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The strength and direction of local (mal)adaptation depends on neighbour density and the environment

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Abstract

1. Populations are embedded in communities, but despite their potential to affect individual fitness, it is unknown whether and how species interactions evolve in communities. Evolutionary outcomes are likely more complex in natural communities because (a) the evolution of interactions may not be evenly distributed among all community members and (b) coevolution is conditional on the environmental conditions within which interactions are playing out.

2. To test the evolution of interaction strengths in natural communities, we performed two common garden experiments in grassland communities in Northern California. In each garden, we transplanted individuals of four populations (one local, three foreign) of an annual invasive grass *Bromus hordeaceus* into natural communities, characterized the interaction neighbourhood around each focal individual, and quantified individual fitness. This method allowed us to fit multispecies competition models to fitness data, estimating interaction strengths between focal *B. hordeaceus* populations and each of seven species that were common in the interaction neighbourhoods, in each garden.

3. We found that interaction strengths significantly differed among local and foreign source populations, but the direction and magnitude of evolution differed among common gardens and among neighbour species—in neither garden were interactions experienced more strongly by foreign populations compared to local populations. The fitness of local populations (relative to foreign populations) decreased when neighbours were removed, strongly enough in one garden to cause strong local maladaptation, and the local population did not perform the best in either garden.

4. *Synthesis.* Together, our results demonstrate how species interactions evolve to determine fitness in ecological communities, providing a richer view of adaptation in natural systems. In our study, this richness included the unique challenges populations face in nature: uneven abundances and a diffuseness of species interactions, nonlinear density effects on fitness, and evidence of (mal)adaptation that is conditional on local conditions. We conclude by hypothesizing the causes and consequences of challenges to adaptation and how they help identify priority areas for the field.

1 | INTRODUCTION

Ecological communities contain a diversity of species maintained dynamically through space and time (Adler et al., 2006; Nuvoloni et al., 2016). This is evident by studies showing how variable the composition of communities can be even among locations with similar environments (e.g. due to dispersal and ecological drift, Chase, 2010; Tuomisto et al., 2003). Given that populations exist and evolve within multispecies communities, an important goal in evolutionary biology is to understand how the community context contributes to adaptation (terHorst et al., 2018; Urban et al., 2008). Theory supports the idea that other species in ecological communities can impose strong evolutionary pressures on populations (e.g. Lankau, 2011; Vasseur et al., 2011). However, many questions remain about when and in what way the biotic community will influence local adaptation. For instance, interactions with other community members (i.e. the biotic environment) can decrease fitness, enough so as to cause the local extinction of populations that are otherwise well-suited to a given abiotic environment (Germain, Mayfield, et al., 2018). Other studies, however, have found that adaptation may be constrained by variable selection (Bell, 2010; Connell, 1980) owing to high spatial and temporal variability in community composition. Resolving these alternate possibilities remains a goal of evolutionary biology. To that end, we need more studies that quantify if, how and why interspecific interaction strengths (i.e. the degree to which population growth rates are depressed by increasing densities of specific species) combine with the abiotic environment to determine individual fitness (Mayfield & Stouffer, 2017) and drive evolution as recent theory predicts (Pastore et al., 2021).

Most theories of how interaction strengths evolve among competitors focus on pairs of strongly interacting, ecologically similar species. Classic evolutionary theories predict that weak competitive interactions should result from coevolution among competitors. For instance, MacArthur and Levin's theory of limiting similarity (1967), a corollary of Gause's competitive exclusion principle (1932), posits that competing species must differ sufficiently in resource use to co-exist stably. If not, species must evolve sufficient differences in resource use or face local extinction. Importantly, 'sufficient difference' can either be defined as the amount of resource partitioning required to overcome any differences in competitive ability (MacArthur & Levins, 1967) or to overwhelm stochastic noise among nearly neutral competitors (May & MacArthur, 1972). Although few experiments explicitly test the evolution of interaction strengths among competitors, existing evidence is equivocal: some studies find that interaction strengths decrease with coevolution (Connell, 1980; Pritchard & Schluter, 2001), whereas others find that interaction strengths actually increase (Hart et al., 2019; Hausch et al., 2017). For example, in Richard Lenski's long-term experimental evolution study, different asexual *Escherichia coli* lineages were allowed to compete in a highly simplified resource environment. In this setting, Gac et al. (2012) found that niche differentiation evolved on short time-scales, only to be overcome by the dominance of one lineage over the other over a much longer time-scale. Based on the evidence above, the evolution of competitive interactions clearly unfolds along a greater range of trajectories than is often considered. Indeed, more recently, the possibility that competing species coevolve to interact more intensely has been considered theoretically (Abrams, 1986; Pastore et al., 2021), for example, when species compete asymmetrically prior to evolution (e.g. native vs. invasive species; Germain, Williams, et al., 2018). We do not yet, however, have a synthetic understanding of what characteristics of species, communities or even abiotic environments set those trajectories in nature.

In addition to our limited understanding of how pairwise competitive interactions evolve, we also lack a comprehensive understanding of how the evolution of interaction strengths is distributed among interspecific competitors within communities (terHorst et al., 2018). Interaction strengths might evolve evenly among all species in the community or evolve between a select few species only (e.g. close relatives or common species)—evolving interactions may increase in strength among some species and decrease among others, or even result in facilitative interactions (Bimler et al., 2018). If interaction strengths evolve in opposing directions, they may cancel each other out, resulting in no net change in the total amount of competition a given species experiences. Knowing how interaction strengths evolve and in which directions is critical to gaining a full understanding of adaptation in dynamic natural communities. If, for instance, negative interaction strengths generally weaken with evolution, local coevolved populations would have higher fitness than naive foreign populations, reinforcing local adaptation (fitness of local > fitness of foreign populations). However, the evolution of increased negative interaction strengths (e.g. through competitive dominance) would disadvantage local populations, enough so as to generate local maladaptation (fitness of local < fitness of foreign populations). Despite the potential for biotic interactions to contribute to local adaptation, a recent meta-analysis found that 57% of local adaptation studies altered biotic interactions in their transplant gardens in some way (e.g. by weeding or using herbicide; Hargreaves et al., 2020), which they argue, removes potentially important biotic drivers of local adaptation.

