 Pearson, D.E., Ortega, Y.K. and Sears, S.J. (2012). Darwin's naturalization hypothesis up-close:
458 Intermountain grassland invaders differ morphologically and phenologically from native
459 community dominants. *Biological Invasions*, 14, 901-913.

460 Pielou, E. C. (1960). A Single Mechanism to Account for Regular, Random and Aggregated
461 Populations. *The Journal of Ecology*, 48(3), 575. doi: 10.2307/2257334

462 R Core Team. (2020). *R* (version 3.6.1).

463 Rice, K. J., & Dyer, A. R. (2001). Seed aging, delayed germination and reduced competitive
464 ability in *Bromus tectorum*. *Plant Ecology*, 155(2), 237–243. doi: 10.1023/a:1013257407909

465 Richardson, P.J., MacDougall, A.S. and Larson, D.W. (2012). Fine-scale spatial heterogeneity
466 and incoming seed diversity additively determine plant establishment. *Journal of Ecology*,
467 100(4), 939-949.

468 Roy, J. R., & Thill, J.-C. (2003). Spatial interaction modelling. *Papers in Regional*
469 *Science*, 83(1), 339–361. doi: 10.1007/s10110-003-0189-4

470 Rudolf, V.H.W., Kamo, M. and Boots, M. (2010). Cannibals in Space: The Coevolution of
471 Cannibalism and Dispersal in Spatially Structured Populations. *The American Naturalist*
472 10.1086/651616, 175, 5, (513-524).

473 Salo, L. F. (2004). Population dynamics of red brome (*Bromus madritensis* subsp. *rubens*): times
474 for concern, opportunities for management. *Journal of Arid Environments*, 57(3), 291–296. doi:
475 10.1016/s0140-1963(03)00110-1

476 Salo, L. F. (2005). Red brome (*Bromus rubens* subsp. *madritensis*) in North America: possible
 477 modes for early introductions, subsequent spread. *Biological Invasions*, 7(2), 165–180. doi:
 478 10.1007/s10530-004-8979-4

479 Schwinning, S., & Fox, G. A. (1995). Population Dynamic Consequences of Competitive
 480 Symmetry in Annual Plants. *Oikos*, 72(3), 422. doi: 10.2307/3546128

481 Schwinning, S., & Weiner, J. (1998). Mechanisms determining the degree of size asymmetry in
 482 competition among plants. *Oecologia*, 113(4), 447–455. doi: 10.1007/s004420050397

483 Serrato-Valenti, G., Mariotti, M. G., Cornara, L., & Corallo, A. (1998). A Histological and
 484 Structural Study of *Phacelia tanacetifolia* Endosperm in Developing, Mature, and Germinating
 485 Seed. *International Journal of Plant Sciences*, 159(5), 753–761. doi: 10.1086/297594

486 Silveira, A. P., Martins, F. R., Menezes, B. S., & Araújo, F. S. (2017). Is the spatial pattern of a
 487 tree population in a seasonally dry tropical climate explained by density-dependent
 488 mortality? *Austral Ecology*, 43(2), 191–202. doi: 10.1111/aec.12556

489 Su, M., Zhang, Y., Hui, C. and Li, Z. (2008). The effect of migration on the spatial structure of
 490 intraguild predation in metapopulations. *Physica A: Statistical Mechanics and its Applications*,
 491 10.1016/j.physa.2008.02.056, 387, 16-17, (4195-4203).

492 Surendran, A., Plank, M.J. and Simpson, M.J. (2019). Spatial structure arising from chase-escape
 493 interactions with crowding. *Scientific Reports*, 10.1038/s41598-019-51565-3, 9, 1.

494 Thébault, A., Stoll, P., & Buttler, A. (2012). Complex interactions between spatial pattern of
 495 resident species and invasiveness of newly arriving species affect invasibility. *Oecologia*, 170(4),
 496 1133–1142. doi: 10.1007/s00442-012-2376-y

497 Turnbull, L., Coomes, D., Purves, D., & Mark Reesi. (2007). How Spatial Structure Alters
 498 Population and Community Dynamics in a Natural Plant Community. *Journal of Ecology*, 95(1),
 499 79-89.

