Unexpected productivity and invasion resistance from plant communities assembled from allopatric populations

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Abstract

Species with shared geographic history may co-evolve, with interactions leading to niche differentiation and improved resource capture. Thus, plant communities assembled from sympatric sources (shared geographic origins) are predicted to be more productive and invasion resistant than those from allopatric sources (different origins), even with identical species composition. We compared performance among communities of four species from 15 locations, assembled from allopatric or sympatric sources. Unexpectedly, allopatric-sourced communities had 29-35% more inflorescences, 19% higher survival, 19% longer growing season, 26-53% greater size, and 108% lower invader biomass than sympatric-sources. Sympatric populations showed trait convergence consistent with strong environmental selection, with trait variation higher in allopatric communities. Variation was associated with higher productivity and invasion resistance, suggesting an advantage of allopatric sources for community reassembly when environmental filters are strong. These findings challenge assumptions about the advantages of shared origins and have implications for understanding competition, community assembly, and ecosystem restoration.

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Title: Unexpected productivity and invasion resistance from plant communities assembled from allopatric populations

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Abstract (150 words)

Species with shared geographic history may co-evolve, with interactions leading to niche differentiation and improved resource capture. Thus, plant communities assembled from sympatric sources (shared geographic origins) are predicted to be more productive and invasion resistant than those from allopatric sources (different origins), even with identical species composition. We compared performance among communities of four species from 15 locations, assembled from allopatric or sympatric sources. Unexpectedly, allopatric-sourced communities had 29-35% more inflorescences, 19% higher survival, 19% longer growing season, 26-53% greater size, and 108% lower invader biomass than sympatric-sources. Sympatric populations showed trait convergence consistent with strong environmental selection, with trait variation higher in allopatric communities. Variation was associated with higher productivity and invasion resistance, suggesting an advantage of allopatric sources for community reassembly when environmental filters are strong. These findings challenge assumptions about the advantages of shared origins and have implications for understanding competition, community assembly, and ecosystem restoration.

Introduction

Plants share demands for common resources such as water, nutrients, and light (Gause 1934; Silvertown 2004), but can reduce competition by evolving strategies that reduce direct overlap in resource use such as offset phenology or variation in rooting depths or leaf morphology (Aarssen 1983; Bakker et al. 2021; Godoy et al. 2020; Hector et al. 2010; Kulmatiski et al. 2020). This niche differentiation can result in reduced negative interactions and even facilitation between plant neighbors, where interacting plants not only experience reduced direct competition but may also promote each other's persistence (e.g., nurse plants, hydraulic lift; Camarretta et al. 2020; Grady et al. 2017; van Moorsel et al. 2018). The results of such plant interactions affect individual fitness and population trajectories but can also have cascading effects on community functions such as productivity and invasion resistance (van Moorsel et al. 2019; Whitham et al., 2020). Indeed, there is a breadth of literature demonstrating that community function is influenced by species-level diversity (Isbell et al. 2015; Mahaut et al. 2020; Tilman et al. 2014).

In addition to the important effects of diversity at the species level, population-level diversity, or ecotypic variation, can also affect plant interactions and thus communities. The existence of intraspecific trait variation has long been recognized (Siefert et al. 2015) and is often correlated with environment and interpreted as evidence of local adaptation (Baughman et al. 2019; Leimu & Fischer 2008). Given substantial phenotypic variation among populations, the same niche partitioning mechanisms that lead to diversity-function relationships at the species level could also be associated with intraspecific differences among populations. Indeed, modeling and manipulative studies have found that growing with neighbors that share site-level origins (hereafter referred to as sympatric populations) can increase community functions such as productivity and invasion tolerance (Aubree et al. 2020; Chen et al. 2022; Dietrich et al. 2024; Grady et al. 2017; van Moorsel et al. 2018), though other studies have found species-specific effects, but no consistent community level responses (e.g., Agneray et al. 2023a; López-Angulo et al. 2023).

Whether at the species or population level, differentiated traits that arise from a shared interaction history may lead to desirable community properties (Germain et al. 2016; van Moorsel et al. 2021; Westerband et al. 2021a; Zuppinger-Dingley et al. 2014). For example, if strong biotic interactions result in niche differentiation and complementarity, we might expect sympatric communities to have the greatest trait diversity and thus show greater productivity and less susceptibility to invasion due to more complete use of resources (Figure 1, high resources; Funk et al. 2008; Moore et al. 2001; van Moorsel et al. 2021). Alternately, strong environmental filters in low resource or otherwise challenging environments could result in greater trait similarity, i.e., convergence, among species in sympatric communities, with multiple species evolving similar characteristics in response to selection (Figure 1, low resources; Bruelheide et al. 2018; Drenovsky et al. 2012; Westerband et al. 2021b), and thus allopatric mixtures could display more trait variability due to their divergent environmental backgrounds. If trait variation is important for community-level functions such as invasion resistance, the relative ability of sympatric or allopatric communities to demonstrate desirable community functions may not be constant across all levels of resource availability. Note that we use the phrases "sympatric communities" and "allopatric communities" throughout to refer to suites of species experimentally assembled from either the same source location or different source locations.

While we are beginning to understand the importance of plant-plant interactions in natural and experimental communities (Genung et al. 2012; Grady et al. 2017; van Moorsel et al.

2018; Zaiats et al. 2021), these interactions are often overlooked when establishing new communities for ecological restoration, a practice essential for recovering biodiversity loss and long considered the “acid test” of ecological knowledge (Bradshaw 1987). There is reason to question if our knowledge of community function is passing this test, as in many cases, restored communities fall short of practitioner goals (Atkinson et al. 2022; Holl et al. 2022; Shackelford et al. 2021). Due to myriad practical constraints, restoration projects may include a limited number of target species with seed sourced from disparate sites (Erickson & Halford 2020; Holl et al. 2022), resulting in low diversity allopatric communities, i.e., a restoration mix composed of a few dominant species established from populations with no co-occurrence history. While some restoration techniques, such as hay transfer in grasslands, include transferring propagules from a single community into restoration sites en masse (Wagner et al. 2021), it is not always possible to employ community-based approaches to seed sourcing, due to a lack of intact sites and the species-specific nature of seed collection and production (e.g., NASEM 2023). Observing the disconnect between restoration practice and the growing evidence that locally adapted plant-plant interactions can affect community outcomes such as productivity and response to invasion (Aubree et al. 2020; Grady et al. 2017; van Moorsel et al. 2018), we investigated whether preserving the shared origin of seed mixes by collecting seeds from multiple species from one location could improve restoration outcomes, based on the potential for a co-evolutionary history to increase community function.

