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RESEARCH ARTICLE

Foundation species promote local adaptation and fine-scale distribution of herbaceous plants

Michael J. O'Brien[1,2] | Elisa P. Carbonell[3,4] | Gianalberto Losapio[5] | Philipp M. Schlüter[6] | Christian Schöb[4]

[1]Área de Biodiversidad y Conservación, Universidad Rey Juan Carlos, Móstoles, Spain; [2]URPP Global Change and Biodiversity, University of Zurich, Zurich, Switzerland; [3]Aprisco de Las Corchuelas, Torrejón el Rubio, Spain; [4]Department of Environmental Systems Science, Swiss Federal Institute of Technology, ETH Zurich, Zurich, Switzerland; [5]Department of Biology, Stanford University, Stanford, CA, USA and [6]Institute of Biology, University of Hohenheim, Stuttgart, Germany

Correspondence
Michael J. O'Brien
Email: mikey.j.obrien@gmail.com

Christian Schöb
Email: christian.schoeb@usys.ethz.ch

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Abstract

1. Interactions among neighbours can alter demography and traits of commingled species via adaptation or plasticity in phenotypic expression, and understanding these two mechanisms in diverse communities is important for determining the ecological and evolutionary consequences of plant–plant interactions.
2. We reciprocally transplanted perennial species (*Arenaria armerina* and *Festuca indigesta*) among patches of two foundation shrub species and open ground to assess whether origin microsite (defined as the spatially distinct abiotic and biotic conditions associated with the two shrubs and open ground) determines germination, recruitment and growth that, in turn, promotes fine-scale distribution of species among microsites. In addition, we tested the effect of origin microsite on traits, competitive ability, drought tolerance and outlier loci to assess whether origin microsite conditions drove differences in traits, strategies and adaptive loci.
3. Germination was consistently greater for seeds planted back into their origin microsite relative to seeds sourced from foreign microsites, although this effect was weakened for recruitment. Plant growth was best in open sites regardless of origin microsite. In the greenhouse, *A. armerina* had conserved traits within origin microsite but distinct trait values among environmental conditions, specifically plants originating from the most productive microsite (e.g. sufficient light, high nutrients and improved water availability) had distinct trait values. *Festuca indigesta* had conserved trait responses among microsites while within microsite, individuals had significant trait plasticity to different environmental conditions. The combined field and greenhouse results suggest that fine-scale distributions are supported by local adaptation among microsites of *A. armerina* and phenotypic plasticity of *F. indigesta*.
4. *Synthesis*. Adaptation or plasticity in phenotypic expression has different implications for demographic rate and persistence of species in changing environments. Local adaptation to neighbours suggests that reductions in foundation species diversity could concomitantly lead to reduced genetic diversity of commingled

species while a plastic response indicates a more robust and broad response to changing climatic and biotic conditions.

KEYWORDS
competition, drought tolerance, evolutionary ecology, facilitation, foundation species, plant–plant interactions, trade-offs, trait plasticity

1 | INTRODUCTION

Interactions among plants, both direct and indirect, are fundamental drivers of community assembly (Kraft et al., 2015), species coexistence (Adler et al., 2018) and responses to climatic changes (Alexander, Diez, & Levine, 2015; O'Brien, Reynolds, Ong, & Hector, 2017). Plants impact their neighbours via a range of interactions including competition for resources (O'Brien, Reynolds, et al., 2017), amelioration of stressful conditions through facilitation (Schöb, Butterfield, & Pugnaire, 2012) and by mediating mutualisms such as pollinators (Losapio et al., 2019) and soil microbes (Hortal et al., 2017). Ecological research has largely focused on the role of plant interactions that drive ecosystem functioning and community resilience (Tilman, Reich, & Knops, 2006; Wagg et al., 2017), while there has been less emphasis on the effect of plant interactions for structuring genetic diversity and species distributions, especially at fine-spatial scales (Castellanos, Donat-Caerols, González-Martínez, & Verdú, 2014; Cheng Choon et al., 2016; Ehlers, Damgaard, & Laroche, 2016; Thorpe, Aschehoug, Atwater, & Callaway, 2011).

Local adaptation is a process driving genetic diversity among plant populations within species. Biotic interactions among plants may promote local adaptation indirectly by altering local abiotic conditions or directly through competition that selects for genotypes with improved acquisitive strategies (Aarssen, 1989; Ehlers et al., 2016; Germain, Williams, Schluter, & Angert, 2018; Hart, Turcotte, & Levine, 2019; Turkington & Harper, 1979). However, connecting local adaptation explicitly to plant interactions is challenging due to the presence of additional environmental and biotic factors such as soil nutrients, soil microbes and climatic conditions (Thorpe et al., 2011). Furthermore, alterations in species strategies can simply stem from phenotypic plasticity without local adaptation (Abakumova, Zobel, Lepik, & Semchenko, 2016). Despite these challenges, understanding whether plant–plant interactions cause local adaptation is fundamental, since genetic diversity will be associated with species diversity, which has implications for species persistence under climate change (Alexander et al., 2015; Lawrence et al., 2012).

The lack of research on the evolutionary consequences of plant–plant interactions is not surprising because of the difficulty in explicitly testing interactions among plants in the presence of other abiotic and biotic factors that may dilute the outcomes of interactions (Thorpe et al., 2011). Indirect evidence for the role of plant–plant interactions in natural selection has been found in some systems (Aarssen & Turkington, 1985; Schöb, Brooker, & Zuppinger-Dingley, 2018; Turkington & Harper, 1979; van Moorsel et al., 2019; Zuppinger-Dingley et al., 2014) by interpreting genetic variation across plant neighbours or assessing plant performance in reciprocal transplant studies (Ehlers et al., 2016; Kawecki & Ebert, 2004; Thorpe et al., 2011; Turkington & Harper, 1979). Beyond demonstrating the effect of plant–plant interactions on natural selection, questions remain regarding the spatial scales at which adaptation can occur (Leibold, Urban, De Meester, Vanoverbeke, & Klausmeier, 2019; Richardson, Urban, Bolnick, & Skelly, 2014; Sutherland et al., 2013), especially for organisms with high phenotypic plasticity in response to environmental factors that may overshadow adaptive responses (Abakumova et al., 2016; Chevin, Lande, & Mace, 2010). Evidence that adaptation can occur at the neighbourhood scale in plant communities exists from studies on old-pasture systems where individuals of *Trifolium repens* grew best when planted within patches dominated by the grass species from which the individual originated (Aarssen & Turkington, 1985; Turkington & Harper, 1979), likely driven by the distinct soil microbial communities among species (Lüscher, Connolly, & Jacquard, 1992; Thompson, Turkington, & Holl, 1990). Since fundamental trade-offs and genetic differentiation were not demonstrated, those results only indirectly support the selection of genotypes as the underlying driver that promotes fine-scale distributions and improved demographic rates among populations.

Here, we used a dry alpine system (characterized by patchy vegetation created by foundation shrub species) as a model system for testing the consequences of plant–plant interactions on demographic trait variation and potentially adaptive genomic differentiation. This system has aggregations of perennial herbs growing within the foundation shrubs alongside nearby open ground where the herbs grow in isolation. We reciprocally transplanted seeds sourced from different microsites (defined as the spatially distinct abiotic and biotic conditions associated with the two shrubs and open ground; Figure S1) to test for patterns of local adaptation (i.e. improved germination, recruitment and growth of seeds in their origin microsite) as a factor determining the fine-scale distribution of individuals. We also used controlled greenhouse experiments to examine trait expression of plants across origin microsites to disentangle local adaptation from phenotypic plasticity as mechanisms underlying the fine-scale distribution of species. We further tested the effects of competition and drought on plants originating from different microsites to examine the potential trade-offs in response to these variables among microsites. We expect that if local adaptation promotes the persistence of perennial species growing within shrubs and gaps, then seeds will perform better in their microsite of origin, and the species will likely show distinct trait differences that are consistent with

adaptation to the conditions of their origin microsite (e.g. traits that improve stress tolerance in open ground versus traits for improved competition in shrubs).

2 | MATERIALS AND METHODS

2.1 | Site description

Field work was conducted in the Sierra Nevada Mountains, SE Spain. The field site (36.9845°N, 3.3232°W) used for the collection of plants and the field experiment was situated on a gentle slope facing southwest (225°) at 2,500 m a.s.l. Climate at the study site is alpine Mediterranean, with dry and hot summers and average annual rainfall of 690 mm and temperature of 3.9°C. The vegetation at the field site is dominated by perennial dwarf shrubs including a cushion-forming legume shrub endemic to the mountains of SE Spain (*Cytisus galianoi* TALAVERA & GIBBS; 40% cover of the field site, estimated through the intersection of the species canopy along five parallel transects of 25 m, with 10-m distance between transects) and a spiny shrub from the Brassicaceae family distributed over the west-Mediterranean mountains (*Hormathophylla spinosa* (L.) P. KÜPFER; 1.2% cover of the field site). We used these two foundation shrub species (*C. galianoi* and *H. spinosa*) and the surrounding open ground to assess the effect of plant–plant interactions on smaller perennial plants that grow across these three microsites.

