

The Evolution of Competitive Ability

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ABSTRACT: Competition drives evolutionary change across taxa, but our understanding of how competitive differences among species directs the evolution of interspecific interactions remains incomplete. Verbal models assume that interspecific competition will select for reducing a species' sensitivity to competition with their opponent; however, they do not consider the potential for other demographic components of competitive ability to evolve, specifically, interspecific effects, intraspecific interactions, and intrinsic growth rates. To better understand how competitive ability evolves, we set out to explore how each component has evolved and whether their evolution has been constrained by trade-offs. By setting sympatric and allopatric populations of an annual grass in competition with a dominant invader, we demonstrate (1) that in response to interspecific competition, populations can evolve increased competitive ability through either reduced interspecific or, surprisingly, reduced intraspecific competition; (2) that trade-offs do not always constrain the evolution of competitive ability but rather that parameters may correlate in ways that mutually beget higher competitive ability; and (3) that the evolution of one species can influence the competitive ability of its opponent, a consequence of how competitive ability is defined ecologically. Overall, our results reveal the complexity with which demographic components evolve in response to interspecific competition and the impact past evolution can have on present-day interactions.

Keywords: coevolution, interspecific competition, intraspecific competition, McLaughlin Natural Reserve, modern coexistence theory, trade-off.

Introduction

The imbalance in nature—where life has the ability to grow exponentially but is limited by finite resources—is what drives individuals to compete (Malthus 1798). Despite the critical role competitive ability plays in determining the ultimate winners and losers of a competitive interaction (Hart et al. 2018) and in predicting the stability and persistence of coexisting species (MacArthur 1972), understanding how competitive ability evolves remains incomplete. To date,

the evolution of competitive ability, that is, the ability to tolerate competition (Hart et al. 2018), has generally been examined through two lenses. The first lens is that of the evolution of specific traits thought to underlie competitive interactions (e.g., beak sizes of finches; Brown and Wilson 1956). While examining the evolution of competitive ability in this way can provide a direct link to the traits under selection under competition (Bernhardt et al. 2020), the consequences of that trait evolution on the outcome of competition is oftentimes impossible to know (Germain et al. 2018). The second lens that of the measurement of per capita interaction strengths and how they evolve among interspecific competitors (Connell 1983; Aarssen 1985; Felker-Quinn 2012). Interestingly, however, competitive ability itself, as we will discuss, is a complex ecological trait that is underlain by several parameters, each of which has some phenotypic basis. Only when examined together can these population parameters predict coexistence or exclusion (MacArthur and Levins 1967; Chesson 2000; Hart et al. 2018). Now that the mathematical underpinnings of competitive ability are well resolved (Hart et al. 2018; eq. [1] below), we can apply tools from coexistence theory to examine how and why competitive ability evolves.

Synthesizing how competitive ability—a complex trait—can evolve in response to different environments presents several challenges. The first challenge is to break down how every parameter that underlies competitive ability evolves, beyond focusing only on the evolution of interspecific interactions (e.g., Zhao et al. 2016). Using the Beverton-Holt competition model (Beverton and Holt 1957), a species' competitive ability can be defined as

$$\kappa_i = \frac{\lambda_i + 1}{\sqrt{\alpha_{ii} \times \alpha_{ij}}} \quad (1)$$

(Chesson 2000; Godoy et al. 2014; Hart et al. 2018). As such, there are three ways to increase competitive ability (κ_i): reducing per capita sensitivity to interspecific competition (α_{ij}), reducing per capita sensitivity to intraspecific competition (α_{ii}), and increasing intrinsic growth rate (λ_i). Note

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that while the exact equation for competitive ability varies depending on the competition model (see the supplementary information to Hart et al. 2018) and the definition of competitive ability being used, each generally includes these three parameters (Weigelt and Jolliffe 2003). Although there are three ways competitive ability may evolve, the competitive environment ultimately dictates which parameter experiences the strongest selective pressure (MacArthur and Wilson 1967; Lankau 2011; Vasseur et al. 2011; Mallet 2012). A reduced sensitivity to interspecific competition, for example, may be selected for in environments dominated by heterospecific competitors, whereas a reduced intraspecific sensitivity may be under selection when conspecific competitors dominate (Vellend 2006; Bolnick et al. 2011). Intrinsic growth rate, on the other hand, is likely always under selection but most strongly so in weakly competitive environments that favor rapid growth (e.g., frequent disturbance; Mallet 2012). To our knowledge, only one recent study has examined the population parameters that underlie the evolution of competitive ability, using competing species of duckweed (Hart et al. 2019).

The second challenge is that coexistence theory tells us that the three parameters that underlie competitive ability (eq. [1]) are not always independent of one another. Intrinsic growth and competitive interactions can be correlated—for example, because each is underlain by common traits of how individuals use and require resources—but can also be uncorrelated depending on how resources are distributed in an environment (MacArthur 1970; Chesson 1990; Fronhofer et al. 2020; Germain et al. 2020). Ultimately, trade-offs prevent the evolution of a single optimal strategy to increase competitive ability, instead leading to alternative solutions that may or may not differ in adaptive value depending on the environment (Marks and Lechowicz 2006). Two trade-offs are predicted to constrain evolution in response to heterospecific competitors. The first trade-off occurs between intrinsic growth (λ_i) and one's sensitivity to competition (α_{ii} , α_{ij} ; as described in eq. [1]), where, for example, a species may be more successful at low densities due to high per capita resource consumption but compete more intensely as densities increase as a result. The second trade-off manifests in high-density environments—that is, theory often assumes evolving to become a stronger interspecific competitor comes at the cost of increased intraspecific competition (Vasseur et al. 2011). Although these trade-offs have been observed in the few empirical studies that have looked for them (Pimentel et al. 1965; Linhart 1988; Lankau 2008), evidence is still scarce, and theory is emerging (e.g., Pastore et al. 2021) but incomplete. Examining these trade-offs would offer insight into constraints on the evolution of competitive ability, as well as whether there are multiple ecological solutions to selection pressures imposed by a given competitive environ-

ment. Notably, due to trade-offs, a species' competitive ability may not evolve even if the underlying parameters evolve to match conditions in a given environment.

A final challenge is that some parameters, namely, the interspecific interaction coefficients (e.g., α_{ij} or the impact of species j on species i), are pairwise quantities, whose change in value due to evolution cannot be clearly attributed to species i (the recipient) or species j (the opponent). Should, for example, α_{ij} evolve to increase, one would not know whether species i had become more sensitive to competition or species j had become more impactful, a point that is rarely explicitly acknowledged yet affects how one might predict how α_{ij} evolves. Although one might predict that α_{ij} would evolve to decrease in response to an interspecific competitor, as this would benefit species i , α_{ij} might actually evolve to increase if species j was under stronger selection to become more impactful, to species i 's detriment (Van Valen 1973; Germain et al. 2020). For clarity, we adopt Hart et al.'s (2018) definition that a single pairwise interaction (e.g., α_{ij}) is a product of two parts: the opponent species j 's effect and the recipient species i 's response (Goldberg 1990; fig. 1C). While theoretically it has been shown that an interspecific competition coefficient can be partitioned into each species' effect and response (MacArthur 1972; Schoener 1974; May 1975; Ackermann and Doebeli 2004), to our knowledge, no study to date has attempted to do so empirically. Note that this partitioning is exactly why competitive ability in equation (1) is defined from the perspective of the recipient species (i.e., α_{ij} in eq. [1], rather than α_{ji}): the recipient species' response is ultimately what dictates its ability to persist (Godoy et al. 2014; Hart et al. 2018). As a result, a critical knowledge gap exists as to how competitive interactions evolve, namely, whether the evolution of interspecific competition coefficients (i.e., α_{ij}) is attributable to the evolution of recipient species (i.e., the response of species i), to the evolution of opponent species (i.e., the effect of species j), or to some combination of both.