Here we asked how community function is affected by population origin, creating 12 different communities from populations of three common native grasses and a native shrub. We worked in the semi-arid, western region of the Great Basin Desert, which has experienced extensive conversion to annual invasive communities and undergoes extensive ecological restoration (Bradley et al. 2018). These communities were composed of the same plant species, but seeds were sourced from populations with a variety of origins (sympatric or allopatric), trait composition, and source environment variation (Agneray et al. 2023b). We asked four specific questions: 1) how do community-level responses (aboveground productivity, facilitation, inflorescence production, and invasive suppression) differ among community mixtures? 2) Do communities with either allopatric or sympatric origins differ in trait variation? 3) Did any *a priori* measurements (source environment or seedling traits) predict community-level performance? and 4) What plant characteristics are most strongly associated with invasion resistance?

We began this experiment expecting that sympatric communities would demonstrate more desirable community-level responses (greater productivity, facilitation, reproduction, and invasive suppression), due to the potential for coevolved communities to have greater niche differentiation and efficiency in resource use (Aubree et al. 2020; Silvertown 2004). However, in a previous study with cold desert plants, we were surprised to find that when origin affected community outcomes, it was an allopatric community that had the highest biomass and invasion suppression (Agneray et al. 2023a). Hence, we approached this experiment with some uncertainty and were curious if a broader assembly of allopatric communities sourced from a greater number of locations would demonstrate this unexpected phenomenon, or if predictions about desirable properties in sympatric communities would hold true.

Material and Methods

Species, site selection and seed collection

We chose native species that co-occur in the Great Basin Desert and are used in restoration: three perennial grasses (*Elymus* spp. L.*, Eriocoma thurberiana* (Piper) Romasch*, Poa secunda* J. Presl), and one shrub (*Artemisia tridentata* Nutt.). Since *Elymus elymoides* (Raf.) Swezey and *E. multisetus* (J.G. Sm.) Burtt Davy co-occur and hybridize in the western Great Basin (Barkworth et al. 2007), our sampling locations included this complexity. For simplicity, we refer to each of the four taxa as "species," though eight *Elymus* spp. collections contain a combination of the two species and refer to each collection as a "population." We collected seeds from 15 sites (Figure 2) where all species co-occur in lower elevation sagebrush steppe communities, with average annual precipitation between 232 and 388 mm (Table S1; Supplemental Methods; PRISM Climate Group 2004).

Experimental mesocosms

We established an outdoor planting site with 151 mesocosms filled with local topsoil (Table S2; 200L, 0.9m depth) at the University of Nevada, Reno (39.537924, -119.804757). Mesocosm locations were randomized and planted with one of 12 possible mixtures, 6 sympatric and 6 allopatric, with 11 replicates each, with 19 mesocosms serving as unplanted control treatments for the invasion experiment

In fall 2019, seeds were planted inside the greenhouse and seedlings were transplanted into outdoor mesocosms starting in spring 2020. Planting density approximated a typical sagebrush shrubland community with one individual of *A. tridentata, Elymus* spp., and *E. thurberiana,* and two individuals of the smaller-statured *P. secunda*. We monitored survival weekly from March 2020 to November 2020 (growing season one) and November 2020 through

August 2021 (growing season two) and monitored green days (presence or absence of photosynthetic tissue) in growing season one. We initially watered to maximum water holding capacity and thereafter, lightly watered once weekly if there had been no precipitation. In November 2020 and March 2021, perished individuals were replaced to ensure complete community establishment. At the end of August 2020 and 2021, every plant was assessed for height, crown size (length x width), senescence (an index between 0-3 from least to most live green tissue), and number of inflorescences.

In December 2020, each container was invaded with *Bromus tectorum* L. (cheatgrass), a competitive invasive annual grass in the Great Basin (Bradley et al. 2018; Monaco et al. 2017). Mesocosms were planted with 130 *B. tectorum* seeds, based on natural seed production assessed in a moderately invaded field site. All *B. tectorum* individuals were harvested at the end of the second growing season, August 2021, oven-dried, and weighed.

Community responses

We use the word "community" to refer to one of 12 possible mixtures for the individual mesocosms (Table S2) and community response variables are the aggregated responses across the five plants in each mesocosm. Productivity was measured as aboveground native plant volume at the end of the first and second growing seasons. Reproductive output was represented by the total number of inflorescences produced by all plants in the mesocosm. The total mass of *B. tectorum* per mesocosm was used as a metric of invasion resistance, with lower values indicating greater suppression. We also quantified potential facilitation, measured by the total mortality experienced by any plant in a mesocosm. We aggregated the number of days plants were photosynthetically active (i.e., green days) in their first growing season prior to invasion as a measure for the community's potential to capture resources, which is particularly important in semi-arid systems with pulsed resource availability (Chesson et al. 2004).

Environmental data

Climate normals, soil, and site characteristics for each collection site were gathered from the PRISM Data Explorer, SSURGO Web Soil Survey, and USGS Digital Elevation Models (PRISM Climate Group 2004; Soil Survey Staff NRCS-USDA 2021; USGS 2019; Table S1) and used to calculate a suite of functionally relevant climate variables. We retained 11 variables with relatively low ($|r| < 0.6$) correlation for analysis (Table S1).

Quantifying seed and seedling traits

We focused on comparing seed and seedling traits among populations, as these characteristics are important for plant recruitment in the Great Basin Desert (James et al. 2011; Larson et al. 2023; Leger et al. 2019). We weighed seeds and grew seedlings of each species and population in a controlled greenhouse environment and measured root, shoot, and phenological traits, employing methods previously used to describe perennial grass seedlings, and reduced these measurements to a selected set of traits (Agneray et al. 2023b; Leger et al. 2021; Supplemental Methods; Tables S3 and S4).

Statistical analysis

Q1: How did community-level responses differ among community mixtures?

We evaluated whether origin (allopatric or sympatric) or individual communities influenced each response using R version 4.4.2 (R Core Team 2024). Model factors included origin and community (nested within origin), with separate linear regression models built for each response variable, transformed as needed to better fit a Gaussian distribution (Table S5). Community was included as a fixed term, rather than random, because some communities were deliberately selected based on their performance in previous experiments (Supplemental Methods). However, it is also the case that all combinations can be viewed as a subset of a much larger pool of possible combinations, thus we present a complementary set of models (Supplemental Methods) in which community was modeled as a random term; this approach does not precisely reflect our original design but the more limited degrees of freedom for testing the main effect in the mixed model provided a conservative and thus informative test of our main hypothesis involving evolutionary history (allopatric vs sympatric origins).

When considering invasion suppression, mesocosms with *B. tectorum* growing alone were not included in the models due to their extremely high production values, but information is presented to illustrate how native communities impacted *B. tectorum* growth.

Q2: Do communities with either allopatric or sympatric origins differ in trait variation?