An additional source of complexity relevant to adaptation is that the strength of pairwise interactions among species can be modified by the environment (Germain, Williams, et al., 2018; Grainger et al., 2019). In nature, the environments that different populations experience vary in several ways, such as in resource availability, environmental stress (e.g. temperature) and the types of species present. A given pair of species might interact strongly in one environment but not in another, for example, if the latter contains a broader spectrum of resources that species can partition (Pastore et al., 2021),

or is so stressful that population sizes are small, reducing encounter rates. As a consequence, we might expect the strength of pairwise interactions, and thus, the intensity of coevolution among competitors, to vary spatially depending on geographical context, a phenomenon referred to as 'the conditionality of coevolution' (O'Brien et al., 2018). Moreover, increased competitive ability can come with costs, such as reduced stress tolerance, and might actually be selected against in some environments (Lancaster et al., 2017). If coevolution is conditional, then we would expect a given pair of species to diverge and evolve along different, location-specific trajectories.

To examine how populations evolve in natural communities, we performed two common garden experiments each using four populations (at each garden: one local, three foreign) of an invasive annual grass, *Bromus hordeaceus*. *Bromus hordeaceus* was introduced to California from Europe ~200 years ago (Jackson, 1985); thus, any differences among the four populations we used in this study most likely have accumulated over this post-invasion timeframe. In this study, we transplanted individuals of each focal population into each common garden, quantified individual fitness in the following growing season, and characterized each individual's 'interaction neighbourhood' (i.e. identity of every neighbour occurring within 7.5 cm). We used these data to fit multispecies competition models, yielding interaction coefficients of the per capita impacts of neighbour species on the fitnesses of each focal population in each common garden. We used these data to ask:

1. How dependent is local adaptation on the presence of neighbours?
2. How are pairwise impacts on *B. hordeaceus* distributed among neighbour species, and do these impacts vary with microevolutionary history?
3. Are (1) and (2) conditional on the local environment?

We predicted that local adaptation would be strongest when tested in intact natural communities (Hargreaves et al., 2020), and that the strength of competitive interactions exerted by neighbouring species would be weaker on local versus foreign populations of *B. hordeaceus* (a baseline expectation from classic theory; Brown & Wilson, 1956; MacArthur & Levins, 1967). As we will discuss, what we found instead was not consistent with any theory we are aware of. Our results show an overriding influence of facilitation, nonlinear density effects on fitness and instances of extreme maladaptation, as well as a strong effect of neighbours on the strength of local adaptation.

2 | MATERIALS AND METHODS

2.1 | Study system

Our fieldwork took place at McLaughlin Natural Reserve (https://naturalreserves.ucdavis.edu/mclaughlin-reserve) in Northern California, USA (38.8739°N, 122.4317°W). The reserve has a Mediterranean climate, characterized by cool wet winters and hot dry summers. We focused on grassland communities that associate with serpentine soils, a unique soil type characterized by low Ca:Mg ratios, high heavy metal content and low productivity (Anacker, 2014; Harrison & Rajakaruna, 2011). Serpentine soils are formed by the emergence and erosion of the Earth's mantle and tend to exist as patches embedded within a non-serpentine matrix habitat. Although conditions in serpentine soils are typically harmful to plant growth, they support a hyper-diverse flora (Anacker, 2014) and are hypothesized to act as refuge habitat for native plants to escape invasive monoculture of *Avena* spp. which fill the non-serpentine habitat matrix (Gilbert & Levine, 2013).

We used soft chess *Bromus hordeaceus* as our transplant species, a primarily self-fertilizing winter annual grass that is widely distributed in California, both on and off serpentine soils (Dean, 2012). As a winter annual, *B. hordeaceus* germinates with the onset of autumn rains (~November) and completes its life cycle by late May. It was introduced to North America by European colonists ~200 years ago (Jackson, 1985). We chose *B. hordeaceus* as the focal species because it tends to reach high abundances at McLaughlin Reserve, particularly in wetter, more productive sites/years (Figure S1). Additionally, our previous research suggests that genetic differentiation of populations has occurred on small spatial scales at the reserve (100 s of meters; Germain et al., 2020). Exploring the evolution of competitive impacts on *B. hordeaceus* by species in its introduced range would elucidate the coevolutionary processes that help or hinder the success of *B. hordeaceus* as an invader.

2.2 | Experimental setup

Seeds of *B. hordeaceus* from four source populations at McLaughlin Natural Reserve were collected in September 2017 from hundreds of individuals, prior to the onset of the fall growing season and following summer heat stratification. The source populations were at least 1.1 km from one another and up to 7.8 km apart (mean of 4.25 km) and were haphazardly selected from eight potential populations we had records of from previous research (Germain et al., 2020; see Discussion for an exposition of possible differences among populations). Two of these populations originated from sites overlapping with our two common garden experiments (garden details described below); thus, each garden included one 'local' population and three 'foreign' populations. Although we intended to use seed grown in a common greenhouse environment prior to our experiments (i.e. to standardize maternal growing conditions), those greenhouse-grown seeds were seized at the US border on our way to the field, forcing us to use field-collected seed in our transplant experiments. To explore how maternal environmental effects might have impacted our results, we supplemented this study with a comparative study of greenhouse-grown seeds and those of the same populations collected directly from the field (see Supporting Information). The main effect of the maternal environment was an early growth advantage to one of the

populations that did not cause populations to differ in success beyond the establishment phase (Figure S2).