Here, we experimentally break the evolution of competitive ability down into its underlying population parameters (eq. [1]), focusing on the evolution of a native species in the face of an invasive competitor. To do so, we placed in competition natural populations of two annual grasses, *Vulpia microstachys* and *Bromus hordeaceus* (for brevity, we refer to *Vulpia* as the native species and *Bromus* the invader), comparing competitive abilities between populations of *Vulpia* with no history of interaction with *Bromus* (allopatric pairs) against populations with a history of interaction (sympatric pairs). Our competition trials were designed to parameterize an annual plant model using manipulations of competitor densities, as well as to partition the degree to which evolutionary changes in interspecific competition coefficients could be attributable to any

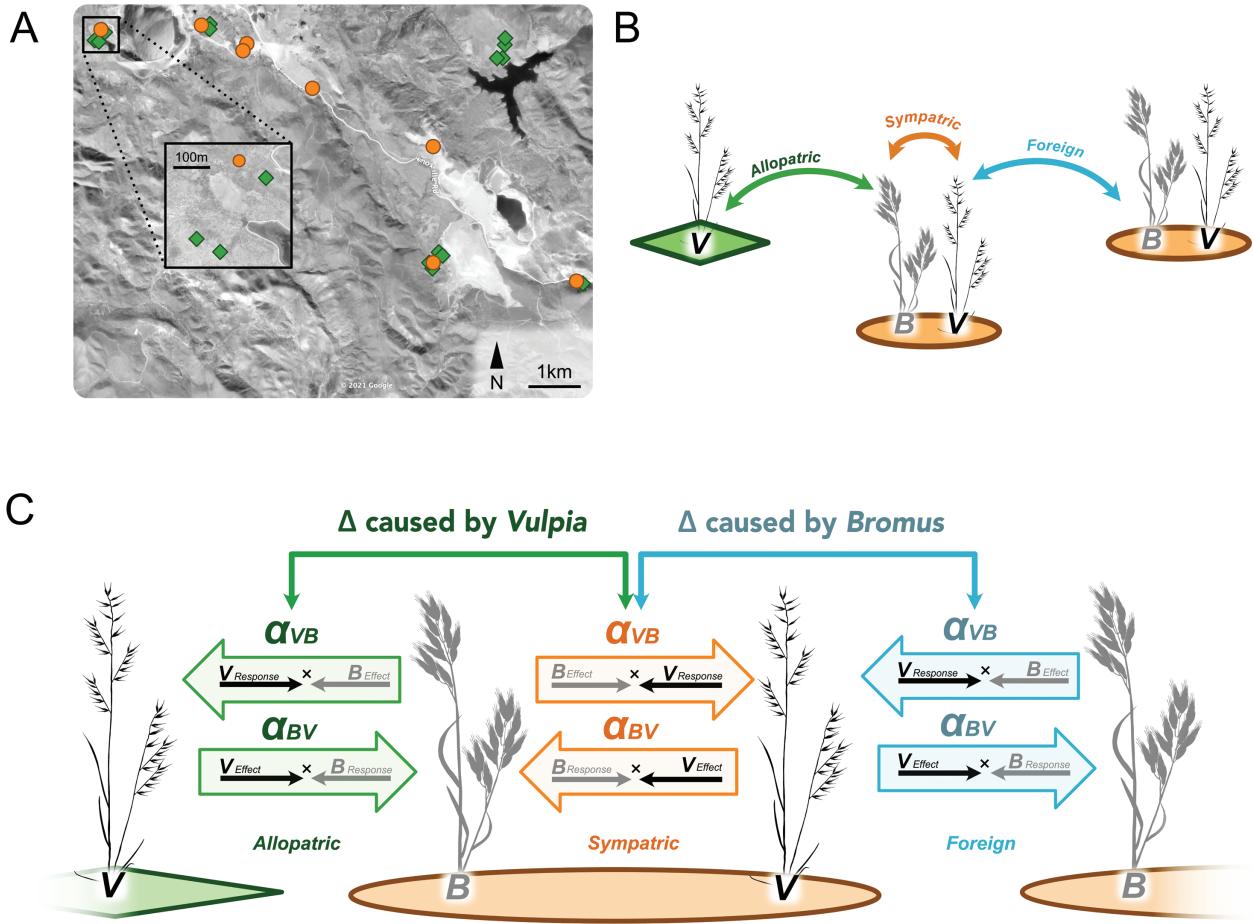


Figure 1: Population origins and experimental design. Panel A shows a map of sites where each population of *Vulpia* (V) and *Bromus* (B) was collected from the McLaughlin Natural Reserve, California (38.85, -122.40). Orange circles represent sites where *Vulpia* is found with *Bromus* (sympatry), whereas green diamonds represent sites with *Vulpia* in the absence of *Bromus* (allopatry). Panel B shows conceptually which populations were competed in our three evolutionary history treatments (see description in “Treatment Comparisons and Hypothesis Testing”). Here, one population of *Bromus* is competed against two populations of *Vulpia* (arrows), each with unique evolutionary histories (green diamonds and shared orange circles in reference to panel A), while each sympatric *Vulpia* is competed against a local and a foreign *Bromus* population. See figure S1 for the full experimental design. Panel C shows what the response and effect are and how their evolution can be attributed to each species. Each single pairwise interaction coefficient, for example, α_{VB} (per capita impact of *Bromus* on *Vulpia*) is a product of two parts: *Bromus*’s effect and *Vulpia*’s response. To maintain consistent language, we only ever use terms “response” and “effect” to describe these two components that make up any one competition coefficient, whereas to refer to an entire competition coefficient (e.g., α_{VB}), we use terms “impact on” or “sensitivity to” the competing species, depending on whether the coefficient is being described from *Bromus*’s or *Vulpia*’s perspective, respectively. Arrows show how comparing competition coefficients between evolutionary history treatments can isolate each species’ contribution to the evolution of each interaction coefficient (see fig. 4). As an example, by comparing α_{VB} between allopatric and sympatric evolutionary histories, any observed difference is due to evolved differences in *Vulpia*’s response, as *Bromus*’s effect is held constant.

one species (i.e., the recipient’s response vs. the opponent’s effect; Hart et al. 2018). We used these data to answer three questions: (1) Do population parameters that underlie competitive ability evolve, and is their evolution driven by a history of interaction in sympatry? (2) Is the evolution of population parameters constrained by trade-offs? And (3) how do the contributions of recipients versus opponents compare when isolating how each has affected the evolu-

tion of interspecific interaction coefficients? For questions 1 and 2, we explicitly examine the consequences of *Vulpia*’s (but not *Bromus*’s) history of sympatry versus allopatry for population parameters, including *Vulpia*’s impacts on *Bromus*, whereas in question 3, we explore and contrast the evolution of *Vulpia* and *Bromus* in tandem.