500 Uriarte, M., & Menge, D. (2018). Variation between individuals fosters regional species
 501 coexistence. *Ecology Letters*, 21(10), 1496–1504. doi: 10.1111/ele.13130

502 Vahl, W. K., Meer, J. V. D., Weissing, F. J., Dullemen, D. V., & Piersma, T. (2005). The
 503 mechanisms of interference competition: two experiments on foraging waders. *Behavioral*
 504 *Ecology*, 16(5), 845–855. doi: 10.1093/beheco/ari073

505 Velázquez, J., Garrahan, J. P., & Eichhorn, M. P. (2014). Spatial Complementarity and the
 506 Coexistence of Species. *PLoS ONE*, 9(12). doi: 10.1371/journal.pone.0114979

507 Vogt, D.R., Murrell, D.J. and Stoll, P. (2010). Testing Spatial Theories of Plant Coexistence: No
 508 Consistent Differences in Intra- and Interspecific Interaction Distances. *The American Naturalist*,
 509 10.1086/648556, 175, 1, (73-84).

510 Waugh, J.M. and Aarssen, L.W. (2011). Spatial indicators of plant community assembly from a
 511 453-year sand-dune chronosequence. *Plant Ecology & Diversity*,
 512 10.1080/17550874.2011.617393, 4, 2-3, (153-165).

513 Weiner, J., Stoll, P., Muller-Landau, H. and Jasentuliyana, A. (2001). The Effects of Density,
 514 Spatial Pattern, and Competitive Symmetry on Size Variation in Simulated Plant Populations.
 515 *The American Naturalist*, 158(4), 438-450.

516 White, E. R., & Smith, A. T. (2018). The role of spatial structure in the collapse of regional
 517 metapopulations. *Ecology*, 99(12), 2815–2822. doi: 10.1002/ecy.2546

Wilson, J.B., Agnew, A.D.Q., and Roxburgh, S. (2019). The Nature of Plant Communities.

546 **Tables and Figures**

547

548 **Table 1.** Summary of Analysis of Deviance for native species (*Phacelia tanacetifolia*) from GLM. Spatial
 549 pattern (clumped vs. dispersed), treatment, and pattern*treatment. Each measure was treated as separate
 550 models. Density refers to quantity of individual germination events and cover refers to a bird's-eye estimate
 551 of the percent of soil covered by plant material. Establishment data was collected at week 4 and final data
 552 was collected at week 8.

		<i>df</i>	Deviance Resid.	<i>df</i> Resid.	Dev	Pr(>Chi)
<u>Establishment:</u>						
<i>P. tanacetifolia</i> Density	NULL			59	55.035	
	pattern	1	3.2913	58	51.744	0.05258
	treatment:rep	3	4.6393	55	47.104	0.15137
	pattern:treatment: rep	3	5.0983	52	42.006	0.12071
<i>P. tanacetifolia</i> Cover	NULL			59	9410.0	
	pattern	1	135.00	58	9275.0	0.34957
	treatment:rep	3	1079.79	55	8195.2	0.07194
	pattern:treatment: rep	3	172.56	52	8022.7	0.77261
<u>Final:</u>						
<i>P. tanacetifolia</i> Density	NULL			59	55.183	
	pattern	1	3.9849	58	51.198	0.02944
	treatment:rep	3	4.1128	55	47.085	0.17971
	pattern:treatment: rep	3	5.9070	52	41.178	0.07097
<i>P. tanacetifolia</i> Cover	NULL			59	3843.3	
	pattern	1	81.67	58	3761.7	0.2598

Comment [jb1]: Match these to the figures – or the figures to these and ensure they match the results. Here is week for but figures are establishment etc

P. tanacetifolia
Biomass

treatment:rep	3	334.21	55	3427.5	0.1579
pattern:treatment:rep	3	83.38	52	3344.1	0.7300
NULL			59	9.596*10 ⁻³	
pattern	1	3.450*10 ⁻⁵	58	9.562*10 ⁻³	0.63744
treatment:rep	3	1.127*10 ⁻³	55	8.435*10 ⁻³	0.06422
pattern:treatment:rep	3	3.567*10 ⁻⁴	52	8.078*10 ⁻³	0.51326

553

Table 2. Summary of Analysis of Deviance for exotic species (*Bromus madritensis ssp. rubens*) from GLM. Spatial pattern (clumped vs. dispersed), treatment, and pattern*treatment. Each measure was treated as separate models. “rep” was included as a nesting factor to model pots to avoid pseudo-replicates. Density refers to quantity of individual germination events and cover refers to a bird’s-eye estimate of the percent of soil covered by plant material. Establishment data was collected at week 4 and final data was collected at week 8.