Seed and seedling trait variation within each community mixture was analyzed using general linear models to ask whether there were overall differences in variation between allopatric or sympatric communities; trait values were measured from field-collected seeds and greenhouse-grown seedlings. These models included origin type (either allopatric or sympatric) with the variation in each seed or seedling trait (Table S3) as response variables, assuming a Gaussian distribution of residuals. Variation in traits was assessed with the coefficient of variation of an individual trait among the populations included in a mesocosm, using population-level means (Table S3; Supplemental Methods).

Q3: Did any a priori measurements predict community-level performance?

After finding significant differences among community mixtures and between origin types for nearly every response variable, we asked whether seedling traits measured at the population-level in the greenhouse or environmental characteristics of the original collection site could predict a subset of community-level responses (productivity, number of green days, inflorescence production, survival or *B. tectorum* biomass) using random forest analysis. We performed the analysis using the randomForest package in R (Breiman et al. 2018), with 10,000 trees and all other parameters set to the package defaults. We considered the total trait values (e.g., the sum of seedling root lengths included in a particular community, estimated from the population averages described in an initial greenhouse experiment) and the variation in each trait value (e.g., variation in total root length among species in a mesocosm, calculated from greenhouse measurements) to determine whether traits or trait variation predicted community responses. For environmental variables, we included the sum of values for each plant's collection sites for both sympatric and allopatric communities (e.g., sum of the mean annual precipitation from represented sites for each plant).

Models were created separately for each community response including totals and variation of trait values alongside total environmental values and the community type (either sympatric or allopatric). We then reported the top ten variables ranked by importance, as measured by the percent increase in Mean Squared Error (MSE), along with the percent of variance explained by the full model. Additionally, we examined the partial dependence plots for each of the top ten variables of each response to report the direction of the observed marginal effects.

Q4: What plant characteristics are best correlated with invasion resistance?

Focusing on invasion suppression, we sought to explain the marked differences in performance among communities using structural equation modeling (SEM; Supplemental Methods). Unlike question 3, which asked whether previously measured traits or environment of origin predicted community outcomes, this analysis focused on the influence of plant characteristics within individual mesocosms. Specifically, we evaluated whether the size, survival, period of active photosynthesis, or reproductive output of plants within a mesocosm had a measurable influence on invasion resistance. For each species, we selected a single variable from within the mesocosm that was most strongly correlated with *B. tectorum* biomass, selecting one variable from measurements taken prior to invasion in the first growing season and one variable measured during invasion in the second growing season, and moved these forward in the SEM. We included potential competitive relationships among native species in the second growing season in the model, along with origin as a potential predictor of native plant characteristics in the first growing season.

Results

Q1: How did community-level responses differ among community mixtures?

Origin types (allopatric or sympatric; Figure 2) and unique community mixtures (Figures 3 and S4) differed in nearly every community response (results were consistent across two modeling approaches with community as a fixed or random effect; Tables 1 and S6). Differences between allopatric and sympatric communities were all in unexpected directions. Allopatric mixtures had 19% fewer deaths and in the first growing season were 53% larger, had 35% more inflorescences, and 19% more green days than sympatric communities overall. In the second growing season, allopatric mixtures were 26% larger, made 29% more inflorescences, and invasion resulted in 108% less *B. tectorum* biomass.

Most mesocosms planted with native plant mixtures suppressed *B. tectorum*, relative to the controls growing *B. tectorum* alone. In mesocosms with native plants, *B. tectorum* biomass ranged from 0.02-73.99g, with an average of 12.43g, which was much lower than *B. tectorum* biomass in control mesocosms (mean: 71.40g, range: 55.75-83.67g). Two communities differed from their treatment group (sympatric or allopatric) in invasion resistance: S2 had low *B. tectorum* biomass, relative to other sympatric communities, and A5 had greater *B. tectorum* biomass, relative to other allopatric communities (Figure 3).

Q2: Do communities with either allopatric or sympatric origins differ in trait variation?

We asked whether species from sympatric populations were more likely to show divergent or convergent traits, relative to allopatric populations. Of the seven seed and seedling traits considered, four differed strongly (average diameter, FRL, RMR, and SRL; all $p < 0.05$) and one differed somewhat (days to emergence; $p = 0.078$) among allopatric and sympatric communities (Table S7). Of the traits that differed, the sympatric mixtures had less variability in all measured traits (i.e., trait convergence), though the magnitude of differences was small (mean CV for allopatric vs. sympatric communities: average diameter, 0.26 vs. 0.24; days to emergence, 0.37 vs. 0.34; FRL, 0.26 vs. 0.24; RMR, 0.4 vs. 0.22; SRL, 1.17 vs. 1.07; Figure S2).

Q3: Did any a priori measurements predict community-level performance?

Prior population-level measurements somewhat predicted community-level performance with all models explaining ≤ 20.15% of the variance (Figure 4). Several community-level performance responses were associated with population-level environmental variables, seedling traits, or origin type (Figure 4). The four models with reasonable fits contained trait totals, trait variation, and environmental variables, and trait totals were in the top ten important variables 10 times, trait variation 11 times, and environmental variables 19 times. Several variables emerged as key predictors of performance across multiple responses. For example, mesocosms with plants from sites with lower mean annual precipitation resulted in larger plants and longer photosynthesis periods during the first growing season, more inflorescences and greater *B. tectorum* suppression in the second growing season, among other environmental predictors (Supplemental Results). Similarly, specific root length appeared in the top ten variables for each reported response. Higher specific root length, which typically means longer, thinner roots, resulted in more inflorescences and *B. tectorum* suppression along with higher volume and more green days in the first growing season, among other important traits (Supplemental Results). Finally, variation in seed and seedling traits was in the top variables for every response: greater variability in root diameter was associated with higher first-season plant volume, longer growing periods, and greater *B. tectorum* suppression, while higher variability in root mass ratio was predictive of *B. tectorum* suppression and greater inflorescence numbers, while lower variability in total root biomass was associated with greater *B. tectorum* suppression.

Q4: What plant characteristics are best correlated with invasion resistance?

Structural equation modeling confirmed that within-mesocosm factors contributed to *B. tectorum* suppression (Figure 5), and our model showed good fit to the data (χ^2 =26.9, p = 0.308; lower test statistic and higher p value indicate better fit) and high explanatory power for *B. tectorum* biomass (R^2 = 0.61). Notably, all species benefited from growing in allopatric mixes during the first growing season, though the strength of the relationship varied. Specifically, in allopatric mixes, *A. tridentata* was on average 67% larger, *Elymus* spp. made 35% more inflorescences, *E. thurberiana* was 11% larger, and *P. secunda* had 26% more green days than plants grown in sympatric mixes. All four species influenced the biomass of *B. tectorum* to some degree, but the largest suppressive effects were observed for *A. tridentata* and *Elymus* spp. with size (season one, pre-invasion for *A. tridentata*, season two, post-invasion for *Elymus* spp.) and propensity to produce inflorescences (post-invasion for *A. tridentata*, pre-invasion for *Elymus* spp.) negatively associated with *B. tectorum* biomass. For these two influential species, the indirect effect of allopatry mediated through *A. tridentata* was -0.66, while the indirect effect for *Elymus* spp. was -0.38. In contrast to the strong competitive interactions between some native species and *B. tectorum*, there was weaker evidence of competitive interactions among native species in the second growing season, with *A. tridentata* having the strongest direct negative effect (-0.26) on *Elymus* spp.