We hypothesized that because *Bromus* tends to be competitively dominant to *Vulpia*, selection on traits underlying

interspecific competition may be asymmetric, that is, experienced more strongly by *Vulpia* than by *Bromus* (see Germain et al. 2020, fig. 1). If this hypothesis were supported, we would predict that sympatric populations of *Vulpia* would have evolved higher competitive abilities than their allopatric counterparts, manifested primarily through a reduced sensitivity to interspecific competition (α_{ij}) at the potential trade-off of other population parameters (i.e., higher α_{ii} , lower λ_i). In turn, we predicted that *Vulpia* would evolve to impact *Bromus* more strongly (i.e., higher α_{ji} in sympatry). As we will show, our hypotheses were largely supported, with two exceptions: some parameters appeared to trade up instead of trade off (i.e., a win-win relationship; see Reding-Roman et al. 2017), and counterintuitively, intraspecific competitive interactions may have in fact weakened with evolution in response to a dominant competitor.

Methods

Competition Model

In order to test how competitive ability has evolved, we performed competition experiments designed to parameterize Beverton-Holt competition models:

$$N_{it+1} = \frac{\lambda_i N_{it}}{1 + \alpha_{ii} N_{it} + \alpha_{ij} N_{jt}}. \quad (2)$$

In this equation, germinable seeds produced by species i (N_{it+1}) depend on the initial number of competing individuals (N_{it} ; i.e., seeds planted initially that germinated), intrinsic growth rate (λ_i), per capita intraspecific competition (α_{ii}), per capita interspecific competition (α_{ij}), and the population size of species j (N_{jt}). Because equation (2) is symmetrical for species i and j , it also describes the dynamics of species j by switching subscripts i and j . Note that Chesson's (1990, 2000) original derivations of terms relevant to coexistence were based on the Lotka-Volterra model and not the Beverton-Holt model, but see appendix A in Godoy and Levine (2014) for derivations showing the alignment between the two models; we use the Beverton-Holt model because it best fits empirical data collected from annual plants, including *Bromus* and *Vulpia* (Levine and HilleRisLambers 2009; Godoy and Levine 2014; Germain et al. 2016). Below, we describe how populations were chosen, how our competition experiments were designed and used to fit the Beverton-Holt model, and what treatment comparisons were used for hypothesis testing.

Study System and Seed Origins

We worked with *Vulpia* (*Festuca*) *microstachys* (Poaceae) and *Bromus hordeaceus* (Poaceae) populations collected from serpentine grassland habitat at the University of Cali-

fornia McLaughlin Natural Reserve (38.8713 N, 122.4188 W) in Northern California. In the California Floristic Province, *Vulpia* and *Bromus* frequently co-occur on serpentine soils, a globally rare soil type commonly found in subduction zones that supports a unique, endemic flora of serpentine-specialized plants (Anacker 2014). *Bromus* was introduced to California by European settlers more than 200 years ago and is competitively dominant to *Vulpia*, a species native to California, in productive soils (Germain et al. 2020). *Vulpia* is more widely distributed and can tolerate harsher abiotic environments than can *Bromus*. Both species reproduce largely through self-fertilization (Adams and Allard 1982; Ainouche et al. 1999), resulting in populations that are phenotypically distinct despite close proximity (see fig. S7). Note that although our methodology was reported in a previous paper with different goals and analyses (see Germain et al. 2020), we repeat the relevant details here.

Seeds were collected October 4–6, 2016, from 16 sites: eight sites containing both *Bromus* and *Vulpia* populations (i.e., sympatric populations of *Vulpia*) and eight sites containing only *Vulpia* (i.e., allopatric populations of *Vulpia*), for a total of 16 populations of *Vulpia* and eight of *Bromus* (fig. 1A). To control for abiotic differences between sites, allopatric and sympatric sites were paired (eight pairs total) based on abiotic similarity (for details, see Germain et al. 2020, “Extended Data”). Doing so meant that allopatric *Vulpia* populations from some of our harshest sites were not included, as there were no sympatric analogs. Seeds were haphazardly collected and pooled among hundreds of plants per population. Individuals grown from field-collected seeds may differ phenotypically among populations due to evolved genetic differences or due to differences in maternal growing conditions that carry over to the offspring (i.e., maternal environmental effects; Kawecki and Ebert 2004). To reduce maternal environmental effects, each population was grown for one generation in a common greenhouse environment prior to our competition experiments, September 2016 to June 2017. Each 2.79-L pot included ~50 seeds of one population (10 replicate pots per population) filled with potting mix (sunshine mix no. 5). Each pot was top-watered during the germination process and bottom-watered thereon after as needed. At first signs of mildew, we applied MilStop fungicide. Greenhouse conditions were set to mimic the natural day/night temperature and light cycles of Northern California, starting at winter (15°/7°C, 11L:13D) and progressively increasing to summer (30°/15°C, 16L:8D). Seeds were collected and dried at 60°C for 72 h for use in our competition experiments.

Competition Experiments

We initiated a competition experiment using growing conditions designed to mirror those populations might

experience in the field. Potting soil for the competition trials was a 1:3 ratio of Sunshine no. 5 potting mix and serpentine soil collected from Grasshopper Mountain in British Columbia (49.5449 N, 120.9339 W). Grasshopper Mountain was selected due to biochemical similarity to soil found at the McLaughlin Natural Reserve (Bulmer and Lavkulich 1994). Similar to conditions in the maternal generation, day/night cycles were set to 15°/8°C with an 11L:13D photoperiod, gradually increased to 30°/15°C and longer days (16L:8D). For the first month, to reflect the onset of autumn rains and a corresponding nutrient pulse within the Californian serpentine system (Parker and Schimel 2011), 350 mL of 1,500 ppm 20-20-20 NPK fertilizer was administered twice early in the growing season, and pots were top-watered twice daily to keep soil moist. After the first month, we switched watering to an automatic drip irrigation system, gradually reducing the frequency of watering to mimic seasonal changes in rainfall (for details, see Germain et al. 2020). Although our phenomenological approach to measuring competition need not require knowledge of what individuals are competing for, competition in greenhouse conditions might occur through differences among species in which, when (i.e., phenology), and where (i.e., in the soil profile) limiting resources are taken up (e.g., nitrogen, phosphorus, and potassium, water, micronutrients, and light; HilleRisLambers et al. 2012).

We chose pairs of *Bromus/Vulpia* populations to compete to represent three evolutionary history treatments (described in “Treatment Comparisons and Hypothesis Testing”; fig. 1B). To fit equation (2) to empirical data, species must be competed at a range of relative and total densities (Hart et al. 2018). To do so for each population pair, we sowed F_1 seeds at the following densities of *Bromus/Vulpia*: 65/5, 35/35, and 5/65 per 2.54-L pot; a total seeding density of 70 individuals per pot (equivalent to 5,525 seeds m^{-2}) mirrors natural seeding densities in the field of 2,500–5,500 m^{-2} (Bartolome 1979; Harrison 1999). Each relative density was replicated four times. To better estimate intrinsic growth rates (λ_i), we also included a low-density trial for each population, specifically, sowing either three or seven seeds of *Bromus* or *Vulpia* (more seeds of *Vulpia* because germination rates are lower) into pots, respectively, recording germination, and then thinning densities to a single germinated individual per pot. Each low-density trial was replicated seven times per population. To summarize, our experiment included 288 two-species competition experiments (3 evolutionary histories \times 8 populations per evolutionary history \times 3 relative densities per pair \times 4 replicate pots per relative density) and 168 low-density experiments (3 evolutionary histories \times 8 populations per evolutionary history \times 7 replicate pots per population), for a total of 456 pots. All pots were arranged in a completely

random design on greenhouse benches. All seed produced by each species in a pot was collected (seeds of the two species were kept separate), which could then be used in model fitting (described in the following section); note that plants within a pot are not independent of one another, but each species’ population parameters can be fit independently as they are based on their own population growth rates (eq. [2]).