		<i>df</i>	Deviance Resid.	<i>df</i> Resid.	Dev	Pr(>Chi)
<u>Establishment:</u>						
<i>B. rubens</i> Density	NULL			39	80.645	
	pattern	1	0.927	38	79.718	0.154830
	treatment:rep	2	55.656	36	24.062	< 2.2*10 ⁻¹⁶
	pattern:treatment:rep	2	7.964	34	16.098	1.68*10 ⁻⁴
<i>B. rubens</i> Cover	NULL			39	7734.4	
	pattern	1	105.6	38	7628.8	0.29706
	treatment:rep	2	3475.3	36	4153.4	1.704*10 ⁻⁸
	pattern:treatment:rep	2	850.6	34	3302.8	0.01255
<u>Final:</u>						
<i>B. rubens</i> Density	NULL			39	82.371	
	pattern	1	0.927	38	81.444	0.175539
	treatment:rep	2	55.802	36	25.642	< 2.2*10 ⁻¹⁶
	pattern:treatment:rep	2	8.323	34	17.319	2.65*10 ⁻⁴
<i>B. rubens</i> Cover	NULL			39	6697.5	
	pattern	1	2.50	38	6695.0	0.87020
	treatment:rep	2	3067.74	36	3627.3	7.675*10 ⁻⁸

<i>B. rubens</i> Biomass	pattern:treatment: rep	2	443.93	34	3183.3	0.09341
	NULL			39	0.048924	
	pattern	1	1.062*10 ⁻³	38	0.047862	0.177155
	treatment:rep	2	2.194*10 ⁻²	36	0.025927	6.77*10 ⁻⁹
	pattern:treatment: rep	2	6.103*10 ⁻³	34	0.019824	5.335*10 ⁻³