In September 2017, we transplanted individuals into two common garden sites (i.e. not as a full reciprocal transplant design), which were separated by 6.4 km. At each garden site, seeds were individually planted into 0.5-inch diameter polypipe (i.e. one seed per tube, since *B. hordeaceus* tends to have high germination rates) that had been cut into 0.75-inch long tubes and filled with field soil. This kept the transplanted seed from washing away from the transplant site and from being contaminated by non-focal *B. hordeaceus* seed. The tubes were unlikely to interfere with natural interactions among species, as roots were free to grow to much deeper depths than the 0.75-inch length of the tube. The tubes were pressed into the ground at 15 cm intervals along seven transects with 60 tubes per transect (see Figure S3 for a schematic).

Along each transect, seeds from the four source populations were sown into tubes in a systematic order, with a single seed sown per tube. A 'neighbour removal' treatment was laid out similarly, except with three transects that lay parallel with a 30 cm buffer from the intact community transect (two transects = 28 tubes each, one transect = 24 tubes each; Figure S3). It was not logistically feasible to randomize the 'intact' versus 'neighbour removal' treatments, but prior to neighbour removal, there was no obvious visual difference in plant communities between what would become different treatments. Seeds in the 'neighbour removal' treatment were removed with a rake and broom during the dry season. Although this method effectively removed the majority of seed, some neighbour species (including perennial species with below-ground regeneration structures) remained at low abundance despite removal efforts—their presence had no effect on our ability to fit our models, which were fit based on abundances and not by treatment groups (i.e. the intercept is fitness in the absence of competitors). In total, there were 105 replicate tubes per source population per common garden (420 total) planted in the intact communities and 20 replicates per source population per common garden (80 total) planted in the competitor removal treatment (see Supporting Information for more details). The high amount of replication and sampling effort per replicate needed to characterize interaction coefficients at any one garden site precluded a full reciprocal transplant design (Johnson et al., 2021), but our design still allows a test of how interactions evolve in the field.

We returned to each common garden in the following growing season, at peak flowering (May 2018), to characterize the interaction neighbourhood around each focal individual of *B. hordeaceus* and to quantify each individual's fitness. We placed a circular (15-cm diameter) sampling frame around each focal individual and quantified the abundance of every species in the circle (Figure S3). We then scored whether the focal *B. hordeaceus* individual germinated ('no' if no plant in tube), survived to reproduce ('no' if a senesced plant was present but with no seed) and collected all seeds (if any). We use the term 'individual fitness' to refer to the lifetime reproductive success of germinated individuals, which includes survival (i.e. 0 seeds produced) and reproduction (see *Analysis* for treatment of ungerminated seeds). Our *B. hordeaceus* transplants had 2.3× higher

reproductive success in one garden compared to the other; thus, we refer to these gardens as 'high fitness' and 'low fitness' to aid our discussion. The low-fitness garden was characterized by low productivity, high species diversity and high species evenness, relative to the high-fitness garden (Figure S4). For 48 and 54 experimental units in the high-fitness and low-fitness gardens, respectively, tubes were missing (e.g. pulled by gophers) or data were missing for at least one neighbour species (e.g. recording error), and thus were excluded from analysis.
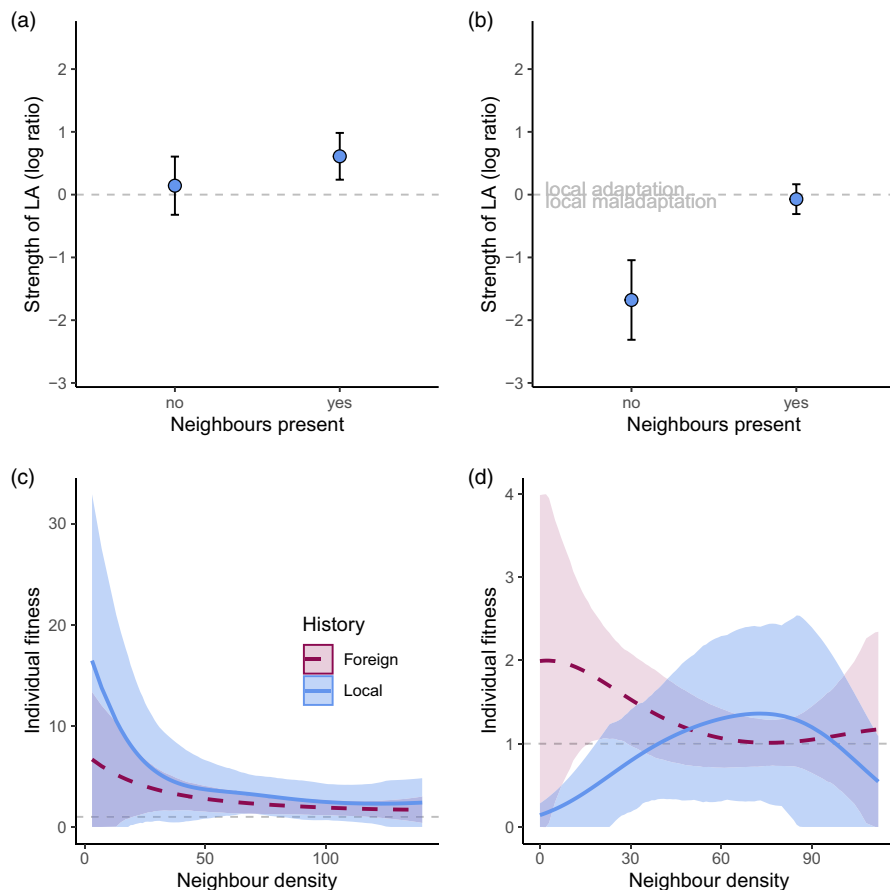
2.3 | Analysis

All analyses were performed in R v. 3.5.2 (2018). All analyses reported below were generalized linear mixed effects (glme) models, implemented using R package GLMMTMB (Magnusson et al., 2017). Response variables were the number of seeds produced per transplanted individual modelled with an 'nbinom2' error distribution (with a log link) and zero inflation, as this distribution was selected as the best fit to our data after AIC-based model comparison (using the function 'anova'). We included 'population' as a random factor to statistically account for three replicate foreign populations, and performed separate analyses for each common garden site (i.e. two analyses total). We focus our main analyses on transplanted individuals that germinated (including germinants that did not survive beyond the seedling stage), as only germinated individuals experience competition. Regardless, the ungerminated component contributed little to patterns we observed (see Results, Table S2; Figure S7).