Model Fitting

To fit equation (2) to data collected during our competition experiments, we used a Bayesian approach (JAGS ver. 4.3.0 via rjags in R package). As we will describe (see “Treatment Comparisons and Hypothesis Testing”), each *Bromus* population was grown in pairwise competition against each of three *Vulpia* populations representing three evolutionary history treatments (fig. 1B); a fourth *Vulpia* was also included for a treatment that is not being considered here but is included in model fitting to enable future research. Thus, we fit separate models to each *Bromus* population, allowing all four *Vulpia* to be fit at once using indexing. For example, α_{11} would be the per capita impact of that *Bromus* population on itself, whereas α_{12} , α_{13} , α_{14} , and α_{15} are the interspecific interaction coefficients of each *Vulpia* on *Bromus*. In other words, our model mirrors both our experimental design (shown in figs. 1B, S1) and our planned treatment comparisons (described in “Treatment Comparisons and Hypothesis Testing” below). Equation (2) can be fit to each population because the number of germinable seeds produced in a pot (N_{it+1}) by each species can be predicted by the densities of individuals sown into pots initially that germinated (i.e., N_{it} and N_{jt}); there are 19 data points per population per species (i.e., seven low-density and 12 two-species competition experiments; see “Competition Experiments”). We have used this same approach in previous research (Germain et al. 2016), which is analogous to the maximum likelihood model fitting approach used by other authors (e.g., Godoy et al. 2014). Future studies testing evolutionary hypotheses with replicated populations should consider a Bayesian hierarchical approach, as doing so would provide knowledge of how among-population variation in population parameters is structured.

We used uninformative priors, with our only constraint being for competition coefficients to be positive (i.e., no facilitation). Specifically, for α and λ , we used uniform priors bound between 0.001 and 100 for α and between 0 and 10,000 for λ , the upper limits of which far exceeded biologically plausible values (for a summary of each parameter’s biological domain, see table S1). We ran four independent Markov chains with 100,000 iterations and an adaptation phase of 50,000 iterations, using JAGS-generated

initial values. We examined trace plots to confirm that posterior samples converged and were well mixed (fig. S7). Medians of posterior distributions were used for significance testing between evolutionary histories, but we note that means and medians were similar (fig. S7). Population growth rates predicted by our estimated parameters closely fit our observed data (fig. S8).

We addressed two issues that arose during model fitting. First, as also identified by previous authors (Godoy et al. 2014; Levine et al. 2017), it became clear that N_{ii} in equation (2) needed to be adjusted (i.e., subtracting the focal individual from N_{ii} ; for details, see the supplemental PDF) to prevent models from allowing self-competition at low density, that is, single individuals competing with themselves, which is biologically implausible and leads to artificial correlations among parameters. This modification did not alter the form of the Beverton-Holt model itself but rather better aligned the model with populations of finite size (as opposed to the infinite populations the model was first based on). Second, one population pair was being fit by our model with parameter estimates that were biologically implausible. For example, α_{jj} was effectively 0 (i.e., an absence of intraspecific competition), leading to carrying capacities in excess of 10,000 individuals per greenhouse pot (fig. S2). Although we are not entirely sure why this occurred for this single population, due to the biological implausibility, our best course of action was to remove this data point, which was a large outlier, from our data set prior to analysis. As such, we report our analyses without the outlier in the main article but also present analyses with the outlier included in the supplemental PDF (figs. S2–S4).

Treatment Comparisons and Hypothesis Testing

To address our research questions, we needed to compare populations with sympatric versus allopatric histories (questions 1 and 2) and use planned contrasts to isolate how each species contributed to the evolution of each interspecific interaction coefficient (question 3). As mentioned earlier in brief, each *Bromus* was competed against three *Vulpia* populations with different evolutionary histories (fig. 1B): (a) a sympatric *Vulpia*, (b) an allopatric *Vulpia*, and (c) a *Vulpia* with a history of competing in sympathy with a different *Bromus* population. To address questions 1 and 2, we compared competitive pairs of *Bromus* and *Vulpia* with sympatric or allopatric evolutionary histories. To address question 3, we needed to test how interspecific interaction coefficients differed when each population of one species was competed twice against two different populations of the other species. For example, if a population of *Bromus* was competed against two different *Vulpia* populations, resulting in different values for *Bromus*'s impact on *Vulpia*

(i.e., α_{VB}), then this difference in impact would be attributable to the evolution of *Vulpia* and not *Bromus* (as the *Bromus* population was held constant). Our experiment was designed so that eight *Bromus* populations (comparing treatments 1 and 2) and eight *Vulpia* populations (comparing treatments 1 and 3) were each competed twice, against a single population of the competing species (see full design in fig. S1). Doing so allowed us to isolate and compare evolved differences attributable to each species, for each interspecific interaction coefficient. To continue the example above, if *Bromus* was held constant, a change in α_{VB} and a change in α_{BV} would be attributable to the evolution of *Vulpia*'s response to and effect on *Bromus*, respectively (fig. 1C). In the absence of evolutionary change, competition coefficients would be insensitive to different populations of either species.

We analyzed differences between competitive histories (research question 1) with a generalized linear mixed effects model (R package glmmTMB; Brooks et al. 2017) and correlations among parameters (e.g., trade-offs; research question 2) using Spearman's rank correlation. For each population parameter, analyzed separately, each model included fixed effects of evolutionary history (sympatric vs. allopatric) and the *Bromus* population as a random effect due to each of eight sympatric versus allopatric contrasts being competed against a common *Bromus* population. We used gamma error distributions for the intrinsic rates of increase (i.e., λ_i) and the competition coefficients (i.e., α_{ii} , α_{jj} , α_{ij} , α_{ji}), as the parameters are positive nonintegers bounded by 0 and their variance is proportional to the mean (for a summary, see table S1). To examine correlations among parameters (i.e., trade-offs), we used Spearman's rank correlation. We chose this method as we do not have to make assumptions of normality or linearity (so long as relationships are monotonic) or regarding which parameter is the dependent variable and which is the independent variable. Note that this analysis is conservative and known to yield type II errors, giving us added confidence when correlations are significant. Because we could not account for random effects with this method, we showed in the supplement how a generalized linear mixed effect model produced qualitatively similar results (table S2). While a Bayesian hierarchical analysis could provide additional knowledge on among-population variation in each parameter, a frequentist approach to model fitting was sufficient to accomplish the goals of our study and is consistent with the methods used in related work (e.g., Godoy et al. 2014; Germain et al. 2016). We also note that correlations are tested against a null hypothesis of no correlation as opposed to a specific trade-off model, as more appropriate null models of trade-offs remain to be developed.

Finally, to test the degree to which the evolution of pairwise interspecific competition coefficients can be attributable

to the evolution of single species (i.e., the recipient's response or the opponent's effect; research question 3), we needed to take a different statistical approach. Point estimates for each population, as used in the mixed models above, are not sufficient because this research goal requires us to identify differences in parameters among pairs of populations (specifically, allowing comparisons shown in fig. 4A). To do so, we made use of the posterior distributions generated for every parameter for every population during model fitting. We interpret parameters as drawn from different distributions if their posterior distributions overlap by 5% or less.

Results

Does Evolutionary History Influence Population Parameters That Underlie Competitive Ability?