Discussion

Our understanding of how population origin influences plant interactions and community function is still developing. Results reported here confirm that community properties can vary dramatically depending on the component source populations, even in relatively simple communities derived from broadly similar environments. However, our findings are in strong contrast with the expectation that a history of co-occurrence produces complementarity in resource use, improved productivity, or reduced opportunity for species invasion (Aubree et al. 2020; Chen et al. 2022; Grady et al. 2017; van Moorsel et al. 2018). Instead, allopatric mixtures consistently outperformed single-source collections in all metrics, demonstrating lower mortality, greater aboveground size and flower production, and longer growing seasons, with a particularly strong impact on invasion resistance. Allopatric communities exhibited larger phenotypic variation than sympatric communities, consistent with trait convergence, rather than divergence in interacting species, consistent with the hypothesis that convergence can occur when abiotic conditions have strong effects on fitness (e.g., Westerband et al. 2021a). Further, allopatry had overall positive effects on individual native plant size, which we observed in a previous experiment (Agneray et al. 2023a), and here, the positive effects of allopatry on *A. tridentata* were particularly impactful for reducing invader biomass. In addition to the effects of co-occurrence history, we found that environment, traits, and trait variation were influential for predicting community outcomes, with more positive community outcomes when plants were sourced from drier environments, had higher specific root lengths, and greater variation in multiple traits. By design, allopatric mixtures encompassed a greater range of environmental variation represented in each mesocosm, which may have contributed to their superior performance via the unintended effect of increased trait variance among plants from different sites.

That our results were unexpected may stem from the fact that much of the foundational diversity-community function literature is from experiments in more productive ecosystems, with a heavy emphasis on temperate grasslands and forests (Balnavera et al. 2006; Cardinale et al. 2011; Duffy et al. 2017). Notably, reviews from drylands have focused on ecosystem functions other than increased productivity from more diverse systems (Maestre et al. 2009). In less productive sites, environmental factors may be stronger selective agents than competitive plant interactions, particularly during early life stages (e.g., Malkinson & Tielbörger 2010). Indeed, we observed little evidence of direct competitive interactions among our native species. Contrary to expectations that strongly outcompeting neighbors would lead to higher survival and fitness, it is possible that plants in less productive systems have higher fitness when they avoid competition, especially during early life stages (Espeland 2018; Atwater et al. 2021). This could have the unexpected outcome of sympatric populations using fewer of the available resources, rather than more, if the fitness of individual plants is increased by minimizing interactions in early life history stages. Our results align with this hypothesis, suggesting that sympatric populations may not fully utilize all available resources, which could help explain the significantly higher biomass of the invasive species, *Bromus tectorum*, in these communities. Conversely, the allopatric communities, with populations lacking a shared history, may not have evolved fine-scaled niche partitioning to avoid direct contact and competition, and thus, may have had the unexpected outcome of a more complete utilization of available resources. A useful follow-up study could focus on resource capture across communities of varying origins to provide further insights into these dynamics.

Despite extensive evidence demonstrating local adaptation of traits to climate and presumably affecting performance in native habitats (Baughman et al. 2019; Hereford 2009; Leimu & Fischer 2008), we found relatively weak associations between community outcomes and either source climate or functional traits. One possible explanation is that our selection of plant collections from ecologically similar plant communities truncated the degree of variation that one would typically see across a species' occupied area, thereby reducing the predictive power of either traits or environment relative to other studies (Baughman et al. 2019; Leimu & Fischer 2008). Further, we measured traits at very early stages and asked if they could predict outcomes for older plants, though traits are known to shift ontogenetically as plants develop (Urza et al. 2019; Zaiats et al. 2021). Nevertheless, even among plants from relatively similar source environments, we found seed and seedling traits and environmental factors that were associated with several desirable community outcomes. Specifically, lower mean annual precipitation and higher specific root length (SRL) among populations in a mesocosm were most often linked to positive community outcomes (larger native plants, more inflorescences, longer active growth periods, and less *B. tectorum* biomass). SRL quantifies the proportional investment of plants towards root length as a proportion of the dry weight of the roots, thus higher SRL indicates a greater investment in thinner, longer roots focused on underground resource capture, but higher SRL also reduces a plant's chance for uprooting and overturning (Freschet et al. 2021). Additionally, our findings align with previous research showing variability in root traits (i.e., root mass, diameter, root mass ratio, and SRL), strongly promote soil resource partitioning and species coexistence (Kulmatiski et al. 2020; Silvertown et al. 2015). The surprise here was that, in order to create communities with variation in important belowground traits, we had to assemble previously isolated populations. It is worth noting that our traits were derived from very young plants (10-35 days old), and the fact they were at all predictive of outcomes multiple years later underscores the importance of early life stages. It is possible that the small differences in trait variability observed at the seedling stage were magnified in older plants. For future studies, we recommend measuring phenotypic traits and trait variation of 1- and 2-year-old plants, as this may provide even stronger predictive insight into final community outcomes.

We found clear evidence of interactions between the invasive *B. tectorum* and our native plants, with native species suppressing the invader (Colautti & Lau 2015; Leger & Goergen 2017; Oduor 2013). Regardless of origin and functional group, native plants suppressed *B. tectorum* biomass, relative to the controls, though the result was strongest in the allopatric communities. While our expectation was that *Elymus* spp. would compete the most directly with *B. tectorum*, we found evidence that *A. tridentata* was a very important component of *B. tectorum* suppression, and all members of the native plant community had a negative impact on *B. tectorum* to some degree, supporting the idea that species diversity confers greater resistance to invasion (Funk et al. 2008; Peng et al. 2019). In the hopes that exceptions could prove the rule, we examined the results for the two community mixtures that defied the overall pattern for their origin type (S2, which was particularly suppressive, and A5, which was not). Anecdotally, S2 was the coldest sympatric site and A5 was the warmest overall allopatric site, but mean annual temperature was not particularly explanatory for any of the community outcomes, so it is not clear that this explains their aberrant behavior. Other differences that may have contributed to the poor invasion suppression of A5 were that those communities had the smallest overall aboveground volume in the first growing season (but not in the second) along with having the largest seeds and the lowest SRL (thicker and fewer roots per gram), all factors that were predictive of invasion suppression to some degree. We did not examine belowground biomass in these mesocosms, due to the challenge of extracting whole plants, but future experiments using a different design may be used to understand whether belowground factors are influencing invasion resistance.