To test our first question of whether there was evidence of local adaptation, and if local adaptation changed in the presence or absence of neighbours, the explanatory variables of our glme were microevolutionary history (local vs. foreign), neighbours (present vs. absent), and their interaction. To visually represent these data, for each garden and neighbour treatment, we calculated log-response ratios of local versus foreign fitness, as per previous authors (Hargreaves et al., 2020), based on fitted means and error estimates (extracted via the 'ggeffects'::'ggpredict' function of type 'fe.zi', which includes the zero-inflated component) from our statistical models. When local and foreign populations perform equally, the log-response ratio is 0. Values >0 indicate local adaptation (i.e. local advantage) and values <0 indicate local maladaptation (i.e. foreign advantage).

Although we predicted that neighbours would impact the strength of local adaptation (i.e. the degree to which log-response ratios were >0), we did not find statistical support for this hypothesis and instead found something entirely unexpected, warranting additional analyses to provide clarity. Specifically, in the low-fitness garden, removing neighbours resulted in extreme local maladaptation (i.e. the local population performed worse; Figure 1b). We describe and interpret this finding later, but by instead visualizing our data by creating a log-response ratio of fitness with versus without neighbours, we found that maladaptation was caused by neighbours having facilitative effects at low densities (i.e. values >0) and competitive effects at high densities (i.e. values <0; Figure S5). To better

understand this result, we compared the density dependence of individual fitness among local and foreign populations. To do so, we used the same model as above, except instead of comparing neighbour treatments, we included total neighbour density as a continuous nonlinear predictor (2° using 'poly' function in R). A switching from positive density dependence to negative density dependence would be interpreted as evidence of positive effects of neighbours at low densities (e.g. facilitation) transitioning into competition (hence nonlinear dependence on density).

To test our second question of how the evolution of pairwise interactions is distributed among community members, we first fit competition models to our fitness data. Our models are modified Ricker models as used in Mayfield and Stouffer (2017), specifically,

$$\omega_{mi} = \lambda_i e^{I_{mi}} e^{D_{mi}}, \tag{1}$$

where the fitness (ω_{mi}) of individual m from focal population i is determined by the intrinsic rate of increase of population i (λ_i) modified by interactions with neighbours (I_{mi}) and overall effects of neighbour density (D_{mi}). I_{mi} is described by the linear function:

$$I_{mi} = \sum_{j=1}^{S} \alpha_{ij} N_j, \tag{2}$$

where each neighbour species j impacts the fitness of individual m by the product of its per capita impact on focal population i (α_{ij}) and its abundance (N_j), summed across all species in the interaction

neighbourhood. When we refer to 'interaction strengths', we are referring to the magnitude of α_{ij} (weaker when closer to 0; Hart et al., 2018). α_{ij} are competitive when values are negative and facilitative when values are positive. For example, if α_{ij} is negative and of value x, then we would interpret this value to represent the magnitude of decrease in log(fitness) of population i for each added individual of species j. Thus, α_{ij} is species specific, and need not be symmetric between two species (i.e. species i may impact species j more than species j impacts species i). I_{mi} can be viewed as the total effect of all neighbours in the neighbourhood surrounding individual m.

Term D_{mi} is needed because we detected nonlinear effects of density on fitness, which may reflect a common effect of density (e.g. through effects on microclimate, conspicuousness to herbivores) that is not attributable to any one neighbour species. D_{mi} is defined by:

$$D_{mi} = L_i \sum_{j=1}^{S} N_j + Q_i \left(\sum_{j=1}^{S} N_j \right)^2, \tag{3}$$

where L_i is the linear effect of total neighbour density (i.e. summed densities of all species) and Q_i is the quadratic effect; L_i and Q_i are computed using the 'poly' function in R, as described earlier. Note the absence of subscript j means that density effects are not species specific, as species-specific effects are absorbed by I_{mi}. Models that included term D_{mi} significantly improved model fit compared to one without this term, and was thus retained in our final model, for the low-fitness garden only

(ΔAIC = 0.7, Δdeviance = 16.7, p = 0.034). Some species in the community occurred at very low relative abundances (Figure S4), meaning that there was not sufficient statistical power to fit a separate α_{ij}. For this reason, for each common garden, we fit separate α_{ij} values for seven of the most abundant species, which made up 95.1% (high-fitness garden) and 96.2% (low-fitness garden) of total abundance—the remaining species were included in D_{mi} as contributing to total neighbour density.

Using Equation 1 as our base model, we used glme models to test whether λ_i, α_{ij}, L_i (linear effect defined in Equation 2), and Q_i (quadratic effect defined in Equation 3) differed among local and foreign populations (i.e. by including microevolutionary history as an interaction term with each). Here we are specifically interested in whether there are instances of significant α_{ij} × microevolutionary history interactions, which species j they occur for, and whether α_{ij} is higher or lower for populations with local versus foreign histories.

3 | RESULTS

3.1 | Summary

We found strong effects of evolutionary history on fitness and interactions with populations of *B. hordeaceus* that differed among our two common garden sites (Figures 1 and 2). As such, below, we describe the results from each common garden separately, and, in our Discussion, explore explanations for differences we observed between the gardens. Our findings run contrary to classic theory of coevolution among competitors, which predict a general weakening of interaction strengths as coevolution proceeds (Brown & Wilson, 1956).