We found support for our hypothesis that evolutionary history (i.e., sympatry vs. allopatry) has shaped the evolution of population parameters, increasing the competitive ability of sympatric populations (fig. 2A). In line with our expectations, interspecific competition evolved in response to a history of interaction with *Bromus*; that is, on average, sympatric *Vulpia* were 1.5 times less affected by competition with *Bromus* (α_{VB}) compared with their allopatric counterparts ($\beta = -0.480$, $\chi^2 = 6.86$, $P = .009$; fig. 2D). Interestingly and unexpectedly, we had not anticipated intraspecific competition to be affected by evolutionary history, yet we found that the sympatric populations self-competed ~ 3.5 times less intensely than did allopatric populations (i.e., α_{VV} was lower; $\beta = -1.243$, $\chi^2 = 5.07$, $P = .024$; fig. 2C). We found no evidence that intrinsic growth rate (λ_v) was affected by competitive history, as expected, given that selection on intrinsic growth rate should not depend on the identity of competitors ($\beta = 0.211$, $\chi^2 = 0.931$, $P = .335$; fig. 2B). Last, while not intrinsic to *Vulpia*'s own competitive ability (eq. [1]), *Vulpia*'s impact on *Bromus* (α_{BV}) did not significantly differ among sympatric and allopatric populations ($\beta = 0.431$, $\chi^2 = 0.996$, $P = .318$; fig. 2E). Together, competitive ability was ~ 2.2 times greater among *Vulpia* populations with a history of occurring sympatrically with *Bromus* (κ_v ; $\beta = 0.771$, $\chi^2 = 5.17$, $P = .023$; fig. 2A).

Is Competitive Ability Constrained by Trade-Offs?

We hypothesized that the evolution of increased competitive ability is constrained by trade-offs between population parameters but instead found evidence to the contrary (fig. 3). Specifically, we found no evidence that there exists a trade-off between growth at low density (λ_v) versus how sensitive *Vulpia* is to competition (α_{VV} , α_{VB}); rather, these parameters are uncorrelated. Our expectation that de-

creased intraspecific competition would beget a decreased ability to depress growth of an interspecific competitor (i.e., an interspecific impact) due to trade-offs was also not supported. Paradoxically, instead of finding correlations among parameters indicative of trade-offs, we found that some parameters were positively related in ways that mutually beget higher competitive ability (i.e., they appear to trade up). Specifically, we found strong negative correlations between the two interspecific interaction coefficients (α_{VB} , α_{BV} ; Spearman's $\rho = -0.57$, $P = .030$), such that populations of *Vulpia* that were less affected by competition with *Bromus* (lower α_{VB}) tended to impact *Bromus* most strongly (higher α_{BV}). Importantly, these correlations we observed are not a statistical artifact of model fitting, as α_{VB} and α_{BV} are fit based on different data sets (i.e., population growth data of *Vulpia* for the former, population growth data of *Bromus* for the latter). Considering that α_{BV} is a parameter we associate with the competitive ability of *Bromus*—for example, in equation (1)—this negative correlation between pairwise parameters (α_{VB} , α_{BV}) shows that competitive abilities may not evolve independently. Critically, this negative correlation, or tug-of-war, between interspecific parameters may represent a different constraint we had not considered a priori, where the evolution of increased competitive ability may be constrained by the competing species, reminiscent of the Red Queen hypothesis (Van Valen 1973).

How Does Each Species (i.e., the Recipient vs. the Opponent) Contribute to the Evolution of a Pairwise Interaction Coefficient?

We found that both interspecific interaction coefficients could be altered due to the evolution of either species (i.e., both the recipient and the opponent). Specifically, by competing each population of *Bromus* against two different populations of *Vulpia*, we found differences in α_{BV} and α_{VB} that could be attributed to the evolution of *Vulpia* alone (as *Bromus* was held constant; fig. 4A). Likewise, we found similar differences in α_{BV} and α_{VB} when competing a single population of *Vulpia* against two different populations of *Bromus* (fig. 4A). While we observed shifts in both α_{BV} and α_{VB} regardless of which species is held constant, we also noted differences. Specifically, when looking at *Vulpia*'s sensitivity to competition from *Bromus* (α_{VB}), four of seven populations showed a shift in interaction due to *Vulpia* (the recipient; i.e., green and orange credible intervals in fig. 4Ai overlapped by less than 5%) compared with only two of eight due to *Bromus* (the opponent; i.e., blue and orange credible intervals in fig. 4Ai overlapped by less than 5%). By contrast, if we focus on *Bromus*'s sensitivity to competition with *Vulpia* (α_{BV}), we find that both the recipient *Bromus* and the opponent *Vulpia* alter the

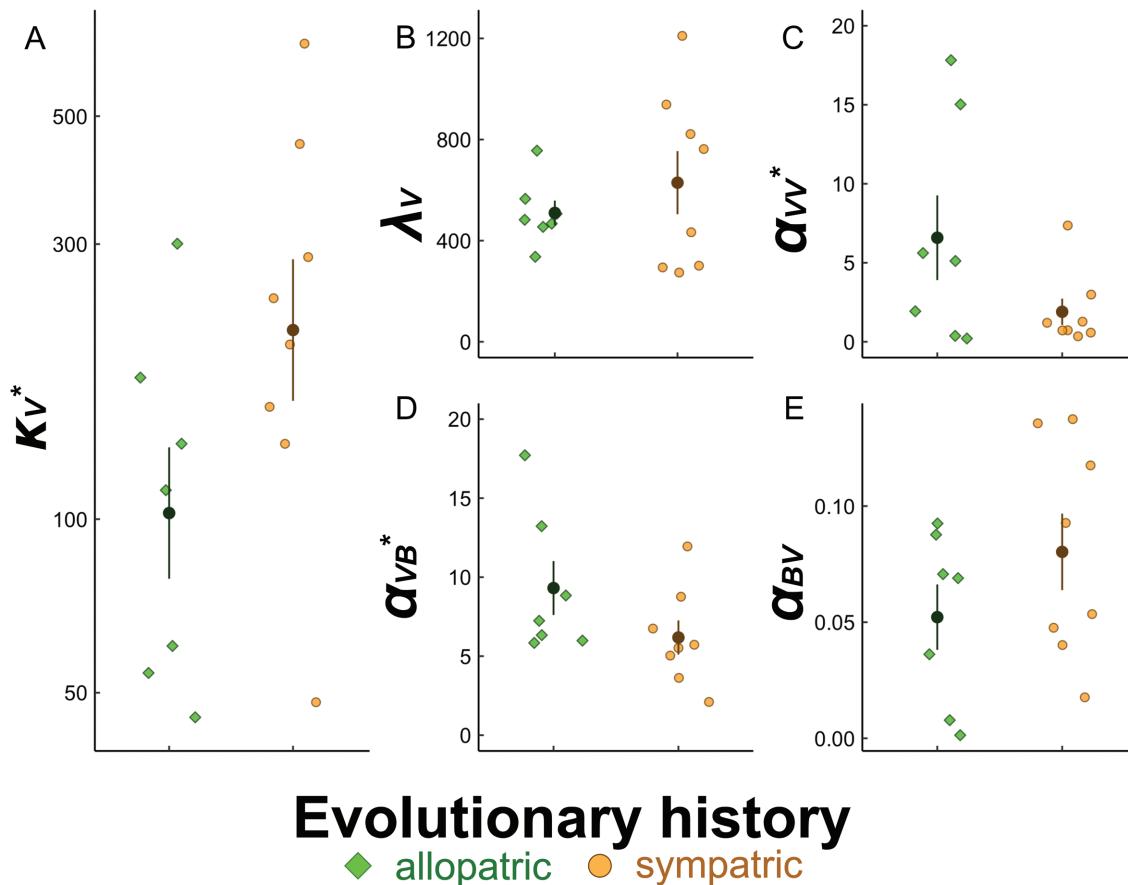


Figure 2: Evolved differences in parameters among populations of *Vulpia* based on evolutionary history. Each data point is a population; orange circles are populations that have a shared history with competitor *Bromus hordeaceus* (sympatric), and green diamonds represent no history of interaction (allopatric). Parameters are as follows: κ_v , competitive ability of *Vulpia* ($\chi^2 = 5.17, P = .023$); α_{vv} , per capita intraspecific competition of *Vulpia* ($\chi^2 = 5.07, P = 0.024$); α_{vb} , per capita interspecific impact of *Bromus* on *Vulpia* ($\chi^2 = 6.86, P = .009$); α_{bv} , per capita interspecific impact of *Vulpia* on *Bromus* ($\chi^2 = 0.996, P = 0.318$); and λ_v , intrinsic growth rate of *Vulpia* ($\chi^2 = 0.931, P = .335$). Error bars represent standard errors.