During a vegetation survey at the study site in summer 2014, we identified 21 vascular plant species within these microsites using 150 plots of 400 cm^2 (50 per microsite) and visually estimated their relative cover per plot. From this characterization, we selected two focal plants that commonly occur in all three microsites. The two focal plants were a polyploid tussock grass (*Festuca indigesta* BOISS; with on average 6.7% cover in the open, 0.9% cover beneath *H. spinosa* and 0.7% cover beneath *C. galianoi*) and a diploid ligneous herb (*Arenaria armerina* BORY with on average 0.3% cover in all three microsites). Both species are long-lived perennial plants, which mature slowly (i.e. reproductive maturity occurs many years after establishment). They differ in their pollination strategy whereby *F. indigesta* is wind-pollinated and *A. armerina* is insect-pollinated.

2.2 | Field experiment

The field experiment consisted of a reciprocal sowing of *F. indigesta* and *A. armerina* among the three microsites (the canopy areas of *C. galianoi* and *H. spinosa* and the surrounding open ground). Between 15 and 19 August 2014, we collected seed material of the two species from >100 individuals per microsite across the entire study area (for *F. indigesta* which clonally propagates in clumps, seeds were collected from separate distinct clumps to ensure collection from multiple genets). Seeds were not significantly different in mass within species across microsites (see Table S1; Figure S2). The seeds were pooled by species and origin microsite. Prior to sowing the seeds in each of the microsites, we established 90 plots of approximately 10 × 10 cm (30 plots in each microsite) within an area of approximately 0.3 ha. A group of three plots (one of each microsite) was clustered together such that the three microsite plots were available within approximately 4 m^2 and distances between clusters were more than 5 m. Consequently, each plot was located beneath a different shrub or in the open, and locations were chosen randomly. Prior to sowing, sparsely occurring herbaceous vegetation within the plot was removed and seeds were sown into bare soil to homogenize the soil environment across microsites. On 20 August 2014, we sowed 100 seeds per species from each microsite in each of the 90 plots. Seedling counts for each species in each plot were recorded 1 (6 July 2015) and 2 (5–6 July 2016) years after sowing. Germination was considered the maximum count recorded for the 2 years, and recruitment was the number of germinates surviving after 2 years (average of $N = 5$ for species by origin microsite by sown microsite).

In each plot, we determined photosynthetically active radiation (PAR), soil moisture and soil C and N content. PAR was measured with a PAR sensor connected to a MINI-PAM-II photosynthesis yield analyser (Heinz Walz GmbH). Soil moisture was measured gravimetrically by determining soil fresh weight of a sieved (2-mm mesh size) composite of three subsamples summing to 10 ml (tube of 100 × 16 mm) per plot, followed by oven-drying the sample for 48 hr at 105°C before determination of soil dry weight. Analyses of soil C and N content was conducted on a CHN analyser (LECO Instrument GmbH) with air-dried subsamples of the above-mentioned composite sample per plot. These measurements showed three distinct environments. Open sites had the highest light and lowest water and nutrients. *Hormathophylla spinosa* had the lowest light but highest water and nutrients, and *C. galianoi* was intermediate in all variables (see Table S2; Figure 1).

2.3 | Drought experiment

For the drought experiment, we grew 10 seeds per pot and 20 pots of the two species from each of the three microsites in a common garden experiment in the greenhouse located at the campus of the University of Zurich (Zurich, Switzerland). Seeds of each species and from each microsite were sown on 4 February 2015 on commercial mineral soil (Rasenerde, Ökohum GmbH) in 1-L pots in the greenhouse. After germination, and due to low germination and high mortality rates, we selected the most vigorous seedling—which was commonly the only healthy individual—and removed all other seedlings from the pot. An additional group of *A. armerina* seeds were sown on 7 December 2015 due to low germination and survival in the first planting. Climatic conditions in the greenhouse were similar between planting rounds with air temperature on average being 19.1 and 18.7°C and air humidity of 57.6% and 55.5% for the first and second rounds respectively. Each pot was thinned to a single individual and initially watered every 3 days to maintain sufficient water availability for the plants to establish—volumetric soil moisture during this establishment phase was 17% (6% *SD*) measured weekly with a ML3 ThetaProbe, Delta-T Devices Ltd.

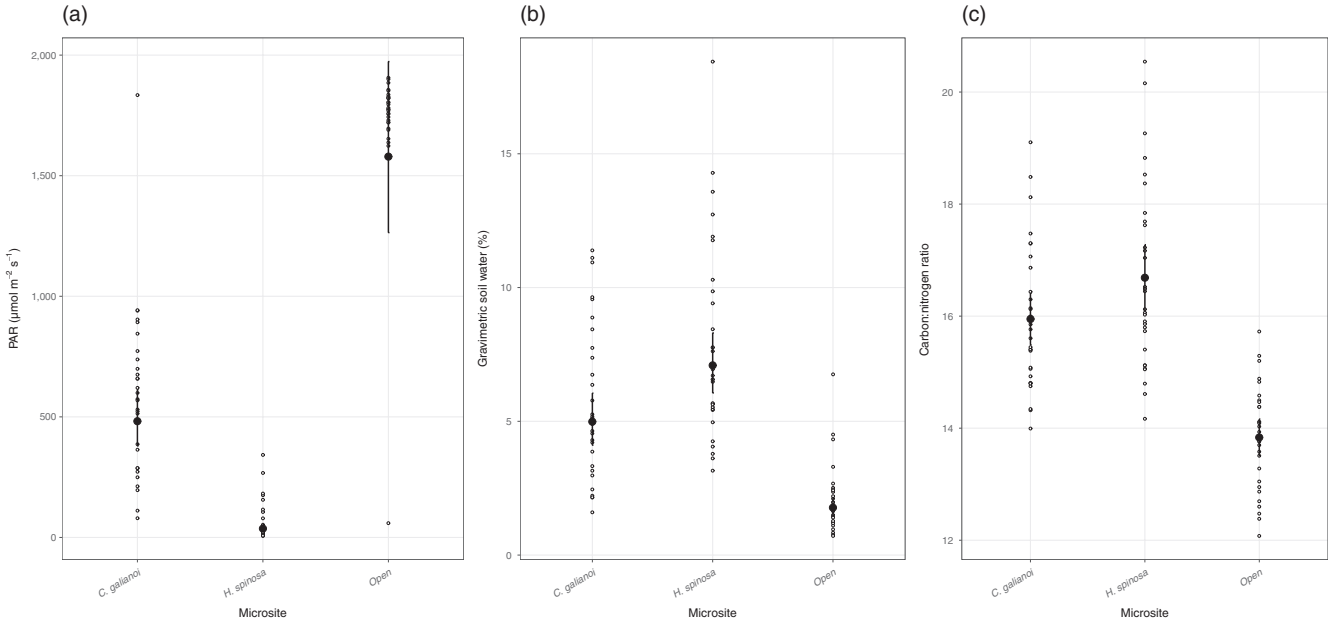

FIGURE 1 Environmental conditions associated with the microsites. Mean with 95% CI for (a) photosynthetically active radiation (PAR), (b) gravimetric soil water content and (c) C:N ratio as a function of the three microsites. Small points represent individual plot measurements

Approximately 1 year after sowing (25 January 2016 for the first round and 6 December 2016 for the second round), the drought treatment was initiated. It consisted of a reduction of the irrigation frequency by 66% of the control watering for 147 days (from watering every 3 days in the control treatment to every 9 days in the drought treatment). The control pots maintained 17% (6% *SD*) volumetric soil moisture, and the drought treatment declined to 7% (6% *SD*). The second round of planting received the drought treatment for 126 days. Volumetric soil moisture of the control was higher during this round (32% with 4% *SD*) relative to the first round, but the drought treatment was similar to the first round of planting (7% with 4% *SD*). At harvest (20 June 2016 and 11 April 2017 respectively), we initially collected the largest, fully developed and healthy leaf, which was saturated with water in the dark overnight and then weighed (i.e. rehydrated leaf mass), scanned for leaf area measurements using the software ImageJ, then dried at 80°C for 48 hr and weighed again. Leaf dry matter content (LDMC) was then calculated as the ratio of leaf dry mass to rehydrated leaf mass, while leaf mass area (LMA) was calculated as the ratio of leaf dry mass to leaf area.

Afterwards, all remaining above-ground plant biomass was collected, separated into living (green) and dead (brown) tissue, dried at 80°C for at least 48 hr and weighed separately. For analyses, we used only the mass of the living tissue. At the end of the experiment, there were on average three individuals of *A. armerina* per microsite per treatment level (drought and control), and on average nine individuals of *F. indigesta* per microsite per treatment level.

2.4 | Competition experiment

For the competition experiment, the target species (*A. armerina* and *F. indigesta*) were grown from seeds in a greenhouse with an average temperature of 19.6°C and humidity of 57.5%. Seeds were sown on 7 December 2015 in 1-L pots filled with commercial mineral soil (Rasenerde, Ökohum GmbH). After germination, on 3 February 2016, we thinned pots to one individual per pot (keeping again the most vigorous individual due to low germination and high mortality rates) and assigned individuals of each species from each microsite (*F. indigesta*: 20 pots per microsite; *A. armerina*: 17 pots for *C. galianoi*, 14 for *H. spinosa* and 11 for the open) into control conditions with no competitor and competition with a neighbour plant from one of three species (*Dactylis glomerata* L., *Festuca nigrescens* LAM. and *Poa pratensis* L.). We aimed at more than one competitor species to avoid potentially species-specific effects of the competitor on one of the target species (Gaudet & Keddy, 1988). Furthermore, we selected competitor species previously used as such in competition studies (e.g. Reader et al., 1994; Wang, Stieglitz, Zhou, & Cahill, 2010). Four seeds of a competitor were sown and, after germination, were reduced to one individual per pot where necessary. On 24 October 2016 (264 days after sowing of the competitors), all above-ground biomass of individuals per pot was harvested, dried at 80°C for at least 48 hr and weighed. At the end of the experiment, there were on average five individuals of *A. armerina* per microsite per treatment level (competition and no competition), and on average nine individuals of *F. indigesta* per microsite per treatment level.