560

561

562

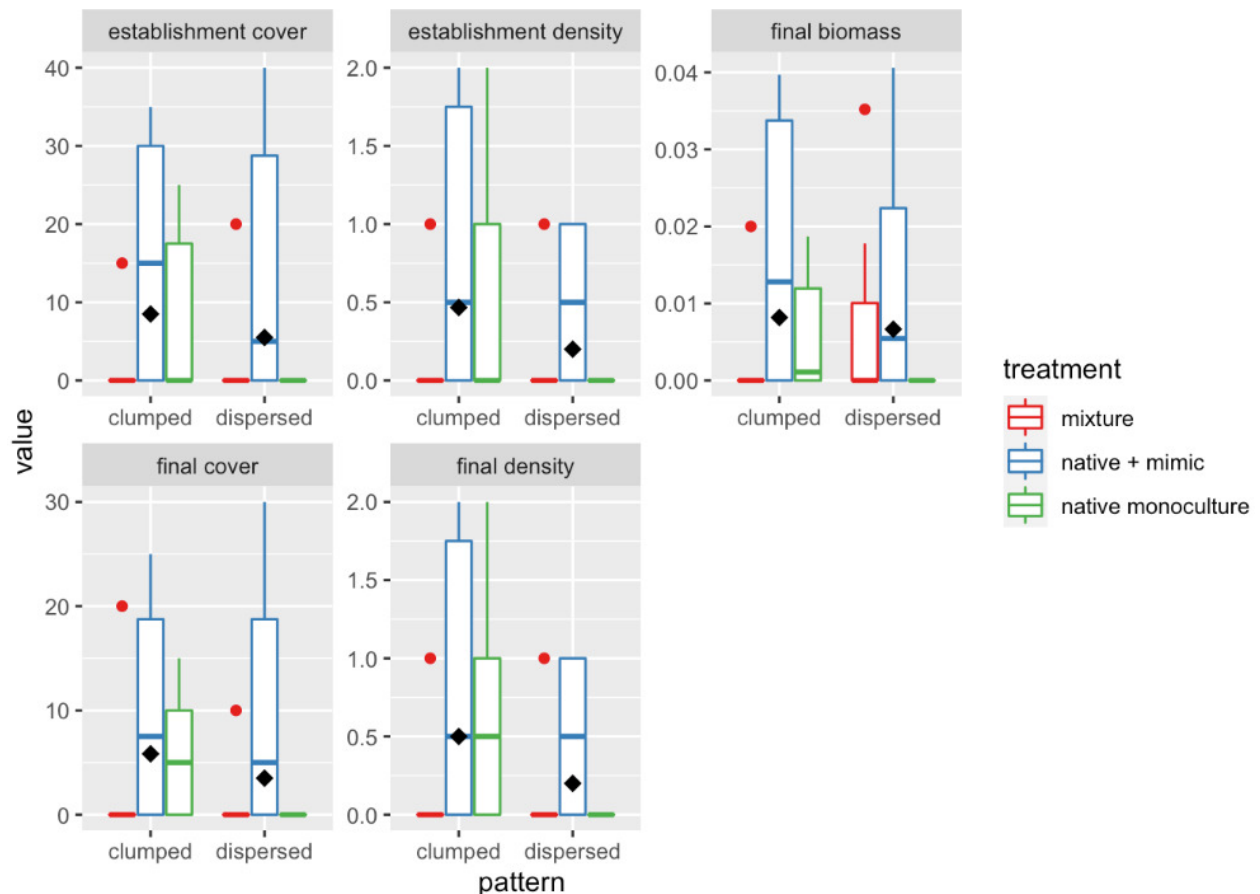


Figure 1. Boxplots of measures percent cover (establishment and final; %), density (establishment and final census), and final biomass (g) of mixture, native + mimic, and native monoculture treatments comparing two spatial patterns (clumped vs. dispersed). Diamond dots represent the mean. Establishment data was collected at week 4 and final data was collected at week 8.