strength of the interaction: seven of seven and six of eight population trials had nonoverlapping credible intervals (95%), respectively (fig. 4Ai). While the mechanism of evolution may not be clear (i.e., evolution is not necessarily adaptive, e.g., due to drift), these results highlight that the evolution of an interspecific interaction can be driven by the evolution of the opponent, not just the recipient, ultimately revealing that the competitive ability of a species may evolve even if the species itself does not.

Our finding that both species are capable of altering either interspecific competition coefficient presents an opportunity for us to examine additional correlations we had not considered a priori. As a reminder, let us first examine what interspecific competition coefficients summarize. We can consider the strength of a single interaction coefficient, α_{ij} , as a product of two parts: the opponent j 's effect and the recipient i 's response. Above, we deconstructed

how evolved differences in competition coefficients among populations of competing species can be attributable to either the recipient species (an evolving response) or the opponent species (an evolving effect), but here we explore the possibility that the evolution of each species' response and effect are correlated. If we first examine potential correlations between responses and effects attributable to the evolution of *Bromus* only, we find that there is no significant correlation (fig. 4Bi; Spearman's $\rho = 0.48, P = .24$). However, when examining correlations attributable to the evolution of *Vulpia* only, responses and effects were negatively correlated (note that a negative correlation is suggestive of a trade-up; fig. 4Bi; Spearman's $\rho = -0.82, P = .034$). Overall, these results show that a species might evolve to increase its own competitive ability while simultaneously decreasing the competitive ability of its opponent (fig. 4Bi), and this evolutionary potential might be

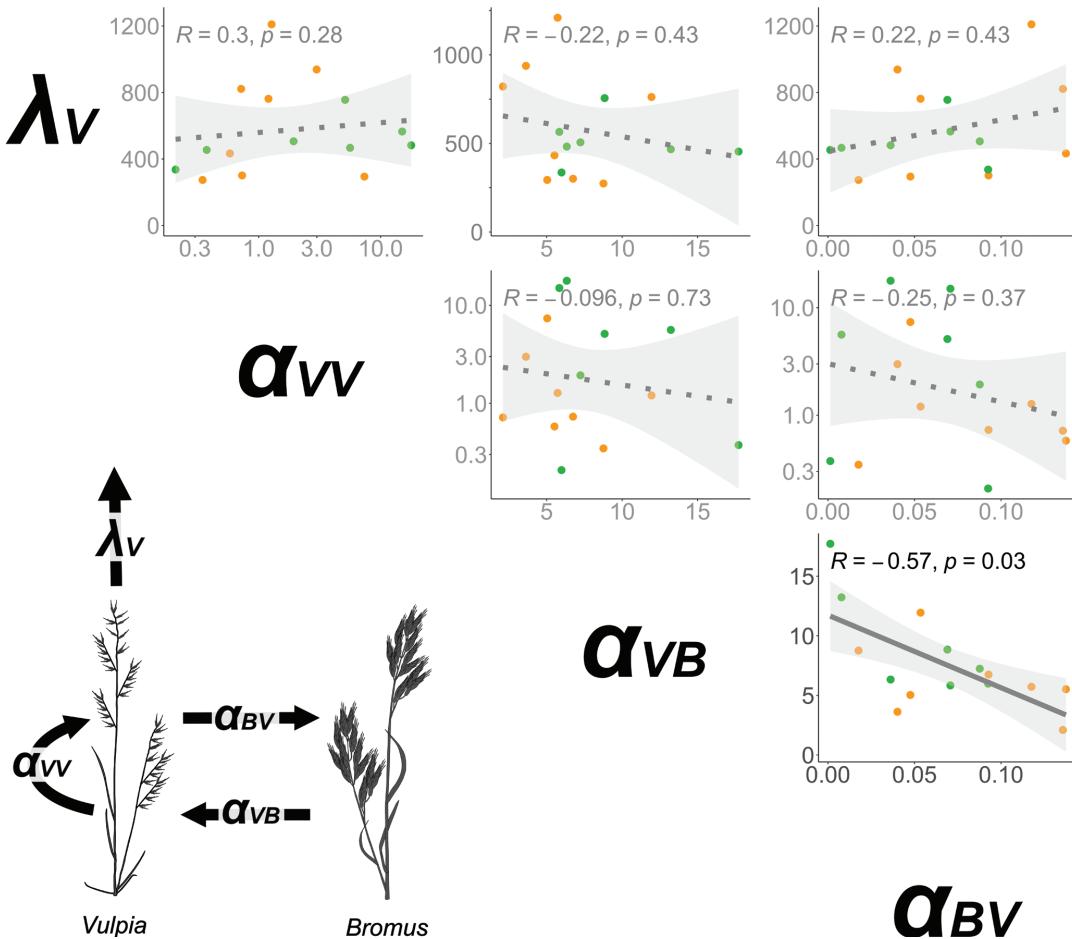


Figure 3: Spearman's rank correlations among the population parameters (median estimates from our model fitting) of competitive ability (see eq. [1]). Solid and dotted lines represent significant ($P < .05$) and insignificant ($P > .05$) correlations, respectively. Orange circles are populations that have a shared history with *Bromus* (sympatric), and green circles represent no history of interaction (allopatric). We additionally show these same figures with full posterior distributions in figure S9, which reveals the same patterns even with uncertainty in parameter estimates. $V = Vulpia$, $B = Bromus$.

asymmetric between competing species (higher for *Vulpia* than for *Bromus*).

Discussion

With recent strides made to explore whether evolution can act as a mechanism for species to persist, coexist, or exclude one another (Lankau 2011; Vasseur et al. 2011; Schrieber et al. 2018; Wittmann and Fukami 2018; Pastore et al. 2021; Yamamichi and Letten 2021), the next step is to understand how this is achieved, by examining the evolution of specific demographic pathways to coexistence. Motivated by this endeavor, we began this research with the specific goal of exploring how and why each component of competitive ability evolved. At the same time, we find no evidence that the parameters constituting competitive abil-

ity are constrained by trade-offs, despite evidence that parameters do evolve and can be correlated in ways that would allow species to evolve toward coexistence (the first empirical demonstration of this outcome, to our knowledge). Below, we discuss contingencies, nuances, and new findings that open up new lines of inquiry on the evolution of competitive ability.