2.5 | Population genomic data generation and analysis

Population genomic data for *A. armerina* were obtained using a modified genotyping-by-sequencing (GBS) protocol (Elshire et al., 2011). Paired-end Illumina HiSeq 2500 sequence data from leaves of 55

individuals (17 individuals from *C. galianoi*, 19 *H. spinosa* and 19 from open areas remained) were analysed as described in Annex A1 of the Supporting Information. To summarize, single nucleotide polymorphisms (SNPs) were identified using STACKS 2.0 (Catchen, Amores, Hohenlohe, Cresko, & Postlethwait, 2011). The VCF file of SNPs was filtered based on a minimum read depth of 10, a minimum of 10,000 variants per individual and a minimum 20% coverage of individuals per loci. We identified outlier loci with elevated F_{ST} using Bayescan 2.1 (Falush, Stephens, & Pritchard, 2003). Because genome-wide differentiation among populations was not expected, we used the outliers to calculate a distance matrix between individuals using an unphased diploid SNP distance (Foll & Gaggiotti, 2008) using snpdist 0.1 from the biOP library (https://sourceforge.net/projects/biop/). Detailed methods of GBS can be found in Annex A1 of the Supporting Information.

2.6 | Statistical analyses

The reciprocal transplant experiment tested the patterns of local adaptation in seedling germination (maximum count per species per plot), recruitment (abundance of plant surviving a year) and growth (biomass). Analysis used generalized linear mixed-effects models with a Poisson distribution and a log link function for germination and recruitment and a Gaussian distribution and identity link function for biomass (see Tables S3–S5). All three variables were analysed with a model designed to test the response of the local seed planted into its origin microsite versus foreign-sourced seeds from the other microsites planted into that same microsite, that is, our main factor of interest. Each response variable was analysed as a function of species (a fixed factor with two levels: *A. armerina* and *F. indigesta*), sown microsite (a fixed factor with three levels: *C. galianoi*, *H. spinosa* and open), a local versus foreign seed source contrast (a fixed factor with two levels: local and foreign), all possible two-way interactions and the three-way interaction (see Tables S4–S6).

A significant effect of the local versus foreign term is interpreted as evidence for local adaptation (Kawecki & Ebert, 2004). A significant interaction between species and the local versus foreign contrast suggests the magnitude of local adaptation varied by species. A significant interaction between sown microsite and local versus foreign contrast suggests sown microsite effects on the magnitude of local adaptation. Finally, a significant three-way interaction among these terms indicates local adaptation is altered by specific species and sown microsite relationships. Random terms were defined as block (a factor with 30 levels) and plot (a factor with 90 levels). The model for biomass was also weighted by abundance to account for variation in seedling density and variance was estimated separately for each species to account for heterogeneity. Biomass was log transformed to meet assumptions of linearity. We also tested a contrast for shrub versus open fit before sown microsite, but this contrast was not significant, which indicates sown microsite explains additional variation beyond the shrub and open categories alone.

Leaf mass area and LDMC from the greenhouse experiments were analysed separately for each species. Each trait was modelled as a function of origin microsite (a fixed factor with three levels: *C. galianoi*, *H. spinosa* and open), watering treatment (a fixed factor with two levels: drought and control) and the two-way interaction using a linear model with a Gaussian distribution and an identity link function (see Table S6). LMA was log transformed to meet assumptions of linearity. These analyses tested for phenotypic variation between control and drought conditions among individuals of a species from a microsite as well as phenotypic variation within species among microsites. If traits were statistically different between treatments within microsite but statistically indistinguishable between microsites, then we assumed phenotypic plasticity in response to environment. Alternatively, if traits were statistically indistinguishable between treatments but different among microsites, then we assumed genetic differentiation in phenotypes.

Drought and competition responses were assessed by first calculating the relative response to these two treatments using the relative interaction index (RII), which is the difference between an individual biomass in a treatment and the mean biomass in the respective control treatment (biomass without a neighbour and biomass in well-watered conditions respectively) divided by the sum of those two terms. The RII was then analysed as a function of species, origin microsite, treatment (a factor with two levels: competition and drought), all possible two-way interactions and the three-way interaction using a linear mixed-effects model with a Gaussian distribution and an identity link function (see Table S7). Values significantly indistinguishable from or above zero indicate equal or improved performance under competition or drought, whereas values significantly below zero indicate reduced performance under competition or drought. Because variation was heterogeneous between treatments, it was estimated separately for the two treatments.

We performed constrained analysis of proximities on the distance matrix of *A. armerina* outlier loci to test the effect of the constraining term, origin microsite (a fixed factor with three levels: *C. galianoi*, *H. spinosa* and open), on marker loci dissimilarity. We tested the significance of the constraining term with a permutation test against a null model with no terms. If the inertia in the permuted models was lower than in the constrained model, then the association was considered statistically significant. To assess relationships between outlier loci and traits, we compared a trait matrix of LMA, LDMC, final height and final biomass (measured on plants in the controlled greenhouse environment) with a matrix of the allele frequency of outlier loci across individuals using redundancy analysis (RDA). This analysis was done on 1,000 resamples of the trait data randomly assigned to each genotype because trait variables were not collected for the plants analysed by GBS. Therefore, the RDA and permutation test were repeated for the 1,000 resamples.

All mixed and linear models were performed with the ASREML-R package (ASReml 4, VSN International) in the R statistical software (version 3.6.3; http://r-project.org). Model R^2 values were calculated with the rsquared function in the PIECEWISESEM package (Lefcheck, 2016) and partial R^2 values were calculated with the r2beta function in R2GLMM package (Jaeger, Edwards, Das, & Sen, 2017).

The constrained analysis of proximity analysis was done using the capscale function (Legendre & Anderson, 1999), and the permutation test was done with the ANOVA function in the VEGAN package (Oksanen et al., 2019). The allele frequencies of outlier loci were calculated with the AD_frequency function in the VCFR package (Knaus & Grünwald, 2017). The RDA was done with the rda function in the VEGAN package.

3 | RESULTS

Germination of *A. armerina* showed the patterns of local adaptation to foundation shrubs with approximately double germination of local versus foreign seeds (Figure 2a) under *C. galianoi* (local = 3.8 germinates; 95% CI: 2.0–7.1 and foreign = 1.9 germinates; 95% CI: 1.1–3.2) and nearly double under *H. spinosa* (local = 2.6 germinates; 95% CI: 1.3–5.2 and foreign = 1.4 germinates; 95% CI: 0.8–2.3). However, germination was not statistically different between local and foreign seeds in open microsites. Germination of *F. indigesta* was similar between local and foreign seeds for open microsites and under *C. galianoi* (Figure 2b) but was significantly greater for local-sourced seeds under *H. spinosa* (local = 10.2 germinates; 95% CI: 5.7–18.2 and foreign = 3.7 germinates; 95% CI: 2.4–5.8).

There was no pattern of local adaptation for recruitment of *A. armerina* (Figure 3a). For *F. indigesta*, individuals under *H. spinosa* still showed local adaptation patterns with local recruitment more than four times that of foreign individuals (local = 3.7 recruits; 95% CI: 1.9–7.1 and foreign = 0.8 recruits; 95% CI: 0.4–1.6; Figure 3b). This result suggests that survival of *F. indigesta* in the first year under *H. spinosa* is ~40% for local individuals versus ~20% for foreign-sourced individuals.

Biomass of individuals did not show a pattern of local adaptation but instead had increased growth in open sites regardless of origin microsite (Figure 4). Biomass of *A. armerina* in open microsite was 11.0 mg (95% CI: 7.1–17.0) in contrast to only 4.2 mg (95% CI: 2.9–6.4) under *C. galianoi* and 2.7 mg (95% CI: 1.7–4.2) under *H. spinosa*. Open site individuals of *F. indigesta* were also larger (25.2 mg, 95% CI: 15.3–41.4) relative to individuals under *C. galianoi* (8.4 mg, 95% CI: 4.2–17.2) and *H. spinosa* (2.6 mg, 95% CI: 1.5–4.3). Biomass trends across microsites tracked the relative light conditions of the microsite (Figure 1).