In conclusion, the sympatric or allopatric origin of plant neighbors affected many elements of community performance, though these effects were more difficult to predict across unique mixtures than expected. While we found that community outcomes differed based on their source environment and traits, the measured variables had limited explanatory power, suggesting that other, unaccounted factors may be at work. From an applied perspective, our results suggest that sourcing from sympatric communities for ecological restoration would not yield benefits in this system. Instead, the trait diversity found in allopatric communities may have clear benefits for invasion resistance. It is important to note that our allopatric populations were selected from relatively similar environments, which is possible in the Great Basin Desert where natural plant communities span relatively large areas. However, this approach might not be replicable in other ecosystems that are more degraded or naturally occur over a smaller land area, and assembling allopatric communities may be a poor approach in highly productive environments, as suggested by the results of others (Aubree et al. 2020; Chen et al. 2022; Grady et al. 2017; van Moorsel et al. 2018). Finally, we acknowledge our experiment was conducted under highly controlled conditions different from a typical restoration scenario, and field results may differ. Nonetheless, our results demonstrate it is possible to manipulate community function simply by assembling mixtures of the same species from different source populations, with compelling evidence that niche differentiation may evolve differently in less productive systems. We recommend further mechanistic mesocosm studies and field trials that test our findings by incorporating higher-than-average trait variation through sourcing seeds from different sites with similar environmental conditions and including a broader range of species could further validate our results.

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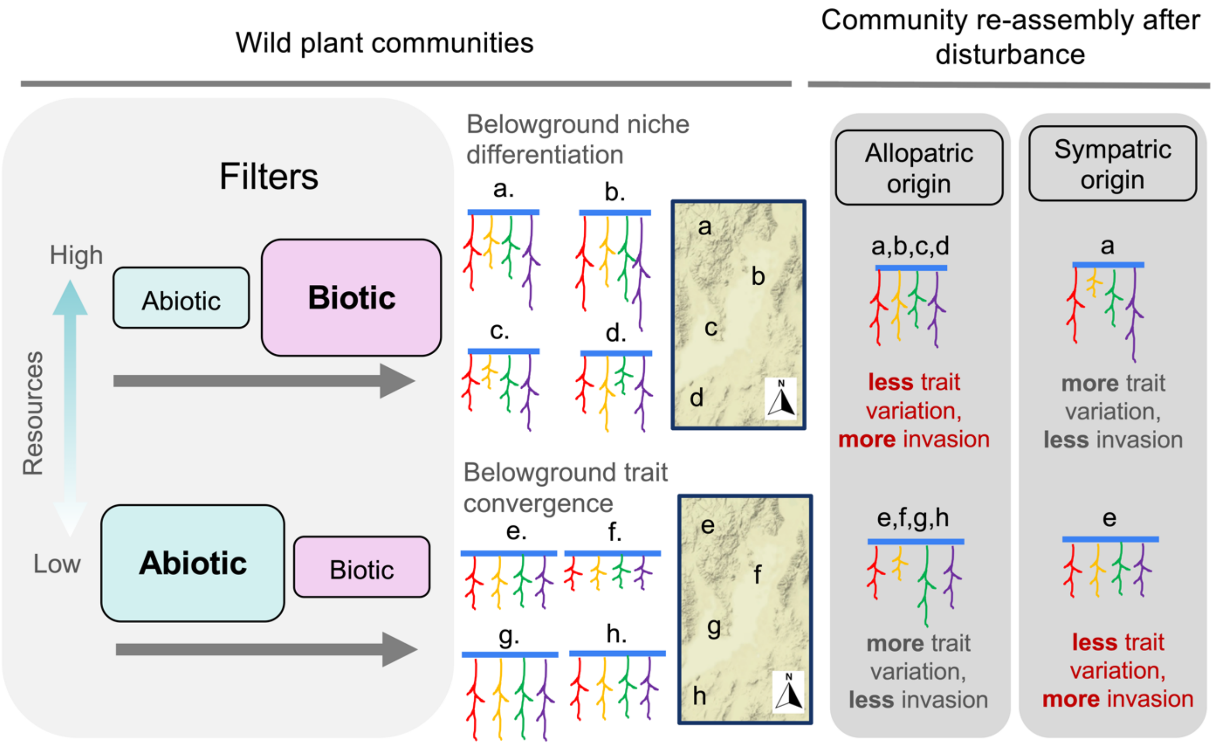
Tables

Table 1. Differences among origin types, either allopatric or sympatric, and communities nested within origin types for the sum (total of all plants in each mesocosm) and CV (variation in each response among plants in each mesocosm) for each response variable. Values reported are from linear regression models, and include the degrees of freedom, a coefficient estimate for the effect of allopatry compared to sympatry, F-test statistics, and the significance of differences; *p* values <0.05 are in bold.

Figures

Figure 1. Hypothesized mechanisms for community-level outcomes based on whether founding plant communities are sourced from allopatric or sympatric collection locations, with expectations varying based on resource availability. Belowground differentiation in root morphology is used as an example trait, though any trait or combination of traits could apply. Similarly, susceptibility to invasion is the community response, though other responses could be included (productivity, growing duration, etc.). In high-resource environments, strong biotic interactions lead to greater niche differentiation, enabling sympatric communities to capture belowground resources more effectively and reduce resource availability for invasive species, conferring an advantage during community re-assembly if sympatry is maintained. In contrast, in low-resource environments, abiotic filters have a greater effect on plant fitness, leading to convergence in adaptive traits among native species, since similar traits are required to access limited resources. Thus, when establishing communities after disturbance in these low-resource settings, allopatric communities have greater trait variation and potential for resource uptake, reducing the available resources for invasive species. Over time, in undisturbed conditions, these allopatric communities may undergo selection for trait convergence, but there is a potential advantage of allopatry in the initial community assembly stage when abiotic filters dominate.



Wild plant communities
Community re-assembly after disturbance
Filters
High
Low
Resources
Abiotic
Biotic
Abiotic
Biotic
Belowground niche differentiation
a.
b.
c.
d.
a
b
c
d
Belowground trait convergence
e.
f.
g.
h.
e
f
g
h
N
Allopatric origin
Sympatric origin
a,b,c,d
less trait variation, more invasion
a
more trait variation, less invasion
e,f,g,h
more trait variation, less invasion
e
less trait variation, more invasion

Figure 2. (a) Fifteen sites (yellow circles) where seeds were collected for all four species used in these experiments, and the location of mesocosms (green triangle). (b-e) Overall differences among allopatric and sympatric communities in volume, survival, and invasion resistance. Native plant size is represented by total plant volume (l x w x h) in the (b) first and (c) second growing season. Overall mortality (d) of native plants in each mesocosm is shown along with (e) *B. tectorum* aboveground biomass from invaded mesocosms. Box plots indicate medians, first to third quartiles, and outliers shown as black points.