Does competitive ability evolve, and if so, how? The answer to the first part of our question is, yes, consistent with coevolutionary theory, competitive ability did evolve among populations in response to a history of interspecific interactions (fig. 2A). Answering how this occurred required us to decompose competitive ability into its three underlying parameters (α_{VB} , λ_V , and α_{VV} ; see eq. [1]). First, consistent with previous work on coevolution among asymmetric competitors (Callaway et al. 2005; Leger 2008; Lankau

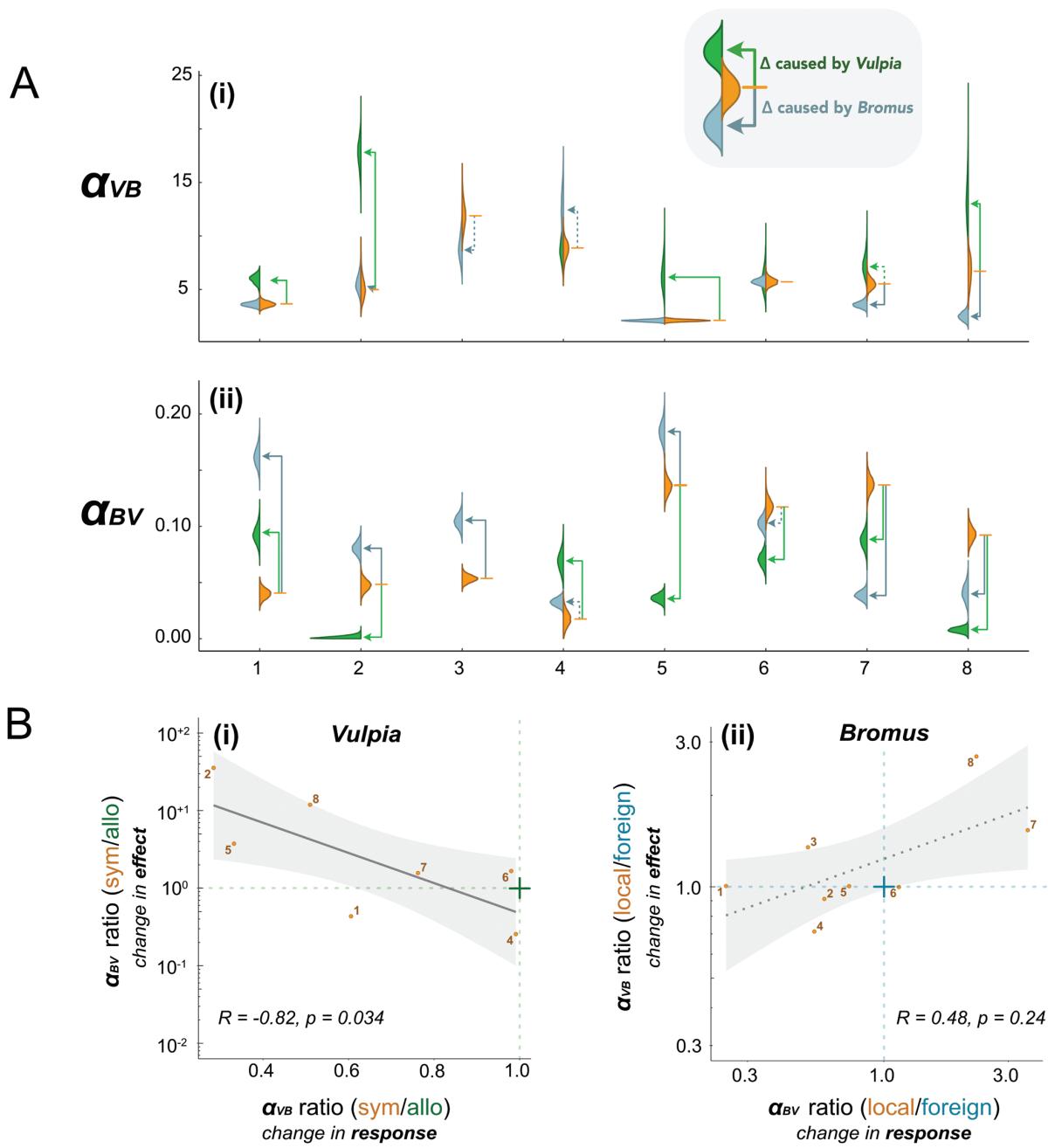


Figure 4: Attributing the evolution of pairwise competition coefficients to individual species. *A*, Posterior distributions of competition coefficients α_{BV} (per capita interspecific coefficient of *Vulpia* on *Bromus*) and α_{VB} (per capita interspecific coefficient of *Bromus* on *Vulpia*) for eight competition trials. Green versus orange = different *Vulpia* populations each competed against the same *Bromus*; blue versus orange = different *Bromus* populations each competed against the same *Vulpia*; see figure S1 for a schematic of the experimental design. For α_{BV} and α_{VB} , a shift from orange to green represents the change associated with *Vulpia*'s effect on *Bromus* and response to *Bromus*, respectively, whereas a shift from orange to blue represents a change associated with *Bromus*'s response to *Vulpia* and effect on *Vulpia*, respectively. Dashed lines mark insignificant differences (>5% overlap). *B*, Partitioning how the evolution of responses and effects attributable to either species (*Vulpia* [i] and *Bromus* [ii]) may be correlated. Relationships between the relative change of α_{BV} against the relative change of α_{VB} between evolutionary histories are as follows: (i) sympatric *Vulpia* divided by allopatric *Vulpia* (competed against the same *Bromus* population) and (ii) local *Bromus* divided by foreign *Bromus* (against the same *Vulpia* population). For *Vulpia*, increased competitive effect is strongly correlated with a reduced competitive response (Spearman's $\rho = -0.82, P = .034$), whereas there is a weak but insignificant correlation between changes in *Bromus*'s effect and response (Spearman's $\rho = 0.48, P = .24$).

and Kliebenstein 2009; Dostál et al. 2013), we found that interspecific sensitivity (α_{VB}) was lower among *Vulpia* populations that had a history of sympatry with *Bromus*. Second, despite evidence to suggest that intrinsic growth rates were capable of evolving (i.e., our 16 *Vulpia* populations did not have identical intrinsic growth rates; fig. S9), intrinsic growth rates were not significantly affected by a history of interaction with *Bromus*. These findings are consistent with classic theory predicting that intrinsic growth rates are always under selection, in both high- and low-competition environments (Mallet 2012). Finally, and most surprisingly, was the evolution of intraspecific competition (α_{VV}). We found that populations with a history of interactions with *Bromus* in sympatry competed less strongly with conspecifics than did allopatric populations (fig. 2C). How did reduced intraspecific competition evolve? Previous studies have shown that increased intraspecific competition evolves when conspecific densities are high (i.e., density-dependent selection). However, sympatric *Vulpia* populations were not found at sites with relatively higher conspecific densities (see the supplemental PDF). An alternative explanation could be that intraspecific competition is mechanistically linked to interspecific interactions via resource use (MacArthur 1972; Chesson 1990), but we find no evidence that such a correlation exists (fig. 4). This final point is particularly interesting because it then suggests that reducing intraspecific competition may be an alternative, independent path for a species to increase competitive ability against a dominant competitor.