In the controlled greenhouse environment, the two species showed different trends within microsites in response to control and drought conditions and among origin microsites. LMA and LDMC of *A. armerina* were different among microsites but conserved between treatments within microsites (Figure 5a,c). In particular, individuals of *A. armerina* originating from *C. galianoi* had lower average LMA (0.03 mg/mm^2, 95% CI: 0.02–0.05) than the other two microsite conditions (*H. spinosa* = 0.06 mg/mm^2, 95% CI: 0.03–0.14 and open = 0.07 mg/mm^2, 95% CI: 0.04–0.13). Average LDMC was also lower for individuals of *A. armerina* originating from *C. galianoi* (177 mg/g, 95% CI: 100–254) than the other two microsite conditions (*H. spinosa* = 300 mg/g^2, 95% CI: 207–395 and open = 303 mg/g^2, 95% CI: 231–375). However, within microsite conditions the traits were not significantly different between

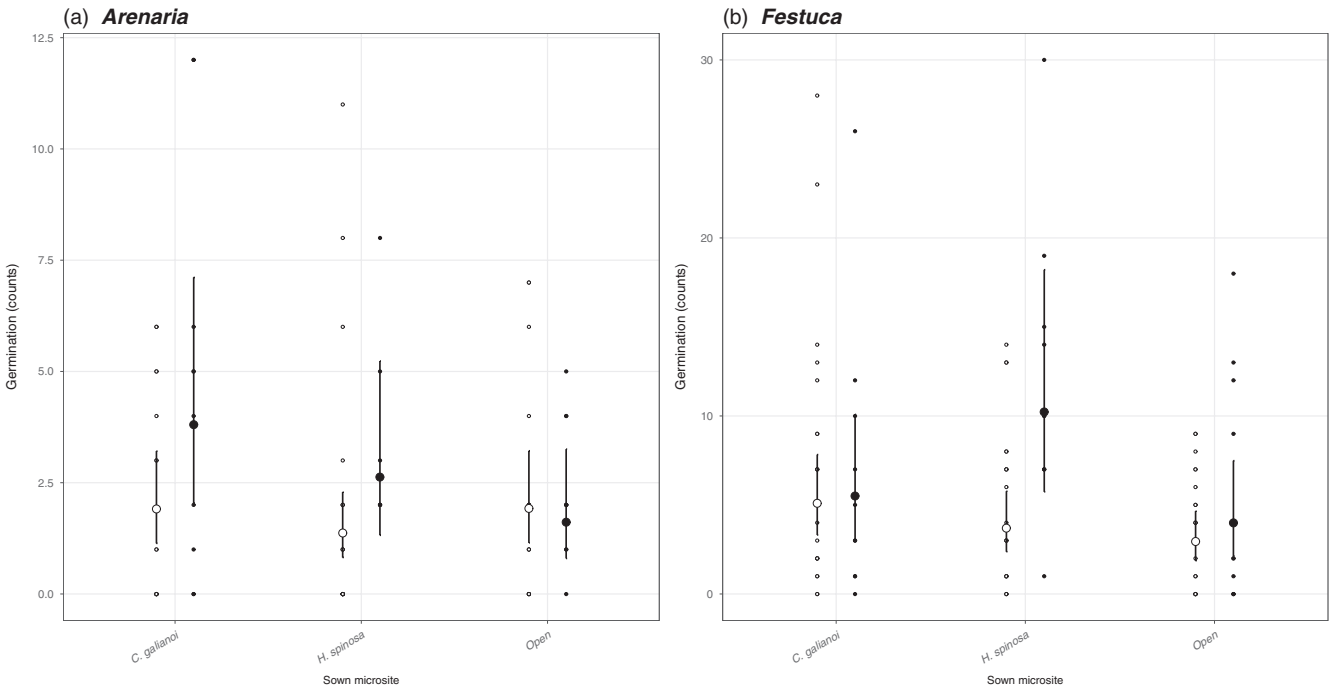

FIGURE 2 Reciprocal transplant germination. The germination of seedlings of *Arenaria armerina* (a) and *Festuca indigesta* (b) sown into each microsite from that same microsite (● local) or from the other two microsites (○ foreign). Large points are mean estimates from all plots with 95% CIs. For the corresponding results of the statistical analyses see Table S3. Data are back-transformed from the log scale for the figure. Comparisons of CIs for local adaptation patterns should be made between local and foreign microsites within a microsite

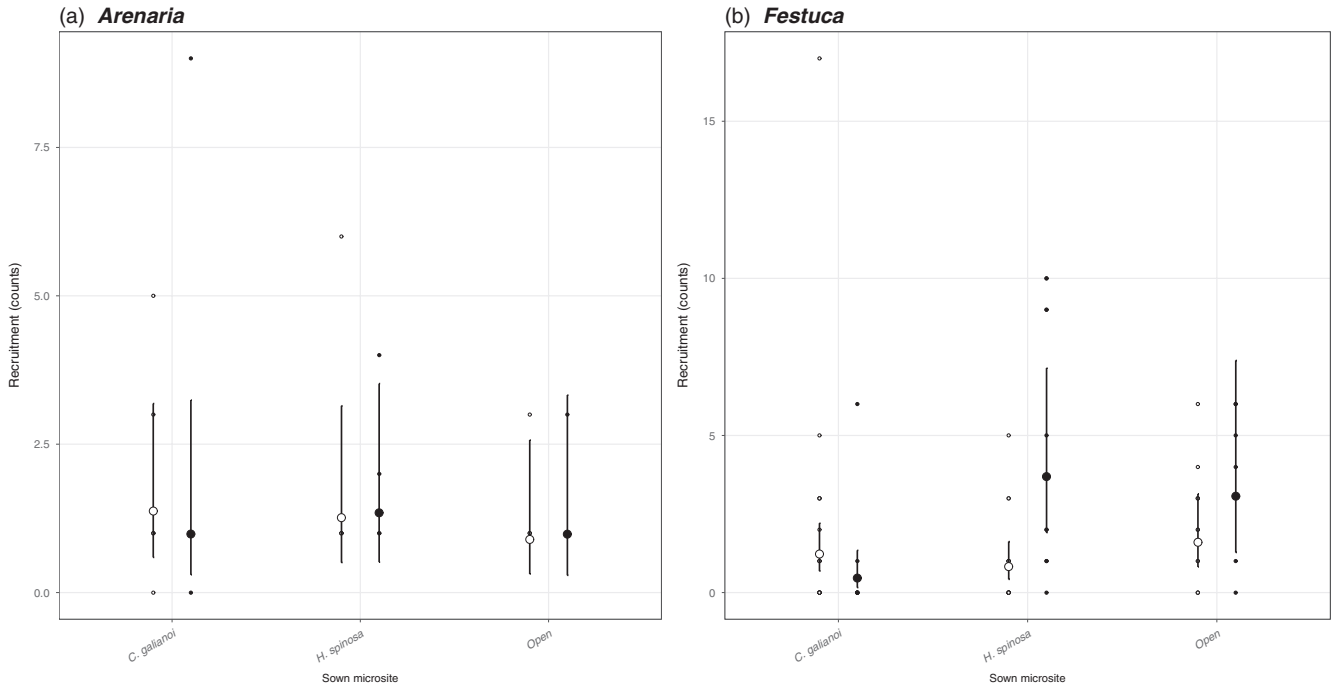

FIGURE 3 Reciprocal transplant recruitment. The recruitment of seedlings of *Arenaria armerina* (a) and *Festuca indigesta* (b) after 2 years planted into each microsite from the same microsite (● local) or from the other two microsites (○ foreign). Large points are mean estimates from all plots with 95% CIs. For the corresponding results of the statistical analyses see Table S4. Data are back-transformed from the log scale for the figure. Comparisons of CIs for local adaptation patterns should be made between local and foreign microsites within a microsite

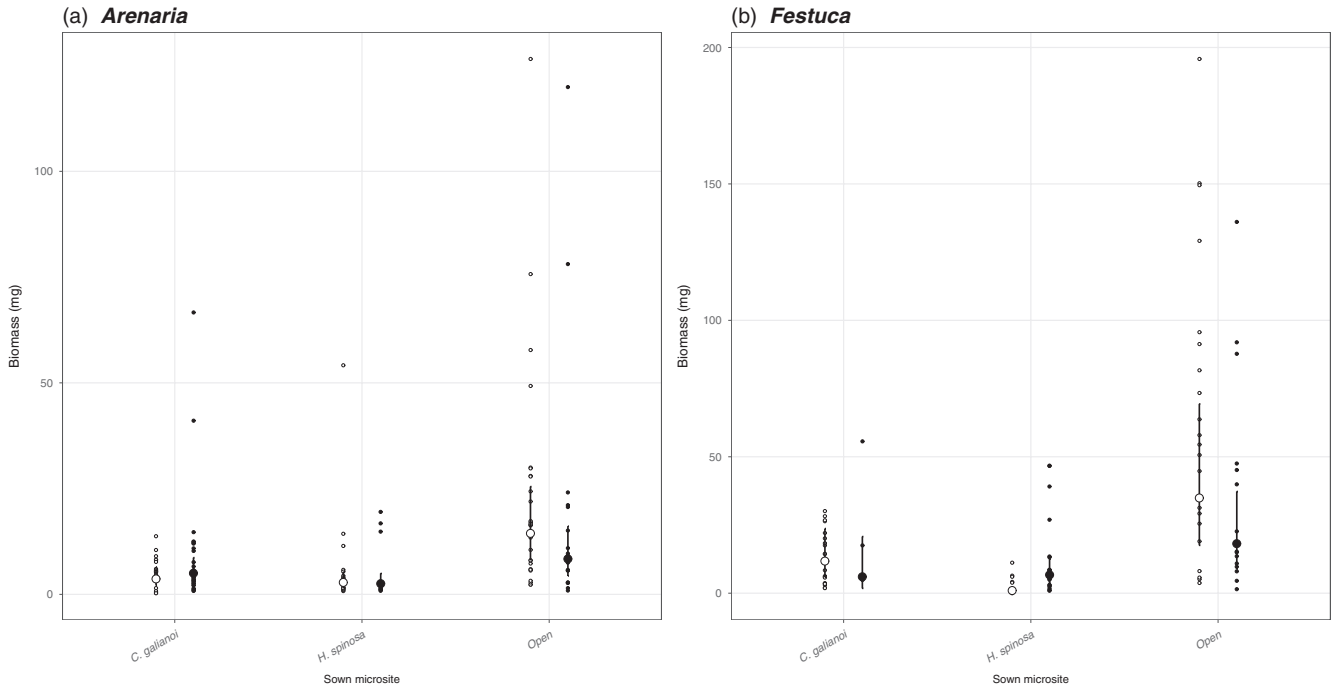

FIGURE 4 Biomass of individuals at the end of the field experiment. The biomass of seedlings of *Arenaria armerina* (a) and *Festuca indigesta* (b) after 2 years planted into each microsite from the same microsite (● local) or from the other two microsites (○ foreign). Large points are mean estimates from all plots with 95% CIs. For the corresponding results of the statistical analyses see Table S5. Data are back-transformed from the log scale for the figure. Comparisons of CIs for local adaptation patterns should be made between local and foreign microsites within a microsite