3.2 | Local (mal)adaptation

Evidence of local adaptation differed between the common gardens, and the strength of this effect depended on the presence or absence of neighbours. At the high-fitness site, in contrast to our hypotheses, local adaptation was statistically unaffected by the presence of neighbours [i.e. insignificant neighbours × microevolutionary history interaction (χ^2 = 2.5, p = 0.118); Figure 1a], in part because we did not find any evidence of local adaptation at all [i.e. local fitness $\ngtr$ foreign fitness (χ^2 = 2.0, p = 0.159)]. This was true even though average fitness of all populations was significantly reduced when neighbours were present (χ^2 = 68.8, p < 0.001), indicating that neighbours strongly competed with *B. hordeaceus* (Figure S5) even if local *B. hordeaceus* did not perform best in this competitive environment. By contrast, at the low-fitness site (Figure 1b), local and foreign populations performed equally in intact communities, whereas
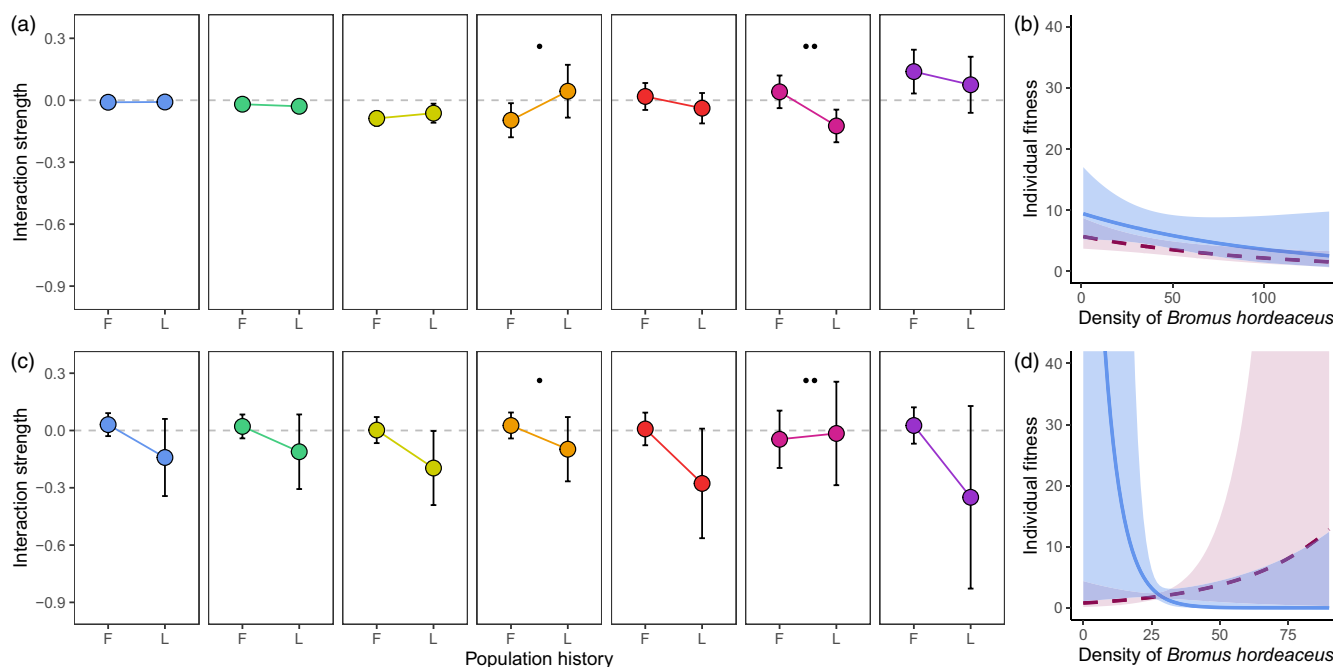

FIGURE 2 Differences in the strength of per capita impacts of each neighbour species on the conditional component of fitness of local versus foreign *Bromus hordeaceus* individuals. (a, c) The per capita direct interaction coefficients of each neighbour species on the fitness of foreign (F) versus local (L) *B. hordeaceus* populations, with 95% confidence intervals. Interaction coefficients are plotted for all species on the same y-axis scales and are fitted estimates from our glmmTMB models. Negative coefficients are competitive interactions and positive coefficients are facilitative interactions. (b, d) The density dependence of *B. hordeaceus* fitness in response to the density of conspecific neighbours, contrasting among contrasted among local (blue, solid line) and foreign (red, dashed line) populations. These graphs correspond exactly to the blue subpanels in (a, c). Data from the high-fitness garden (a, b) and low-fitness garden (c, d) are shown separately. Point colours correspond to different species, shown in Figure 3. Dots at the top of panels indicate significance of differences among local and foreign populations ('.' = p < 0.10, '..' = p < 0.05). See Figure 3 for outputs from the conditional component

the removal of neighbours led to extreme maladaptation of the local population [i.e. neighbours × microevolutionary history interaction ($\chi^2 = 4.4$, $p = 0.035$); Figure 1b]. Fitness of local populations decreased when neighbours were removed, indicating that neighbours had a facilitative effect, whereas the fitness of foreign populations declined in the presence of neighbours (Figure S5).

We additionally tested how fitness was affected by neighbours when neighbours were treated as a continuous predictor variable (Figure 1c,d; Figure S6). Although these analyses reveal the same general insights as our analyses based on the presence or absence of neighbours, they additionally show that fitness responds nonlinearly to neighbour density. For nearly all populations in both gardens, fitness decreased with increasing neighbour density (i.e. significant neighbour density effect in both gardens [$p < 0.001$]), and these density effects were most pronounced (i.e. steepest slope) at low to intermediate densities. However, there was one interesting exception—fitness of the local population in the low-fitness garden experienced positive-density dependence at low densities, peaking at a density of ~70 neighbours, then transitioned to negative-density dependence at greater densities. This form of nonlinearity, where density dependence is positive at low densities, is characteristic of facilitation due to microsite amelioration.