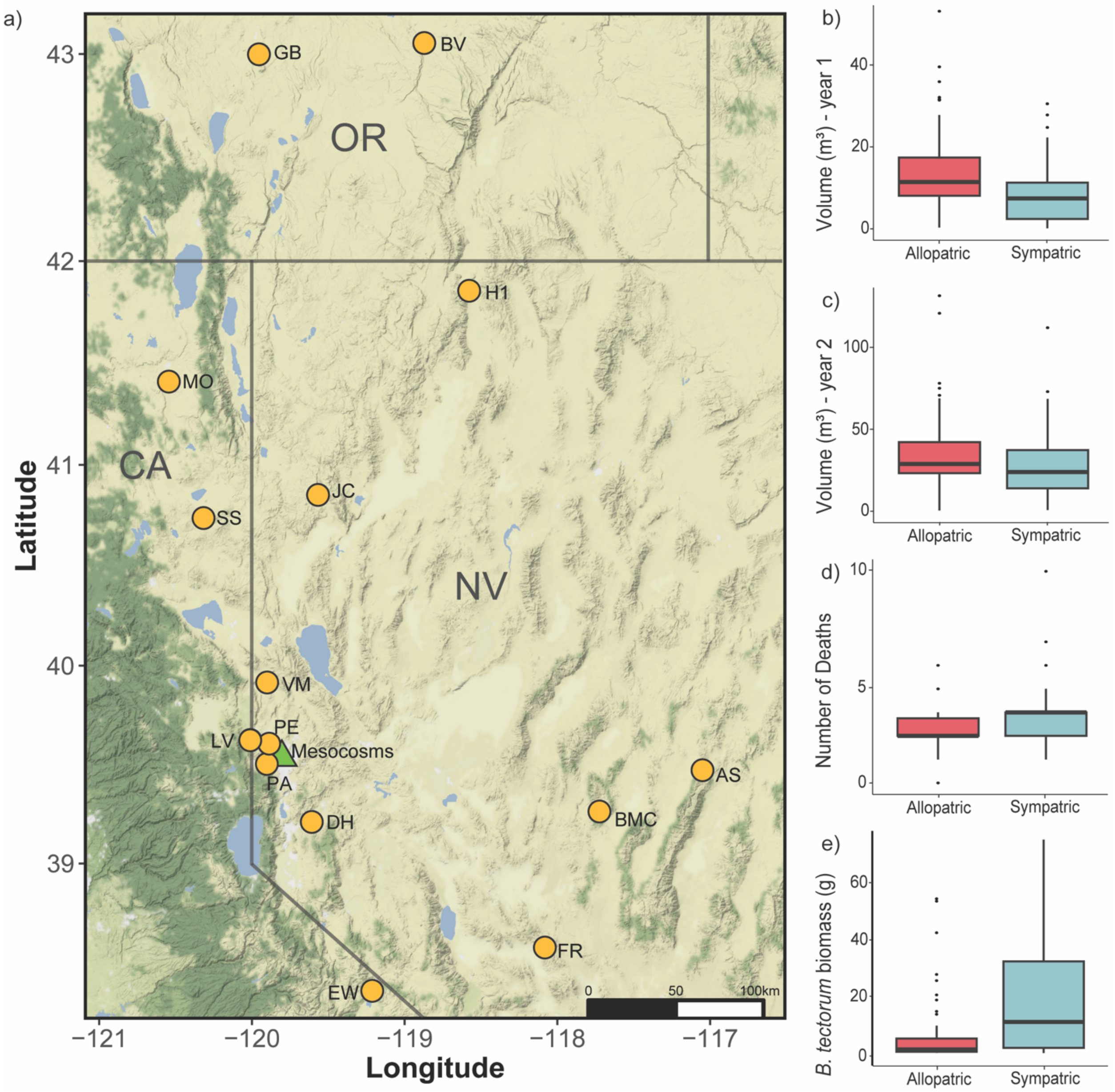

a)
OR
CA
NV
GB
BV
H1
MO
JC
SS
VM
PE
LV
Mesocosms
PA
DH
AS
BMC
FR
EW
0
50
100km
43
42
41
40
39
Latitude
−121
−120
−119
−118
−117
Longitude
b)
Volume (m³) - year 1
0
20
40
Allopatric
Sympatric
c)
Volume (m³) - year 2
0
50
100
Allopatric
Sympatric
d)
Number of Deaths
0
5
10
Allopatric
Sympatric
e)
B. tectorum biomass (g)
0
20
40
60
Allopatric
Sympatric

Figure 3. Differences among unique allopatric (A) and sympatric (S) communities ordered by rank in volume, survival, and invasion resistance. Native plant size is represented by total plant volume (l x w x h) in the (a) first and (b) second growing season; note the change in y axis scale. Overall mortality (c) of all native plants in each mesocosm is shown along with (d) *B. tectorum* aboveground biomass from invaded mesocosms, (e) the number of inflorescences in the second growing season, and (f) the number of green days. Box plots indicate medians, first to third quartiles, and outliers shown as black points; specific source populations included in each community are in Table S2.