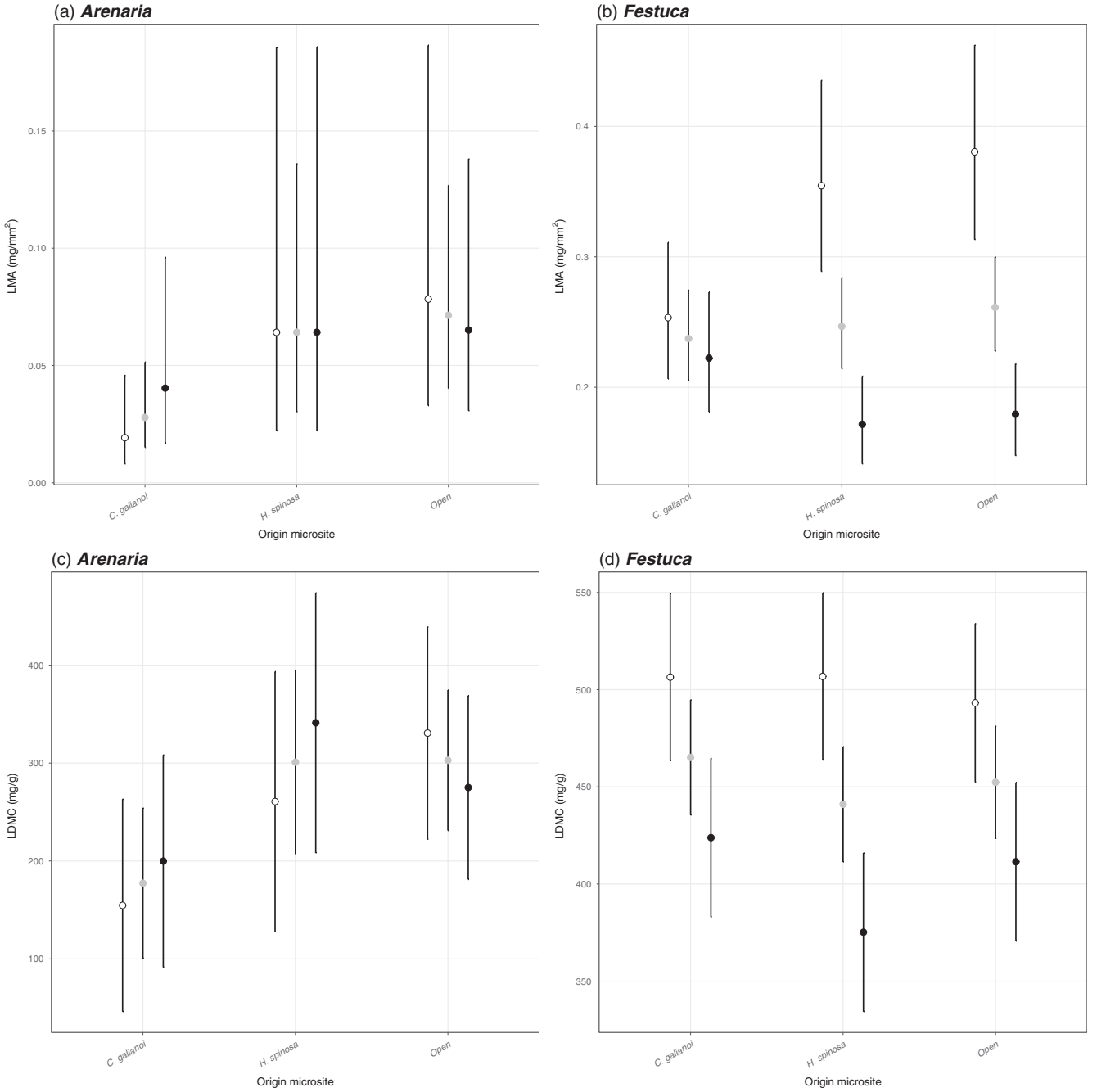

FIGURE 5 Trait differences among plants from the microsites. The leaf mass area (LMA) and leaf dry matter content (LDMC) of *Arenaria armerina* (a and c) and *Festuca indigesta* (b and d) as a function of origin microsite for control (○) and drought (●) treatments from individuals in a greenhouse with a standard soil, temperature and humidity (● are average values per microsite). If traits were statistically different between treatments within microsite but statistically indistinguishable between microsites, then we assumed phenotypic plasticity in response to environment. Alternatively, if traits were statistically indistinguishable between treatments but statistically different among microsites, then we assumed genetic differentiation in phenotypes. Large points are mean estimates from all plots with 95% CIs. Observations were left off the graph for readability. For the corresponding results of the statistical analyses see Table S6

treatments for either trait (95% CIs overlap means between drought and control for each microsite condition Figure 5a,c). The partial R^2 values for both LMA and LDMC (see Table S6 for partial R^2) further indicate the importance of origin for determining trait variation of *A. armerina*.

In contrast, *F. indigesta* showed conserved traits among microsites but significant differences between treatments (Figure 5b,d). Leaf mass area was similar across all microsites (*C. galianoi* = 0.3 mg/mm^2, 95% CI: 0.22–0.35; *H. spinosa* = 0.25 mg/mm^2, 95% CI: 0.20–0.32 and open = 0.25 mg/mm^2, 95% CI: 0.20–0.32). The same was true for LDMC from all microsites (*C. galianoi* = 456 mg/g^2, 95% CI: 388–524; *H. spinosa* = 432 mg/g^2, 95% CI: 364–499 and open = 443 mg/g^2, 95% CI: 375–510). However, traits were always significantly different between control and drought treatments within microsite,

except for LMA under *C. galianoi* (Figure 5b). The partial R^2 values for both LMA and LDMC (see Table S6 for partial R^2) further indicate the importance of water treatment for determining trait variation of *F. indigesta*.

The competition and drought manipulations showed two distinct responses from the species. Origin microsite of *A. armerina* determined the response to competitors (Figure 6) whereby the growth of individuals from *C. galianoi* was better in the presence of competitors (0.2 RII, 95% CI: 0.1–0.4) but the response shifted to a significantly negative effect on individuals from *H. spinosa* (−0.4 RII, 95% CI: −0.7 to −0.2) and open (−0.6 RII, 95% CI: −0.8 to −0.4) microsites. These results show a pattern of decreasing competitive

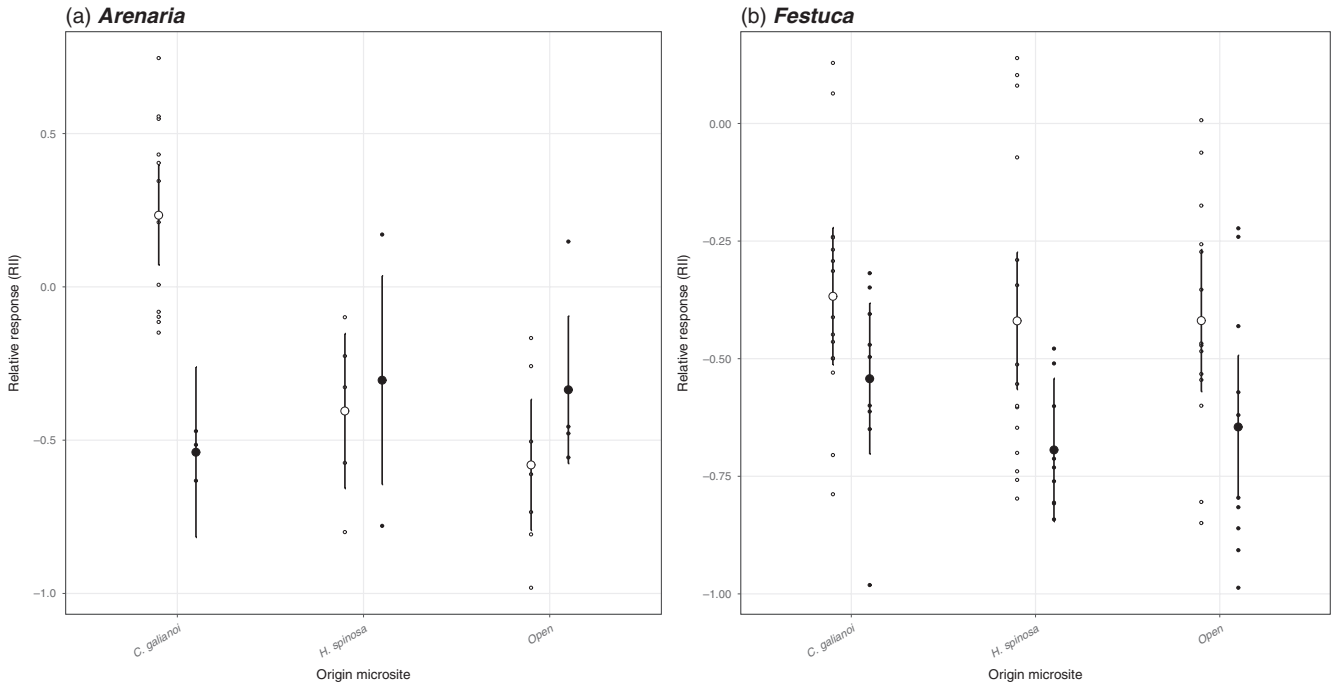

FIGURE 6 Response to competition and drought of individuals from the microsites. The response of *Arenaria armerina* (a) and *Festuca indigesta* (b) to competition (○) with other species or reduced water availability (●). The large points represent the average relative interaction index (RII; 95% CI) between control and competition or drought treatments, and small points are individual RIIs. Confidence intervals that do not overlap zero are statistically different from control biomass and significantly negative values suggest sensitivity to competition or drought. For the corresponding results of the statistical analyses see Table S7