Lastly and interestingly, because zero-inflated models best fit our data, we were able to decompose the reproductive success of germinated individuals into the conditional and zero-inflated components (Table S1); here, the closest biological interpretation of these two components is seed production of plants that survived to reproduce versus those that died before reproducing, with the latter causing an excess of zeros beyond those predicted by a negative binomial distribution (Blasco-Moreno et al., 2019). At both sites, both the conditional and zero-inflated components were negatively affected by neighbour density. However, in the low-fitness garden, the significantly reduced fitness at low densities of the local populations was driven by the zero-inflated component only (i.e. significant microevolutionary history effect; $\chi^2 = 1.0$, $p = 0.003$), whereas the difference in response to neighbour density among local and foreign populations was caused by the conditional (i.e. count) component only (i.e. significant neighbour density × microevolutionary history effect; $\chi^2 = 9.8$, $p = 0.023$). Note that these analyses were performed on individuals that germinated. If we repeat our analyses to include non-germinated individuals, which further inflates the non-zero component, our results are qualitatively unchanged (Table S2). Germination rates were unaffected by microevolutionary history (Table S3; Figure S7).

3.3 | Evolution of interaction strengths

We asked whether the evolution of interaction strengths evolved evenly and consistently across all community members, or if evolution was caused by a few species with disproportionately strong effects. Evidence from our study was most consistent with the hypothesis that the evolution of interaction strengths is driven by a few species with disproportionately strong effects, though patterns differed somewhat between the two gardens. In the high-fitness garden, two of seven species had distinguishable impacts on the fitness of *B. hordeaceus* [one via the conditional model component (Figure 2a), one via the zero-inflated model component (Figure S8a)]. The nature of these impacts depended on whether *B. hordeaceus* was local or foreign to the garden site (i.e. significant species × microevolutionary history interaction; Table S1). Competition with a non-native exotic congener *Bromus diandrus* (magenta points; $p = 0.006$) was more intense for the local *B. hordeaceus* population compared to foreign populations (Figure 2a), whereas with a non-native herb *Centaurea melitensis* (purple points; $p = 0.032$), competition was significantly weaker (Figure S8a). Three other species had marginally significant differences in impact on local versus foreign populations (Figure 2a; Figure S8a), some of which involved a weakening or strengthening of facilitation.

In the low-fitness garden, we obtained two main results, which contrast those of the high-fitness garden. First, local populations were impacted by competition more strongly than foreign populations by nearly every neighbour species (Figure 2b)—in other words, the direction of evolved differences was consistent. For two neighbour species, these differences in impact were significant differences ($p < 0.05$), specifically, *Clarkia gracilis* (yellow points; $p = 0.0346$) and *Hemizonia congesta* (red points; $p = 0.024$). Two additional species exhibited marginally significant higher impacts on local populations of *B. hordeaceus* [i.e. *Bromus hordeaceus* (blue points; $p = 0.057$) and *Lolium multiflorum* (purple points; $p = 0.089$)]. Second, unlike in the high-fitness garden, significant differences in impacts among local and foreign *B. hordeaceus* populations were only observed through the conditional model component and not through the zero-inflated model component (Figure S8b). As described earlier, the biological interpretation of the conditional model component in our dataset can be thought of as the probability that plants that successfully reached reproductive maturity produced × number of seeds. By contrast, the zero-inflated component relates to the probability that plants failed to reach reproductive maturity at all, causing an excess of zeros.

4 | DISCUSSION

An unresolved question in evolutionary biology is how evolution proceeds in diverse ecological communities (Strauss et al., 2005; Thompson, 1999). Ecological theory recognizes that the maintenance of species depends on species' interaction strengths—whether populations are more strongly influenced by many weak or a few strong interactions (Levine et al., 2017; McCann et al., 1998). We applied this theory to an experiment conducted in diverse natural communities to show that interaction strengths depend on species' microevolutionary histories. We show that the strength of local (mal)adaptation within populations depends on whether fitness was tested in the presence or absence (or more generally, with density) of neighbours, as well as on the environmental conditions of common

gardens. As we will describe, our findings are not consistent with common theories in interesting ways, generating new, general hypotheses that emerge from our specific findings.

A recent meta-analysis of 125 local adaptation studies performed under natural field conditions found that, on average, biotic interactions had no effect on the strength of local adaptation (Hargreaves et al., 2020), a finding with two alternative explanations that can be distinguished with our data. The first explanation is that biotic interactions simply do not influence local adaptation, whereas the second is that biotic interactions have opposing (and thus averaged out) effects, both between gardens within studies and across different studies, helping local adaptation in some cases and hindering it in others. Our results point towards the latter explanation: the presence of neighbours impacted the strength of local adaptation at only one common garden site and in an unexpected way (Figure 1b), with two levels of inference. First, differences between common gardens arose even though local adaptation was tested at each site using the same four populations in the same year at the same reserve. This suggests that details of the environment are hugely important for whether local adaptation is observed or not (O'Brien et al., 2018), and that across an environmental gradient, one might find opposing outcomes for local adaptation. Second, as an extension, the scope of studies included in a meta-analysis, performed with different species in many different parts of the world, would likely yield an even greater diversity of outcomes, a reality that is likely to show an average of no difference when taken together.