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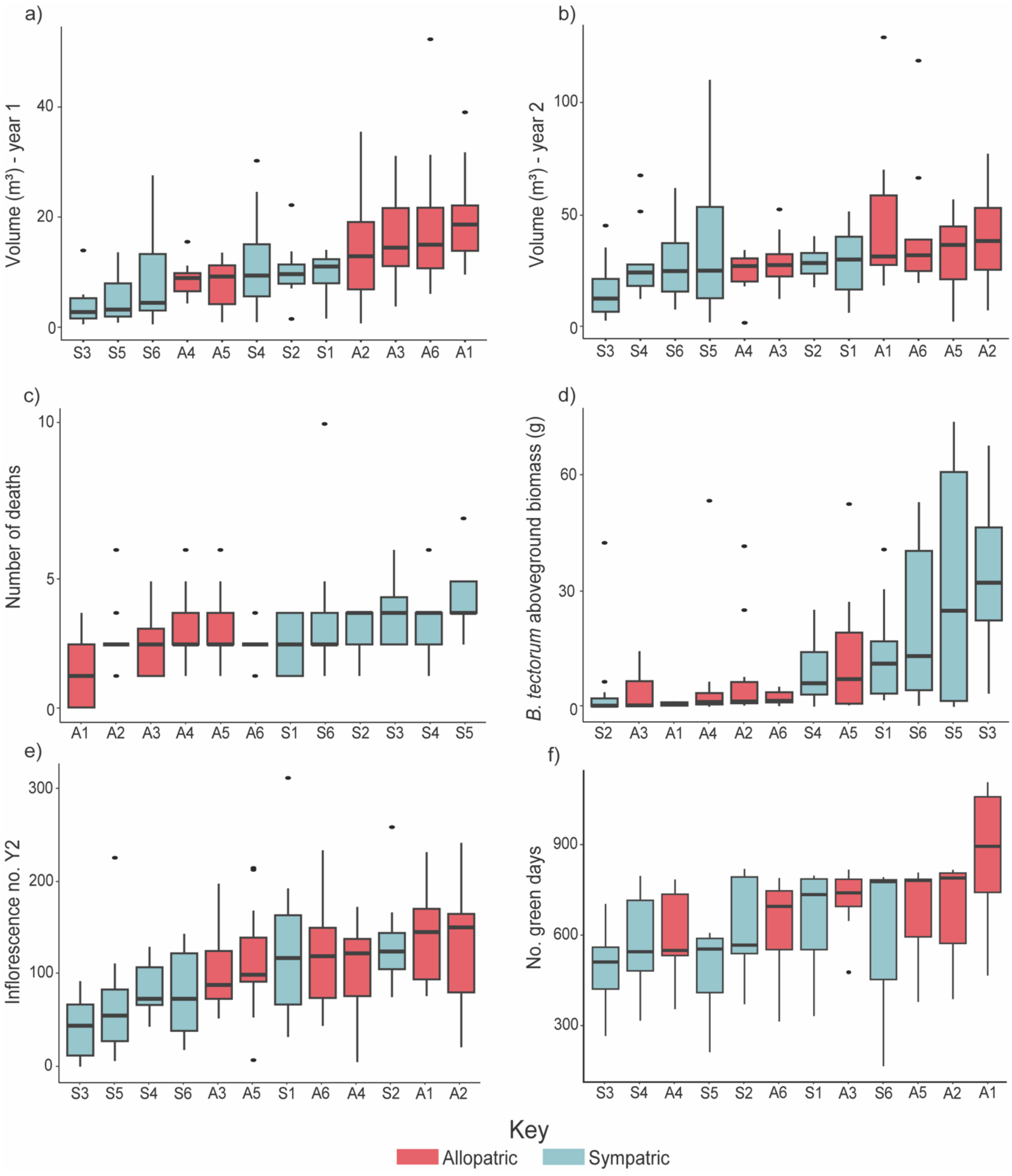


a)
Volume (m³) - year 1
0
20
40
S3 S5 S6 A4 A5 S4 S2 S1 A2 A3 A6 A1
b)
Volume (m³) - year 2
0
50
100
S3 S4 S6 S5 A4 A3 S2 S1 A1 A6 A5 A2
c)
Number of deaths
0
5
10
A1 A2 A3 A4 A5 A6 S1 S6 S2 S3 S4 S5
d)
B. tectorum aboveground biomass (g)
0
30
60
S2 A3 A1 A4 A2 A6 S4 A5 S1 S6 S5 S3
e)
Inflorescence no. Y2
0
100
200
300
S3 S5 S4 S6 A3 A5 S1 A6 A4 S2 A1 A2
f)
No. green days
300
600
900
S3 S4 A4 S5 S2 A6 S1 A3 S6 A5 A2 A1
Key
Allopatric
Sympatric

Figure 4: Influence of seedling and environmental variables across both allopatric and sympatric communities on (A) volume in the first growing season, (B) *B. tectorum* biomass, (C) number of inflorescences in the second growing season, and (D) number of green days in the first growing season. Variables shown are the top ten most important traits as measured by the percent increase in MSE calculated using Random Forest with 10,000 trees, along with the total percent variance explained.