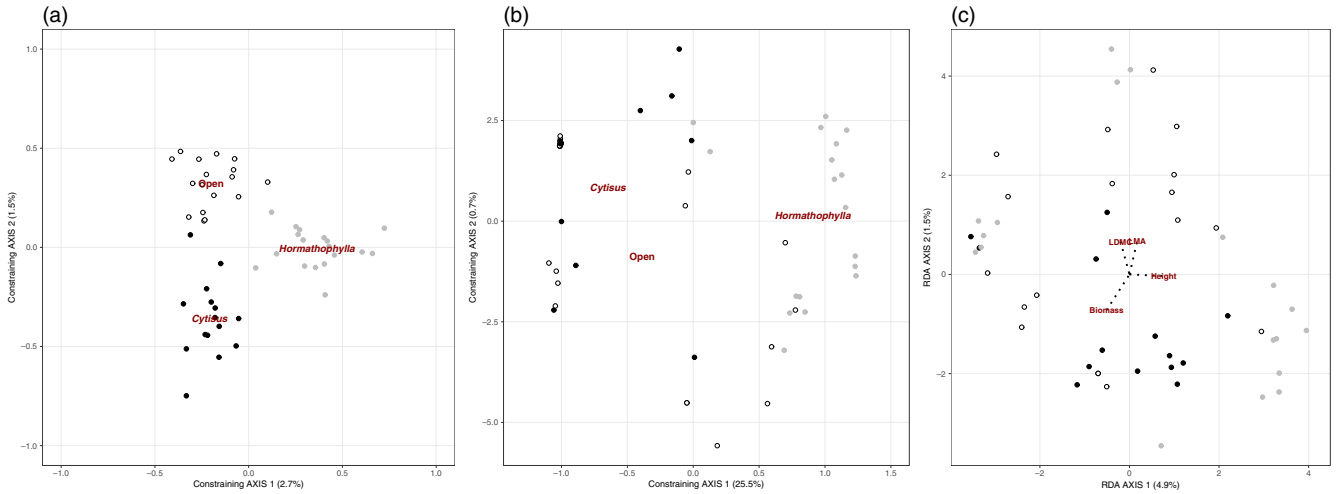

FIGURE 7 Dissimilarity and allele frequency of *Arenaria armerina*. Constrained analysis of proximities of pairwise genetic distances among samples of *A. armerina* from the three microsites (*Cytisus galianoi* ●, *Hormathophylla spinosa* ● and Open ○), based on single nucleotide polymorphisms (SNPs) of all loci (a; 69,623 SNPs) and with elevated F_{ST} loci (b; 46 SNPs). Text are centroids of the population, and small points are individual samples. Microsites were significantly different in elevated F_{ST} loci based on a permutation test against a null model of no differences ($p = 0.001$). The matrix of allele frequency (c) was not significantly associated with the matrix of traits measured in the controlled greenhouse conditions

tolerance of *A. armerina* from the most (*C. galianoi*) to the least (open) productive microsite. In contrast, the effect of drought was statistically indistinguishable among microsites (*C. galianoi* = −0.5 RII, 95% CI: −0.8 to −0.3; *H. spinosa* = −0.3 RII, 95% CI: −0.7 to 0.04 and open = −0.3 RII, 95% CI: −0.6 to −0.1), and *A. armerina* from *H. spinosa* was unaffected by drought. All microsites of *F. indigesta* responded similar to competition (all 95% CIs overlap all means across microsite conditions; Figure 6b) and drought (all 95% CIs overlap all means across microsite conditions; Figure 6b).

We identified 69,623 marker loci of *A. armerina* after filtering the total SNPs for read depth and coverage, of which 46 showed elevated F_{ST} values among individuals from the three microsites (F_{ST} of neutral loci = 0.01 and F_{ST} of outlier loci = 0.12). Five individuals were also removed after filtering due to low coverage leaving 50 individuals (15 individuals from *C. galianoi*, 18 *H. spinosa* and 17 from open areas). The constrained analysis of proximities of the total loci showed that pairwise distances between individuals from the three microsites were not significantly different from the null model (Figure 7a). However, outlier loci of *A. armerina* were significantly differentiated among microsite conditions, which support the likelihood of differences in adaptive loci among these microsites (Figure 7b; $p = 0.001$). In particular, axis 1 explained 25% of the variation and showed a clear separation between outlier loci from *H. spinosa* and the other two microsites while axis 2 highlighted differences in the centroids of *C. galianoi* and open microsites (Figure 7b). The trait matrix was not significantly related with the allele frequency of outlier loci (mean permutation *p*-value from 1,000 resampled trait matrices = 0.48, 95% CI: 0.02–0.94), indicating there was limited connection between outlier loci and the phenotypic traits measured in the greenhouse experiment.

4 | DISCUSSION

Our reciprocal transplant of seeds among foundation shrubs and open ground showed that individuals of *A. armerina* from shrubs had higher germination in their origin microsite relative to foreign seeds from the other two microsites, which supports a pattern of local adaptation (Kawecki & Ebert, 2004), although this pattern was not evident in open microsites. Individual biomass tracked the light conditions of the three microsite conditions whereby biomass was greatest for seedlings planted in open microsites followed by *C. galianoi* microsites and finally *H. spinosa* microsites. This pattern suggests that shrubs limited growth relative to open microsite conditions. The contrasting response of germination with biomass between foundation shrubs and open sites shows that shrubs facilitate the understorey perennial plants in these semi-arid systems while also inhibiting growth via reduced light (O'Brien, Pugnaire, Armas, Rodríguez-Echeverría, & Schöb, 2017; Schöb, Armas, & Pugnaire, 2013). The trait assessment in the greenhouse indicated that *A. armerina* traits were more conserved among individuals of the same microsite but varied among microsites, while *F. indigesta* traits varied within each microsite in response to environmental conditions but were conserved across microsites. Furthermore, outlier loci of *A. armerina* were dissimilar among origin microsites, and dissimilarity showed distinct differences between the lowest light origin (*H. spinosa*) and the two higher light sites. This consistent pattern of demographic, trait and allele frequency differences provides evidence for local adaptation of *A. armerina* among microsites. It suggests the selection of locally adapted genotypes during germination within the microhabitats, which is supported by significant differences in potentially adaptive loci among microhabitats.

Despite the reduction of growth under shrubs relative to open microsites, foundation shrubs supported greater germination and equal or greater recruitment of local relative to foreign individuals. This response was strongest for germination, which suggests a selective force on local genotypes at this stage of development. Although our reciprocal transplant experiment cannot determine the mechanism driving adaptation, based on the environmental conditions of the site, we propose a process that first separates shrub and open microsites and then distinguishes between the foundation shrubs. Light—and likely temperature due to shading (O'Brien, Pugnaire, et al., 2017)—decreases from open to *C. galianoi* to *H. spinosa* microsites (Figure 1). Therefore, seeds originating from the shrubs likely germinate better than open sites in darker and cooler conditions. Light may then have a further impact between the shaded conditions under *C. galianoi* (30% direct sunlight) versus the dark conditions under *H. spinosa* (2% direct sunlight)—that is, local seeds from *H. spinosa* germinate well in very low light and temperature conditions. The large dissimilarity between outlier alleles from the darkest microsite conditions of *H. spinosa* and the other two microsites provides evidence for light as an important mechanism promoting local adaptation—suggesting dark conditions are potentially selecting specific adaptations.

Alternative processes, like inhibited germination of open microsite seed by the additional nutrients and water associated with the shrub microsites, seem unlikely. However, other studies have shown the benefits of local soil environments for improving germination (O'Brien et al., 2018), which may, for example, be due to specific interactions with the rhizobial bacteria cultivated by the foundation shrubs (Delshadi, Ebrahimi, & Shirmohammadi, 2017; Lozano, Armas, Hortal, Casanoves, & Pugnaire, 2017; Shweta et al., 2008). Maternal effects may also promote differences in germination, especially if offspring are produced under higher water availability and nutrient conditions (Donohue, 2009; Roach & Wulff, 1987). Our data do not provide direct evidence of maternal effects in that no differences in seed mass existed among origin microsites nor were there consistently higher germination of a single origin microsite (a common pattern of a maternal effect). Therefore, we suggest temperature and light strongly influence the adaptive patterns with indirect influence from soil variables.