Classic evolutionary theory predicts a weakening of competitive interactions as competitors evolve in each other's presence (Brown & Wilson, 1956; Grant, 1972), an outcome that has been countered by more recent theory (Abrams, 1986; Fox & Vasseur, 2008) and experiments that compete pairs of species (Germain et al., 2020; Hart et al., 2019). In our study, instances in which local populations evolved weaker interspecific interactions with some species were matched by those that evolved stronger interactions. Several neighbour species did not differ in their impacts on local and foreign *B. hordeaceus*, and some were facilitative instead of competitive; note that we cannot predict the ultimate outcome of evolution for the persistence of *B. hordeaceus* populations, as doing so would require knowledge of evolved differences in *B. hordeaceus*'s impact on other species (Levine et al., 2017; Pastore et al., 2021). Neighbour species evolved similarly consistent effects in one garden (the low-fitness garden) but not the other (the high-fitness garden). Despite a clear understanding that the biotic and abiotic environment influence evolution, our understanding of how and in what ways evolutionary outcomes will differ among neighbour species and environments remains surprisingly understudied (O'Brien et al., 2018). Although answering this question would require many replicated gardens and enough species to perform statistical tests, at its core are two interrelated factors: (a) per-capita interaction strengths (α_{ij}) and (b) total abundances of individuals (N_j; Billick & Case, 1994; Germain, Williams, et al., 2018; Hart et al., 2019). Mathematically, we know that α_{ij} and N_j determine the total amount of competition species *j* exerts on species *i* (i.e. $\alpha_{ij} \times N_j$), which by extension, affects how strongly a given species at a given

site imposes selection pressures on another species. Whether interaction strengths evolve to increase or decrease depends on whether the greatest fitness gains are to be made by specializing to better compete for the same or a different set of resources/microsites used by a competitor (see figure 2 in Germain et al., 2020), which in part depends on the resource environment itself (Germain, Hart, et al., 2021; Pastore et al., 2021).

Although we expect the above arguments to apply to any interaction involving two or more species, when applied to diverse communities, one additional factor complicates the evolution of interaction strengths. Connell (1980) and Hubbell (2006) predicted that the possibility of coevolution between pairs of interacting species declines as competition becomes increasingly diffuse. Diffuse competition is defined as 'the combined, usually weak, effects of many or most members of a community upon a given species' (Moen, 1989). In order for interaction strengths to evolve between a given pair of species in a community, they must interact often enough and strongly enough for selection to be consistent. The consistency of selection between any pair of species decreases as diversity increases (both species richness and evenness), especially if one or both species are relatively rare (Pease, 1984). We can make some inferences about the consistency of selection by looking at two aspects of community structure at both gardens. First, at each, the abundances of species varied dramatically in space, even among adjacent neighbourhoods (Figure 3a,b) and certainly below the spatial scale of dispersal (Richardson et al., 2014). This means that, for a hypothetical example, *B. hordeaceus* individuals with genotypes able to compete well against *V. microstachys* may be positively selected for in one neighbourhood but selected against in another, causing variation in the strength of selection across neighbourhoods. Second, at both gardens, *B. hordeaceus* was by far the most abundant species, making up over half (low-fitness garden) to two-thirds (high-fitness garden) of all neighbours in an average neighbourhood (Figure 3). As a consequence, every species had a high probability of interacting with *B. hordeaceus*, including *B. hordeaceus* itself, and rarer species might have additionally been more subject to genetic drift. Under these conditions, we might hypothesize that neighbour species would experience selection pressure to better contend with local *B. hordeaceus* (Lankau, 2011), to a much stronger degree than the selection pressure *B. hordeaceus* would experience to contend with specific (rarer) neighbour species. This would explain why evolution was frequently to the detriment of local *B. hordeaceus* (causing local maladaptation) and why several of the strongest differences in neighbour impacts on local versus foreign *B. hordeaceus* populations we observed came from neighbour species that, relative to *B. hordeaceus*, were rare (e.g. *Centaurea melitensis*).

In the low-fitness garden, our process of analysis to understand an unintuitive result has led to a new hypothesis on the possible scale of biological organization to which populations are evolving in communities (e.g. species specific vs. community specific). As described earlier, adding nonlinear effects of total density on fitness into our model significantly improved model fit. The question now becomes, are species-specific interaction coefficients truly
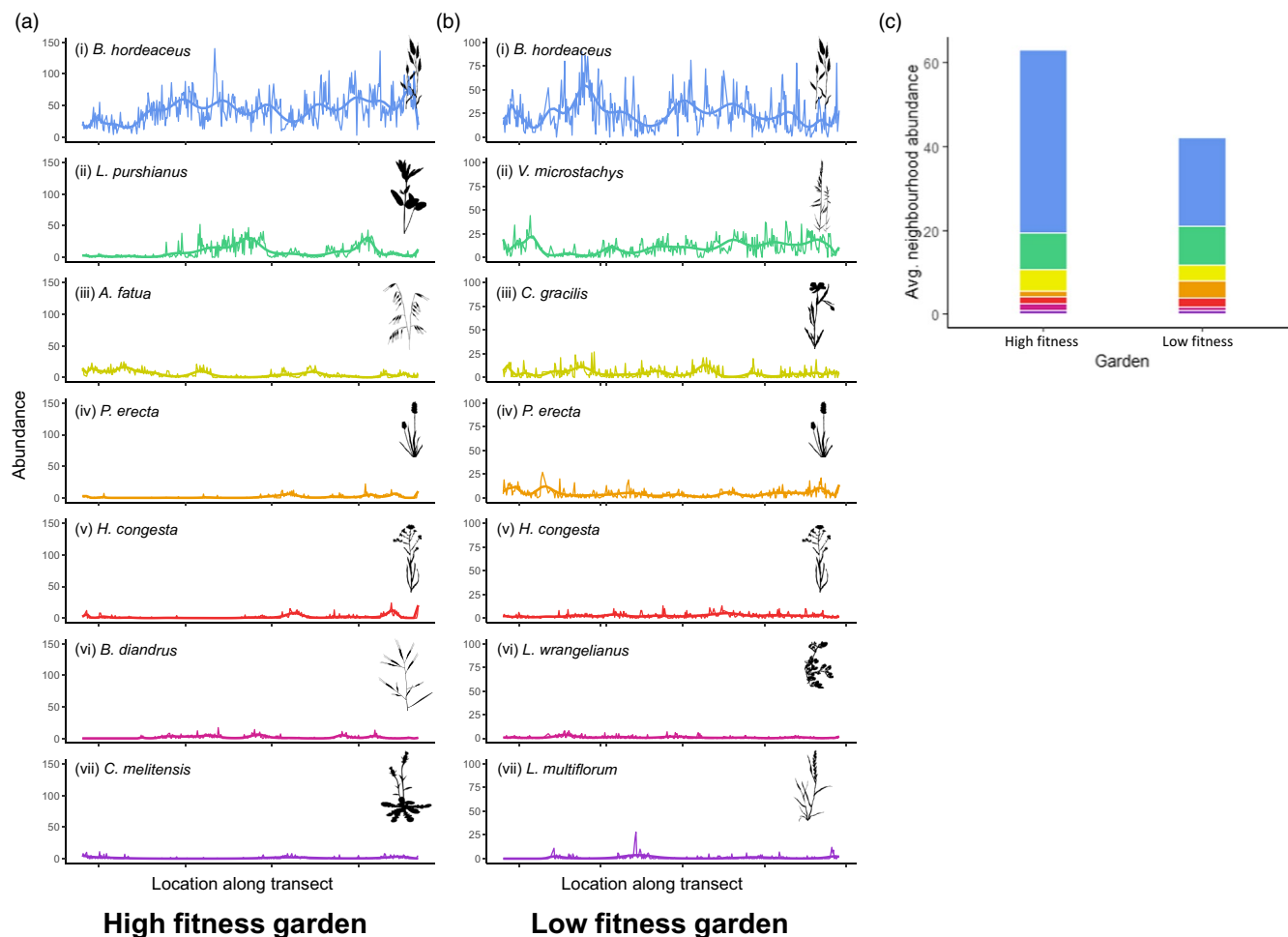
FIGURE 3 Abundances of seven focal species at the neighbourhood scale (a, b) spatially along transects and (c) on average, in the high-fitness garden (a, c) and in the low-fitness garden (b, c). In panels (a) and (b), the jagged line is actual observed abundance in each neighbourhood in the transect, whereas the smooth line is a weighted moving average (loess smoothing) to illustrate coarse-scale trends in abundance over the transect. In panel (c), the heights of the bar charts indicate differences in overall neighbourhood density, whereas the colours indicate proportionally how abundance is split between the seven focal species