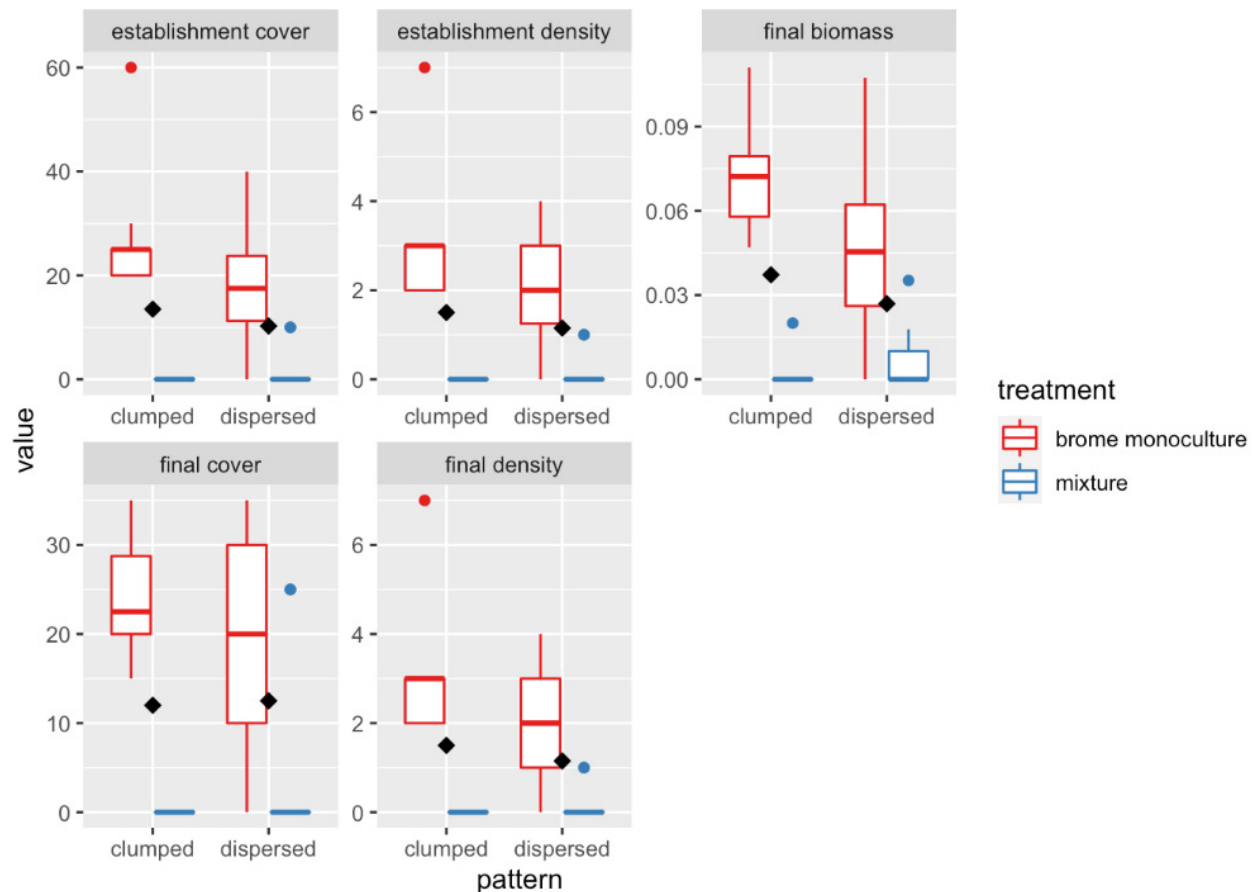


Figure 2. boxplots of measures percent cover (establishment and final; %), density (establishment and final census), and final biomass (g) of red brome monoculture and mixture treatments comparing two spatial patterns (clumped vs. dispersed). Diamond dots represent the mean. Establishment data was collected at week 4 and final data was collected at week 8.

Supplementary Appendix A



A. Plastic red brome mimic used in fake brome trials. Each seedling mimic was created by cutting off a strand 9 cm from the tip.



B. Red brome seeds obtained from Outsidepride.com.



583 C. Setup of trials in greenhouse.

584

Supplementary Appendix B

Table 3. Pattern Post hoc test results. df = infinite. Density refers to quantity of individual germination events. Establishment data was collected at week 4 and final data was collected at week 8.

	Pattern	emmean	SE	df	z ratio	p value
<u>Establishment:</u> <i>P. tanacetifolia</i> Density	clumped	-0.95	0.321	Inf	-2.954	0.0031
	dispersed	-54.01	6574.268	Inf	-0.008	0.9934
<u>Final:</u> <i>P. tanacetifolia</i> Density	clumped	-0.886	0.309	Inf	-2.870	0.0041
	dispersed	-54.008	6439.020	Inf	-0.008	0.9933

Table 4. Pattern*treatment Post hoc test results. df = infinite. Density refers to quantity of individual germination events. Biomass was measured in grams. Establishment data was collected at week 4 and final data was collected at week 8.

	Pattern	treatment	emmean	SE	df	z ratio	p value
<u>Establishment:</u> <i>B. rubens</i> Density	clumped	Brome monoculture	1.100	1.24*10 ⁻¹	Inf	8.872	< 0.0001
	dispersed	Brome monoculture	0.624	1.62*10 ⁻¹	Inf	3.863	0.0001
	clumped	Mixture	-95.792	1.43*10 ⁴	Inf	-0.007	0.9946
	dispersed	Mixture	-2.571	8.78*10 ⁻¹	Inf	-2.929	0.0034
<u>Final:</u> <i>B. rubens</i> Density	clumped	Brome monoculture	1.102	1.30*10 ⁻¹	Inf	8.487	< 0.0001
	dispersed	Brome monoculture	0.592	1.75*10 ⁻¹	Inf	3.393	0.0007
	clumped	Mixture	-95.982	1.47*10 ⁴	Inf	-0.007	0.9948

***B. rubens*
Biomass**

dispersed	Mixture	-2.649	9.41×10^{-1}	Inf	-2.813	0.0049
clumped	Brome monoculture	0.06744	7.34×10^{-3}	Inf	9.184	< 0.0001
dispersed	Brome monoculture	0.03857	7.34×10^{-3}	Inf	5.253	< 0.0001
clumped	Mixture	0.00974	7.04×10^{-3}	Inf	1.383	0.1668
dispersed	Mixture	0.01631	7.04×10^{-3}	Inf	2.315	0.0206

595

596

597

598

599

600

601

602