The field study suggests that local individuals of *A. armerina* germinate best back in their origin microsite for both foundation shrub species, and the greenhouse traits, competition and drought responses provided reasoning for this adaptive benefit under

C. galianoi. However, the mechanistic support under *H. spinosa* is less clear, which may be due to the different forces driving selection under these two shrub species. The environment created by *C. galianoi* has increased nutrients and water relative to open microsite conditions without being light limiting (Figure 1) while *H. spinosa* provides the greatest soil nutrients and water but with very low light conditions (Figure 1). Therefore, selection of *A. armerina* under *C. galianoi* may be associated with competition due to the productive conditions—more light than under *H. spinosa* and more water and nutrients than open microsites—while under *H. spinosa* selection may be due to tolerance to low light (Von Wettberg, Remington, & Schmitt, 2008) and competition for soil resources. Our trait measurements were focused on aboveground variables which may have overlooked important adaptive traits under selection in the environment under *H. spinosa*. The benefit of locally sourced *F. indigesta* under *H. spinosa* may also be due to below-ground traits. This bias also explains the clear contrast of traits between individuals of *A. armerina* from *C. galianoi* and open sites in a controlled setting, which were consistent with adaptation to these two distinct environments.

Two distinct mechanisms appear to be governing the demography and fine-scale distributions of these two species. Origin microsite promoted distinct leaf phenotypes of *A. armerina*, which led to divergent competitive ability of individuals, especially between *C. galianoi* and open microsites. These results, therefore, suggest evolutionary adaptation to microsites associated with species-specific interactions with shrubs (Baron, Richirt, Villoutreix, Amsellem, & Roux, 2015; Brachi et al., 2013; Hart et al., 2019), particularly along the decreasing light environment from open to *C. galianoi* to *H. spinosa* microsites. Alternatively, *F. indigesta* expressed similar leaf phenotypes and tolerances to competition and drought among individuals sourced across the three microsites in the controlled setting, which indicates the presence of this species within these three microsites is due, in part, to phenotypic plasticity of individuals sourced from all three microsites. The major force exerting selection on *A. armerina* at these fine-scales appears to be light (and its association with temperature), but, in addition to the selection on germination, a possible explanation can be attributed to the differences in the pollinators associated with foundation shrubs and isolated patches. In an independent study at nearby site, Losapio et al. (2019) found more than 60% dissimilarity between pollinator communities visiting the flowers of herbaceous plant species growing in the presence and absence of foundation species. Distinct pollinators may decrease gene flow between plant populations across these microsites and facilitate reproductive barriers that may contribute to isolation and divergence of sympatric plant populations. *Arenaria armerina* is an insect-pollinated species suggesting pollinator difference could promote local adaptation while *F. indigesta* is a wind-pollinated species that is not subject to this gene flow limitation.

These different strategies in response to foundation shrubs have implications for understanding the responses of species to climate change and for the maintenance of biodiversity. For example, the relationship between *A. armerina* genotypes and foundation shrubs suggests these biotic interactions may maintain specific genotypes of this species under hotter and drier conditions (O'Brien, Pugnaire, et al., 2017). Therefore, the loss of foundation shrub species may result in the loss of within-species genetic diversity (i.e. greater species diversity promotes greater genotypic diversity within species), which supports predictions for the plant communities in Sierra Nevada (Losapio & Schöb, 2017) and trends in other systems (Cheng Choon et al., 2016). Alternatively, in the controlled setting, *F. indigesta* showed a conserved trait response to drought across microsite conditions (i.e. plants from all origins responded similar to drought) but plastic phenotypes within microsite condition. This suggests that individuals of this species may be more tolerant to climate fluctuations and less sensitive to losses in genotypic diversity because populations have a broader range of phenotypic expression in response to environmental conditions than *A. armerina*.

Our study supports the argument that fine-scale plant–plant interactions can contribute to local adaptation within species thereby promoting genetic diversity. We demonstrate that stress-ameliorating foundation shrubs can induce a shift along the competition–stress tolerance trade-off axis towards more competitive ability and less drought tolerance of understorey perennial plants. However, we also show that phenotypic plasticity is an alternative mechanism for species persistence in these diverse neighbourhoods. Importantly though, the response of species to climate change and biodiversity shifts will depend on the process driving the fine-scale distribution, whereby species differentiated across microsite conditions are likely susceptible to reduced genetic diversity if foundation species are lost.

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AUTHORS' CONTRIBUTIONS

M.J.O. analysed the data and wrote the manuscript; E.P.C. and G.L. contributed to the conceptual design, field implementation, data collection and revisions; P.M.S. oversaw molecular analyses and contributed to the analysis of the sequencing data; C.S. designed and carried out the experiment, co-wrote the manuscript and contributed to revisions.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13461.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xksn02vcs (O'Brien, Carbonell, Losapio, Schlüter,

& Schöb, 2020). No custom R code was used, only built-in functions in standard software packages and all parameters are stated in the methods. Custom code for calculation of pairwise SNP distances is provided at https://sourceforge.net/p/biop/git/ci/master/tree/examples/pas/snpdist.dpr.

ORCID

Michael J. O'Brien https://orcid.org/0000-0003-0943-8423
Gianalberto Losapio https://orcid.org/0000-0001-7589-8706
Christian Schöb https://orcid.org/0000-0003-4472-2286

REFERENCES

Aarssen, L. W. (1989). Competitive ability and species coexistence: A 'plant's-eye' view. *Oikos*, *56*(3), 386–401. https://doi.org/10.2307/3565625

Aarssen, L. W., & Turkington, R. (1985). Biotic specialization between neighbouring genotypes in *Lolium perenne* and *Trifolium repens* from a permanent pasture. *Journal of Ecology*, *73*(2), 605–614. https://doi.org/10.2307/2260497

Abakumova, M., Zobel, K., Lepik, A., & Semchenko, M. (2016). Plasticity in plant functional traits is shaped by variability in neighbourhood species composition. *New Phytologist*, *211*(2), 455–463. https://doi.org/10.1111/nph.13935

Adler, P. B., Smull, D., Beard, K. H., Choi, R. T., Furniss, T., Kulmatiski, A., … Veblen, K. E. (2018). Competition and coexistence in plant communities: Intraspecific competition is stronger than interspecific competition. *Ecology Letters*, *21*, 1319–1329. https://doi.org/10.1111/ele.13098

Alexander, J. M., Diez, J. M., & Levine, J. M. (2015). Novel competitors shape species' responses to climate change. *Nature*, *525*, 515–518. https://doi.org/10.1038/nature14952

Baron, E., Richirt, J., Villoutreix, R., Amsellem, L., & Roux, F. (2015). The genetics of intra- and interspecific competitive response and effect in a local population of an annual plant species. *Functional Ecology*, *29*(10), 1361–1370. https://doi.org/10.1111/1365-2435.12436

Brachi, B., Villoutreix, R., Faure, N., Hautekèete, N., Piquot, Y., Pauwels, M., … Roux, F. (2013). Investigation of the geographical scale of adaptive phenological variation and its underlying genetics in *Arabidopsis thaliana*. *Molecular Ecology*, *22*(16), 4222–4240. https://doi.org/10.1111/mec.12396

Castellanos, M. C., Donat-Caerols, S., González-Martínez, S. C., & Verdú, M. (2014). Can facilitation influence the spatial genetics of the beneficiary plant population? *Journal of Ecology*, *102*(5), 1214–1221. https://doi.org/10.1111/1365-2745.12278

Catchen, J., Amores, A., Hohenlohe, P., Cresko, W., & Postlethwait, J. (2011). Stacks: Building and genotyping loci de novo from short-read sequences. *G3: Genes*, *Genomes*, *Genetics*, *1*, 171–182. https://doi.org/10.1534/g3.111.000240

Cheng Choon, A., O'Brien, M. J., Ng, K. K. S., Lee, P. C., Hector, A., Schmid, B., & Shimizu, K. K. (2016). Genetic diversity of two tropical tree species of the Dipterocarpaceae following logging and restoration in Borneo: High genetic diversity in plots with high species diversity. *Plant Ecology and Diversity*, *9*(5–6), 459–469. https://doi.org/10.1080/17550874.2016.1270363

Chevin, L. M., Lande, R., & Mace, G. M. (2010). Adaptation, plasticity, and extinction in a changing environment: Towards a predictive theory. *PLoS Biology*, *8*(4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Delshadi, S., Ebrahimi, M., & Shirmohammadi, E. (2017). Influence of plant-growth-promoting bacteria on germination, growth and nutrients' uptake of *Onobrychis sativa* L. under drought stress. *Journal of Plant Interactions*, *12*(1), 200–208. https://doi.org/10.1080/17429145.2017.1316527

Donohue, K. (2009). Completing the cycle: Maternal effects as the missing link in plant life histories. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*, 1059–1074. https://doi.org/10.1098/rstb.2008.0291

Ehlers, B. K., Damgaard, C. F., & Laroche, F. (2016). Intraspecific genetic variation and species coexistence in plant communities. *Biology Letters*, *12*, 20150853. https://doi.org/10.1098/rsbl.2015.0853

Elshire, R. J., Glaubitz, J. C., Sun, Q., Poland, J. A., Kawamoto, K., Buckler, E. S., & Mitchell, S. E. (2011). A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE*, *6*(5), e19379. https://doi.org/10.1371/journal.pone.0019379

Falush, D., Stephens, M., & Pritchard, J. (2003). Inference of population structure using multilocus genotype data: Linked loci and correlated allele frequencies. *Genetics*, *164*, 1567–1587. https://doi.org/10.1111/j.1471-8286.2007.01758.x

Foll, M., & Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: A Bayesian perspective. *Genetics*, *180*(2), 977–993. https://doi.org/10.1534/genetics.108.092221

Gaudet, C. L., & Keddy, P. A. (1988). A comparative approach to predicting competitive ability from plant traits. *Nature*, *8*, 242–243. https://doi.org/10.1038/334242a0