nonlinear or have *B. hordeaceus* populations evolved to an environment that is defined by a specific composition of neighbours? Said another way, if individuals perform poorly at low densities (e.g. suboptimal microclimate, conspicuous to herbivores), then does it matter if individuals are surrounded by specific neighbour species *x* versus neighbour species *y*, or by a general community of neighbour species? This work highlights the need for a more nuanced biological interpretation of an interaction coefficient: that positive and negative interactions are not simply indicative of facilitation or competition, respectively, but their net balance (Martyn et al., 2021; O'Brien et al., 2018). Although disentangling negative and positive interactions are not necessary to understand the dynamical consequences of a given interaction, doing so may be crucial if the goal is to understand *why* interactions change in strength in different environments (e.g. does an interaction weaken with evolution in a certain environment because competition is weakening or because facilitation is strengthening?). Unfortunately, we do not have environmental or community data for all four source populations, but anecdotally,

both foreign populations were from sites similarly or more 'harsh' abiotically (from the perspective of our non-native *B. hordeaceus*) than the low-fitness garden. This suggests that the facilitative effect of neighbours on the fitness of the local population is not purely a consequence of adaptation to harsh conditions, but rather, how that abiotic harshness is experienced within that garden's specific biotic community. Recovery from low densities is an important strategy for persistence in our study system (Levine & Rees, 2004), a system that is subject to extreme episodic drought and made more difficult by harsh soil substrates that lack a protective litter layer and hinder survival (hence, strongest effects through the zero-inflated model component; Armstrong et al., 1992; Elmendorf & Harrison, 2013).

In sum, we provide a rare glimpse into how the evolution of pairwise interactions is distributed among species in natural, heterogeneous ecological communities. We began with simple predictions of how interspecific interactions might have evolved in ecological communities and how past evolution might influence local adaptation, with clear alternative expectations of where and why our predictions

might fail. Our predictions were derived from a multispecies extension of what has been learned from individual studies involving species pairs. What we found instead was not consistent with any theory we are aware of—maladaptation, non-linear density effects, large differences in outcomes among garden sites, and microevolutionary history having some of the strongest effects on interactions with rare species. Future research could consider repeating our experiments with many source populations in a reciprocal transplant design, to better identify characteristics of source and garden populations that combine to shape interaction strengths. An additional point worth making is that the link between absolute individual fitness and per capita population growth rates is often described as a natural bridge for eco-evolutionary research (Edelaar & Bolnick, 2019); however, it is not often acknowledged that when we are dealing with average fitness of individuals in populations, these two quantities are one in the same. In other words, we are able to understand dynamical feedbacks that regulate populations through individual fitness.

Although our findings open up more new questions than they answer, here is what we have learnt in our system:

1. testing local adaptation in the absence of neighbours can result in erroneous estimates of its strength under natural conditions
2. the evolution of pairwise interactions is conditional on site conditions and unfolds differently among species
3. density dependence can be shaped by recent microevolutionary history

We view these results as evidence expanding our knowledge of what *can* happen in evolving communities, not of what happens most of the time or of why it happened. In general, the complexity and nuance of our results, and their lack of alignment with any theory we know of, highlights the need for a more extensive, integrative, and eventually, reductionist theory of how evolution unfolds in diverse natural communities. Such a theory should examine ecological processes that determine how strongly interactions are realized between any two species across space and through time (Poisot et al., 2015), affecting the strength, direction and consistency of selection acting on populations.

CONFLICT OF INTEREST
The authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS
R.M.G. conceived of this research and its design; R.M.G., M.U.-C. and N.T.J. performed all the fieldwork; R.M.G., M.R. and N.T.J. analysed the data; R.M.G. wrote the first draft of the paper, and all authors provided substantial feedback and revisions.

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