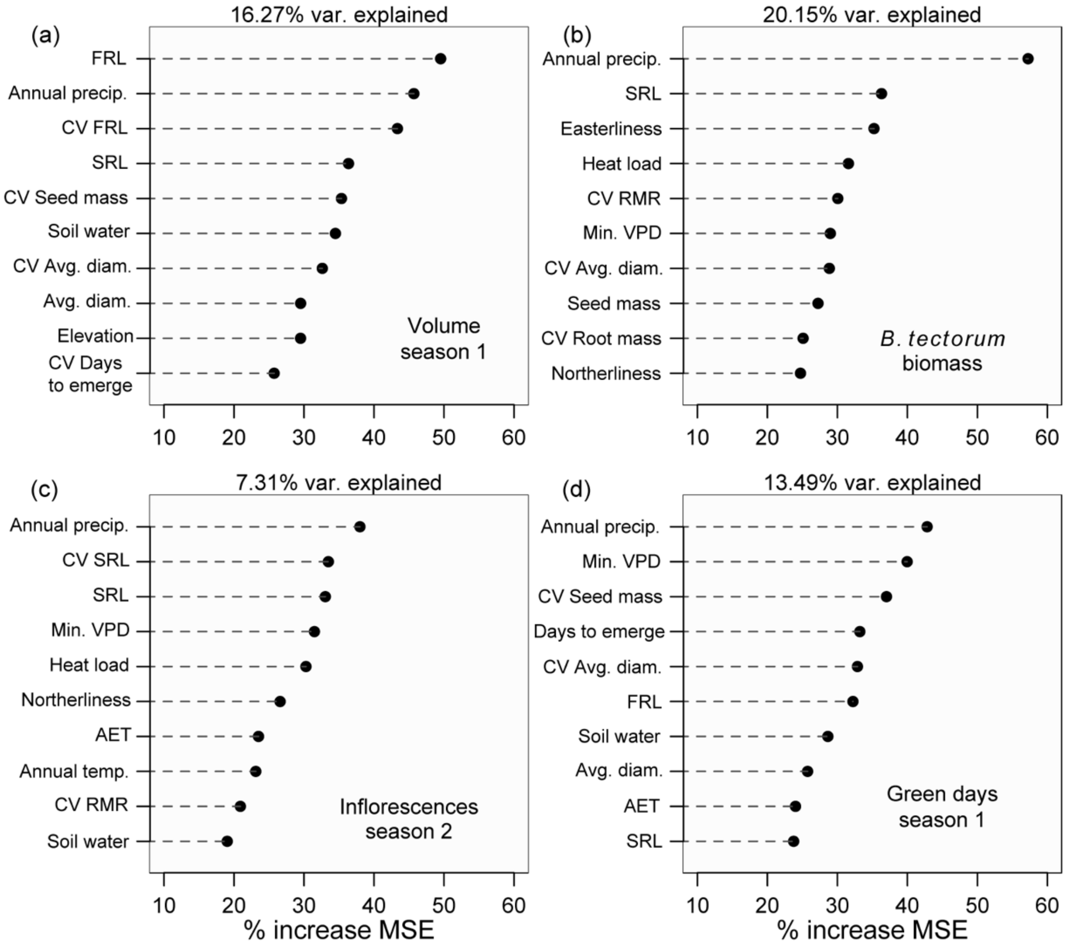
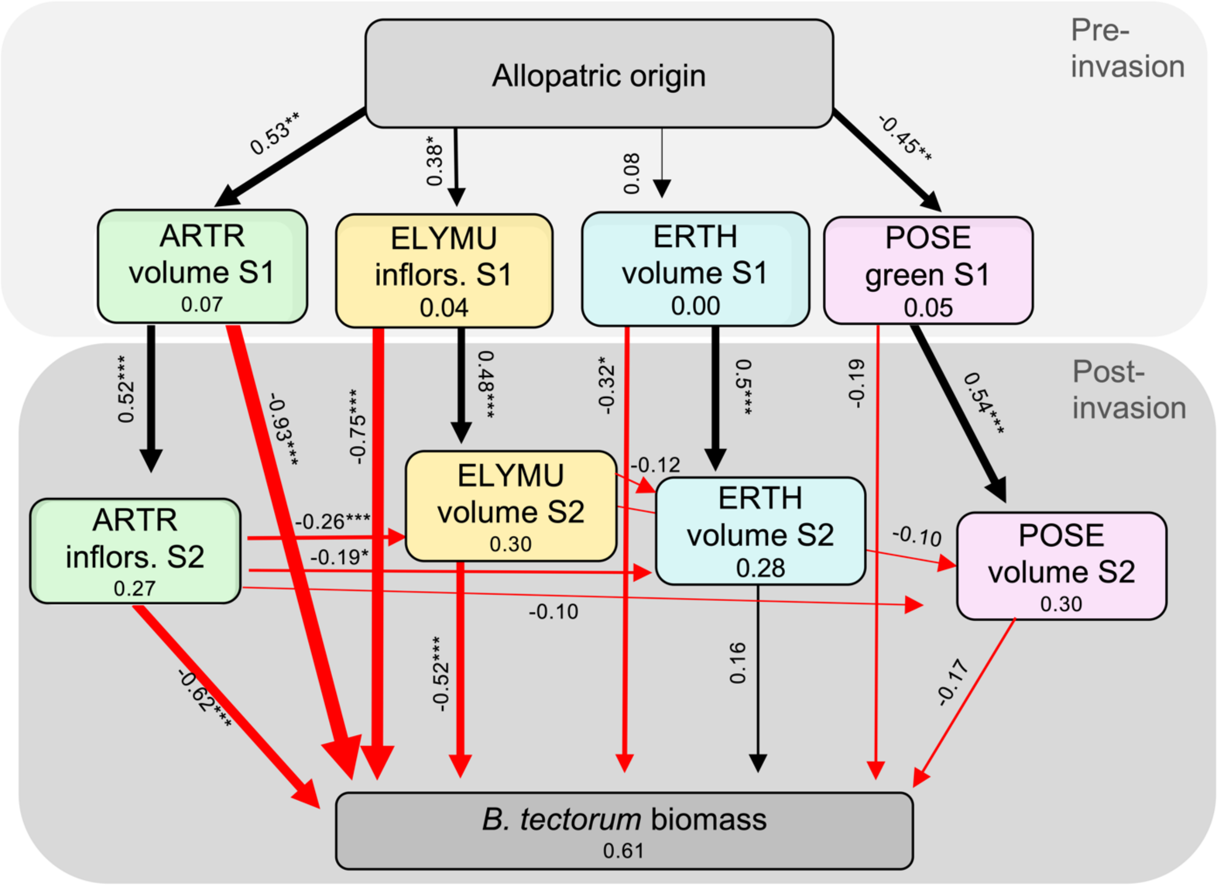
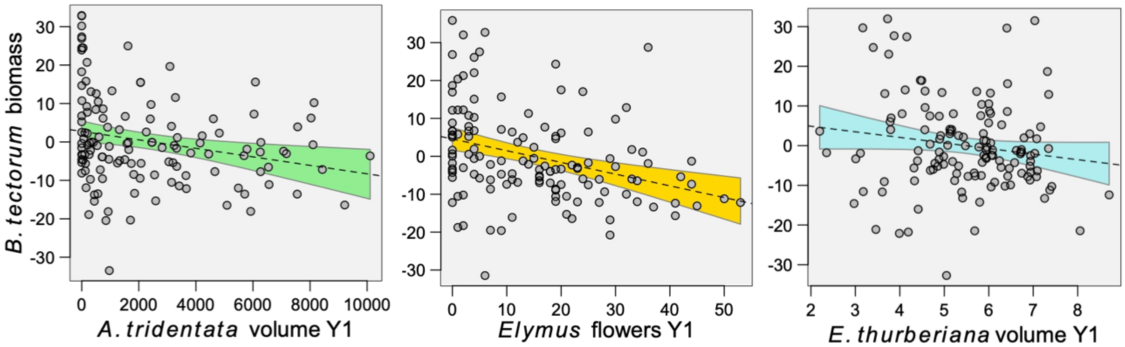


Figure 5. Path diagram illustrating coefficients estimated in structural equation model predicting *B. tectorum* biomass from plant measurements within mesocosms. Plants include *A. tridentata* (ARTR), *Elymus* spp. (ELYMU), *E. thurberiana* (ERTH), and *P. secunda* (POSE), with measurements taken pre-invasion (the first growing season, S1) and post-invasion (the second growing season, S2). A single characteristic was selected among measures of size (volume), number of inflorescences (inflors.) or phenology (number of green days; green), and in-box numbers show corresponding R^2 values. Negative effects are indicated by red lines, and positive effects by black lines; width of lines is scaled to the magnitude of the coefficients, which are shown alongside arrows. Scatterplots are semi-partial plots showing example relationships between a native plant characteristic and *B. tectorum* biomass, with the y-axis adjusted for other variables included in the SEM. The x-axis has no such adjustment. Photos correspond to the scatterplot above. Photo credits: *A. tridentata*, Shannon Swim; *Elymus* spp. and *E. thurberiana*, Elizabeth Leger.


Pre-
invasion
Allopatric origin
0.53**
0.38*
0.08
-0.45**
ARTR
volume S1
0.07
ELYMU
inflors. S1
0.04
ERTH
volume S1
0.00
POSE
green S1
0.05
Post-
invasion
0.52***
-0.93***
-0.75***
0.48***
-0.32*
0.5***
-0.19
0.54***
-0.12
ARTR
inflors. S2
0.27
ELYMU
volume S2
0.30
ERTH
volume S2
0.28
POSE
volume S2
0.30
-0.26***
-0.19*
-0.10
-0.10
-0.62***
-0.52***
0.16
-0.17
B. tectorum biomass
0.61


B. tectorum biomass
30
20
10
0
-10
-20
-30
0
2000
4000
6000
8000
10000
A. tridentata volume Y1
0
10
20
30
40
50
Elymus flowers Y1
2
3
4
5
6
7
8
E. thurberiana volume Y1