Germain, R. M., Williams, J. L., Schluter, D., & Angert, A. L. (2018). Moving character displacement beyond characters using contemporary coexistence theory. *Trends in Ecology & Evolution*, *33*(2), 74–84. https://doi.org/10.1016/j.tree.2017.11.002

Hart, S. P., Turcotte, M. M., & Levine, J. M. (2019). Effects of rapid evolution on species coexistence. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(6), 2112–2117. https://doi.org/10.1073/pnas.1816298116

Hortal, S., Lozano, Y. M., Bastida, F., Armas, C., Moreno, J. L., Garcia, C., & Pugnaire, F. I. (2017). Plant-plant competition outcomes are modulated by plant effects on the soil bacterial community. *Scientific Reports*, *7*(September), 1–9. https://doi.org/10.1038/s41598-017-18103-5

Jaeger, B. C., Edwards, L. J., Das, K., & Sen, P. K. (2017). An R2 statistic for fixed effects in the generalized linear mixed model. *Journal of Applied Statistics*, *44*(6), 1086–1105. https://doi.org/10.1080/02664763.2016.1193725

Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*(12), 1225–1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Knaus, B. J., & Grünwald, N. J. (2017). VCFR: A package to manipulate and visualize variant call format data in R. *Molecular Ecology Resources*, *17*(1), 44–53. https://doi.org/10.1111/1755-0998.12549

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*(5), 592–599. https://doi.org/10.1111/1365-2435.12345

Lawrence, D., Fiegna, F., Behrends, V., Bundy, J. G., Phillimore, A. B., Bell, T., & Barraclough, T. G. (2012). Species interactions alter evolutionary responses to a novel environment. *PLoS Biology*, *10*(5), e1001330. https://doi.org/10.1371/journal.pbio.1001330

Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in r for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, *7*(5), 573–579. https://doi.org/10.1111/2041-210X.12512

Legendre, P., & Anderson, M. J. (1999). Distance-based redundancy analysis: Testing multispecies responses in multifactorial experiments. *Ecological Monographs*, *69*(1), 1–24. https://doi.org/10.1890/0012-9615(1999)069[0001:DBRATM]2.0.CO;2

Leibold, M. A., Urban, M. C., De Meester, L., Vanoverbeke, J., & Klausmeier, C. A. (2019). Regional neutrality evolves through local adaptive niche evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *116*, 2612–2617. https://doi.org/10.1073/pnas.1808615116

Losapio, G., Fortuna, M. A., Bascompte, J., Schmid, B., Michalet, R., Neumeyer, R., … Schöb, C. (2019). Plant interactions shape pollination networks via nonadditive effects. *Ecology*, *100*(3), e02619. https://doi.org/10.1002/ecy.2619

Losapio, G., & Schöb, C. (2017). Resistance of plant–plant networks to biodiversity loss and secondary extinctions following simulated environmental changes. *Functional Ecology*, *31*(5), 1145–1152. https://doi.org/10.1111/1365-2435.12839

Lozano, Y. M., Armas, C., Hortal, S., Casanoves, F., & Pugnaire, F. I. (2017). Disentangling above- and below-ground facilitation drivers in arid environments: The role of soil microorganisms, soil properties and microhabitat. *New Phytologist*, *216*(4), 1236–1246. https://doi.org/10.1111/nph.14499

Lüscher, A., Connolly, J., & Jacquard, P. (1992). Neighbour specificity between *Lolium perenne* and *Trifolium repens* from a natural pasture. *Oecologia*, *91*(3), 404–409. https://doi.org/10.1007/BF00317630

O'Brien, M. J., Carbonell, E. P., Losapio, G., Schlüter, P. M., & Schöb, C. (2020). Data from: Foundation species promote local adaptation and fine-scale distribution of herbaceous plants. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.xksn02vcs

O'Brien, M. J., Pugnaire, F. I., Armas, C., Rodríguez-Echeverría, S., & Schöb, C. (2017). The shift from plant-plant facilitation to competition under severe water deficit is spatially explicit. *Ecology and Evolution*, *7*(7), 2441–2448. https://doi.org/10.1002/ece3.2875

O'Brien, M. J., Pugnaire, F. I., Rodríguez-Echeverría, S., Morillo, J. A., Martín-Usero, F., López-Escoriza, A., … Armas, C. (2018). Mimicking a rainfall gradient to test the role of soil microbiota for mediating plant responses to drier conditions. *Oikos*, *127*(12), 1776–1786. https://doi.org/10.1111/oik.05443

O'Brien, M. J., Reynolds, G., Ong, R., & Hector, A. (2017). Resistance of tropical seedlings to drought is mediated by neighbourhood diversity. *Nature Ecology & Evolution*, *1*(11), 1643–1648. https://doi.org/10.1038/s41559-017-0326-0

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., … Wagner, H. (2019). *vegan: Community ecology package*. R package version 2.5-6. Retrieved from https://github.com/vegandevs/vegan

Reader, R. J., Wilson, S. D., Belcher, J. W., Wisheu, I., Keddy, P. A., Tilman, D., … Beisner, B. E. (1994). Plant competition in relation to neighbor biomass: An intercontinental study with *Poa pratensis*. *Ecology*, *76*(6), 1753–1760. https://doi.org/10.2307/1941691

Richardson, J. L., Urban, M. C., Bolnick, D. I., & Skelly, D. K. (2014). Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology & Evolution*, *29*(3), 165–176. https://doi.org/10.1016/j.tree.2014.01.002

Roach, D. A., & Wulff, R. D. (1987). Maternal effects in plants. *Annual Review of Ecology & Systematics*, *18*, 209–235. https://doi.org/10.1146/annurev.es.18.110187.001233

Schöb, C., Armas, C., & Pugnaire, F. I. (2013). Direct and indirect interactions co-determine species composition in nurse plant systems. *Oikos*, *122*(9), 1371–1379. https://doi.org/10.1111/j.1600-0706.2013.00390.x

Schöb, C., Brooker, R. W., & Zuppinger-Dingley, D. (2018). Evolution of facilitation requires diverse communities. *Nature Ecology & Evolution*, *2*(9), 1381–1385. https://doi.org/10.1038/s41559-018-0623-2

Schöb, C., Butterfield, B. J., & Pugnaire, F. I. (2012). Foundation species influence trait-based community assembly. *New Phytologist*, *196*(3), 824–834. https://doi.org/10.1111/j.1469-8137.2012.04306.x

Shweta, B., Maheshwari, D. K., Dubey, R. C., Arora, D. S., Bajpai, V. K., & Kang, S. C. (2008). Beneficial effects of fluorescent pseudomonads on seed germination, growth promotion, and suppression of charcoal rot in groundnut (*Arachis hypogea* L.). *Journal of Microbiology and Biotechnology*, *18*(9), 1578–1583.

Sutherland, W. J., Freckleton, R. P., Godfray, H. C. J., Beissinger, S. R., Benton, T., Cameron, D. D., … Wiegand, T. (2013). Identification of 100 fundamental ecological questions. *Journal of Ecology*, *101*(1), 58–67. https://doi.org/10.1111/1365-2745.12025

Thompson, J. D., Turkington, R., & Holl, F. B. (1990). The influence of *Rhizobium leguminosarum* biovar. trifolii on the growth and neighbour relationships of *Trifolium repens* and three grasses. *Canadian Journal of Botany*, *68*(2), 296–303. https://doi.org/10.1139/b90-040

Thorpe, A. S., Aschehoug, E. T., Atwater, D. Z., & Callaway, R. M. (2011). Interactions among plants and evolution. *Journal of Ecology*, *99*(3), 729–740. https://doi.org/10.1111/j.1365-2745.2011.01802.x

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*(7093), 629–632. https://doi.org/10.1038/nature04742

Turkington, R., & Harper, J. L. (1979). The growth, distribution and neighbour relationships of *Trifolium repens* in a permanent pasture: IV. Fine-scale biotic differentiation. *Journal of Ecology*, *67*(1), 245–254. https://doi.org/10.2307/2259345

van Moorsel, S. J., Schmid, M. W., Wagemaker, N. C. A. M., van Gurp, T., Schmid, B., & Vergeer, P. (2019). Evidence for rapid evolution in a grassland biodiversity experiment. *Molecular Ecology*, *28*(17), 4097–4117. https://doi.org/10.1111/mec.15191

Von Wettberg, E. J., Remington, D. L., & Schmitt, J. (2008). Partitioning adaptive differentiation across a patchy landscape: Shade avoidance traits in *Impatiens capensis*. *Evolution*, *62*(3), 654–667. https://doi.org/10.1111/j.1558-5646.2007.00309.x

Wagg, C., O'Brien, M. J., Vogel, A., Scherer-Lorenzen, M., Eisenhauer, N., Schmid, B., & Weigelt, A. (2017). Plant diversity maintains long-term ecosystem productivity under frequent drought by increasing short-term variation. *Ecology*, *98*(11), 2952–2961. https://doi.org/10.1002/ecy.2003

Wang, P., Stieglitz, T., Zhou, D. W., & Cahill, J. F. (2010). Are competitive effect and response two sides of the same coin, or fundamentally different? *Functional Ecology*, *24*(1), 196–207. https://doi.org/10.1111/j.1365-2435.2009.01612.x

Zuppinger-Dingley, D., Schmid, B., Petermann, J. S., Yadav, V., De Deyn, G. B., & Flynn, D. F. B. (2014). Selection for niche differentiation in plant communities increases biodiversity effects. *Nature*, *515*(7525), 108–111. https://doi.org/10.1038/nature13869

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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