Can parameters evolve independently of one another, or are there trade-offs that constrain the evolution of competitive ability? Previous work has been mixed. Classic *r/K* theory tells us density-dependent and density-independent parameters should trade off (MacArthur and Wilson 1967), yet many studies have failed to find this trade-off when estimated from empirical data (Hendriks et al. 2005; Reding-Roman et al. 2017; Zhang et al. 2017). This was thought to be, in part, because the *r* versus *K* parameterization does not mathematically decouple density dependence from density independence (Kuno 1991; Mallet 2012)—in other words, *K* necessarily increases with *r*. To our surprise, even after decoupling density-independent parameters (*r* or, here, λ_V) from density-dependent parameters (α_{VV} , which is independent of λ_V ; see Mallet 2012), we still found no evidence of a trade-off; this contrasts potential trade-offs observed in duckweed (Hart et al. 2019). An additional trade-off is the possibility that evolving decreased sensitivity to an interspecific competitor (decreased α_{VB}) comes at the cost of increased intraspecific competition (increased α_{VV}). While many have found evidence to support this trade-off (Pimentel et al. 1965; Linhart 1988; Lankau 2008), again, our results conflict with this expectation. This result is interesting as such a trade-off is thought to aid in stabil-

lizing intransitive interactions that maintain genotypic diversity between intraspecific and interspecific competitors (Lankau 2008).

If trade-offs are unavoidable constraints of life, why did we not observe any? Trade-offs occur when there is a mechanistic constraint between optimizing two tasks. However, when we assume the existence of trade-offs in a study, we assume our focal species is close to an optimized form (Novak et al. 2006; Shoval et al. 2012; Sheftel et al. 2018). We may observe trade-ups rather than trade-offs if two parameters (or tasks) are far from optimized (Novak et al. 2006). Given that the dominant competitor *Bromus* was introduced ~200 years ago and that we observed significant variation in parameter values among *Vulpia* populations (fig. 2), it is possible that the competitive ability of *Vulpia* may not yet have had enough time to be constrained by trade-offs. Alternatively, we may not observe trade-offs because we are not looking at all the dimensions in which they could occur. For example, trade-offs may only be observable in a multispecies community context through higher-order (Abrams 1983; Mayfield and Stouffer 2017), multi-trophic (Jessup and Bohannan 2008), or intransitive (Pianka 1974; Godoy et al. 2017) dynamics. Other possible dimensions may be trade-offs between different abiotic environments (Goldberg and Lande 2006) or investment in enhanced dispersal ability (Yu and Wilson 2001). Finally, we may not observe trade-offs because they are weak relative to other factors that affect variance in fitness, for example, environmental variation (Snyder and Ellner 2018) or individual variation (Hereford 2009).

The implication that a species' competitive ability contains parameters that, in part, are controlled by their opponent (eq. [1]) suggests that competitive abilities between species may not evolve independently. Indeed, we show that the parameters that underlie the competitive abilities of two competing species are negatively correlated (fig. 3) and that even one species can evolve to simultaneously increase its own competitive ability while reducing the competitive ability of its opponent (fig. 4). Fundamentally, this occurs because the definition of competitive ability includes a parameter (i.e., α_{ij}) that is shared between two species, *i* and *j*, with both species capable of changing this one pairwise trait. This phenomena is analogous to one found in host-parasite interactions, where the evolution of the trait responsible for resistance of a host may change if either the host or parasite evolves (Friman and Buckling 2013). We note that while we have focused on a single definition of competitive ability (eq. [1]), this problem extends to at least 50 others that also incorporate pairwise parameters in their own definitions (Weigelt and Jolliffe 2003). Ultimately, this finding highlights the potential pitfalls of applying competitive ability “as is” in an evolutionary context and how an experimental design like

ours can help attribute evolutionary changes to individual species.

Some have argued that population-level parameters, such as competitive ability, could be considered complex traits that undergo selection (Orr 2009), albeit through a complex mapping to multiple genes or phenotypes (Losos 2011). However, if we wish to translate our discussion of competitive ability to actual phenotypic traits measurable on individual organisms, we need to connect the evolution of population parameters to mechanisms that underlie them (e.g., using a consumer-resource model). However, decomposing changes in interspecific interactions as changes in effect and response might provide such a mechanistic connection. Effect and response can be mechanistically described as how a species impacts its opponent's resources (effect) and how a species responds to the reduction of said resource (response; Goldberg 1990, 1996; Leibold 1995). While these may seem like two sides of the same coin, there are key differences. A change in effect would be a change in how a competitor depresses the availability of the shared resource, either through consumption or interference (MacArthur 1970; Case and Gilpin 1974). However, a species' change in response is more complex, as it relies on consumption rates but also depends on its own metabolic requirements and metabolic efficiency in converting those resources to energy for survival (see MacArthur 1972). Critically then, finding that the reduction in *Vulpia*'s response correlates with the increase in effect (fig. 4B), we suggest that the reduction in response we observed occurred in part due to traits responsible for metabolic differences or increased consumption of new, unshared resources (i.e., increased niche breadth). While examining the evolution of competitive responses and effects may provide a new link between competition coefficients, niche differentiation, and the biological mechanisms that underlie them, our deductive process is speculative at this point but could guide future empirical work.

One might wonder what the net effect of all population parameters is for the evolution of species coexistence and how our findings might compare with theoretical expectations. Although we cover this issue in a recent article using the same data set (Germain et al. 2020) and in this paper are able to delve more into the underlying mechanisms, the take-home message is that coexistence is enhanced by a history of interaction in sympatry. Contrary to classic expectations (e.g., character displacement selecting for reduced competition; Germain et al. 2018), enhanced coexistence is most likely achieved via *Vulpia* (the inferior, native competitor) evolving to better compete against *Bromus*. A recent article suggests that coevolution may frequently be a destructive force for coexistence (Pastore et al. 2021)—in other words, coexistence may be enhanced on short timescales only to be overturned on longer timescales as

adaptive landscapes shift with competition and new mutations arise (Kotil and Vetsigian 2018). However, we wish to raise an important caveat: theory in this area is actively being developed, and thus it may be too early to compare our findings to theoretical predictions in an explicit way. For example, Pastore et al. (2021) constrain their model so that only species' niche positions evolve, whereas other possibilities may broaden outcomes and warrant future examination (Germain et al. 2021). Note also that although theoretical developments show that different coexistence mechanisms may be constrained by interdependencies in certain situations (Song et al. 2019), these developments do not extend to interdependencies between population parameters that underlie coexistence (but may arise for other reasons, such as pleiotropy in underlying traits, e.g., nutrient uptake).

We have seen a recent surge of interest in the evolutionary ecology of species coexistence, whether it is needed to better explain the process of speciation (Rosenblum et al. 2012; Rabosky 2013; Germain et al. 2021) or to better predict how species will evolve in response to the selective pressures of rapid anthropogenic change (Kinnison and Hairston Jr. 2007; Bell 2017). As we have discussed, the parameters that impact competition and coexistence are unlikely to evolve in isolation, similar to other suites of traits (e.g., life history traits; Lankau 2011). Thus considering the evolution of all parameters at once conceptually begins to unify theoretical predictions from different but related subfields of biology, namely, life history, coevolutionary, and coexistence theories. Together these theories help guide our understanding of when and how coexistence or exclusion might evolve (as envisioned by MacArthur [MacArthur and Levins 1967; MacArthur and Wilson 1967; MacArthur 1970] and laid out by Lankau 2011). Future efforts to explicitly align these theories are a fruitful research direction toward examining (1) when population parameters that underlie coexistence evolve, (2) how trade-offs might arise due to phenotypic correlations and due to constraints imposed by the resource environment, and (3) when and why interaction coefficients evolve via response versus effect.

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Statement of Authorship

J.S. and R.M.G. conceived the research. J.S. wrote the initial manuscript and carried out the analysis. R.M.G. collected the data, performed Bayesian model fitting, and provided substantial feedback and revisions at all stages.

Data and Code Availability.

Full data and code are archived in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.dfn2z354n>; Sakarchi and Germain 2022).

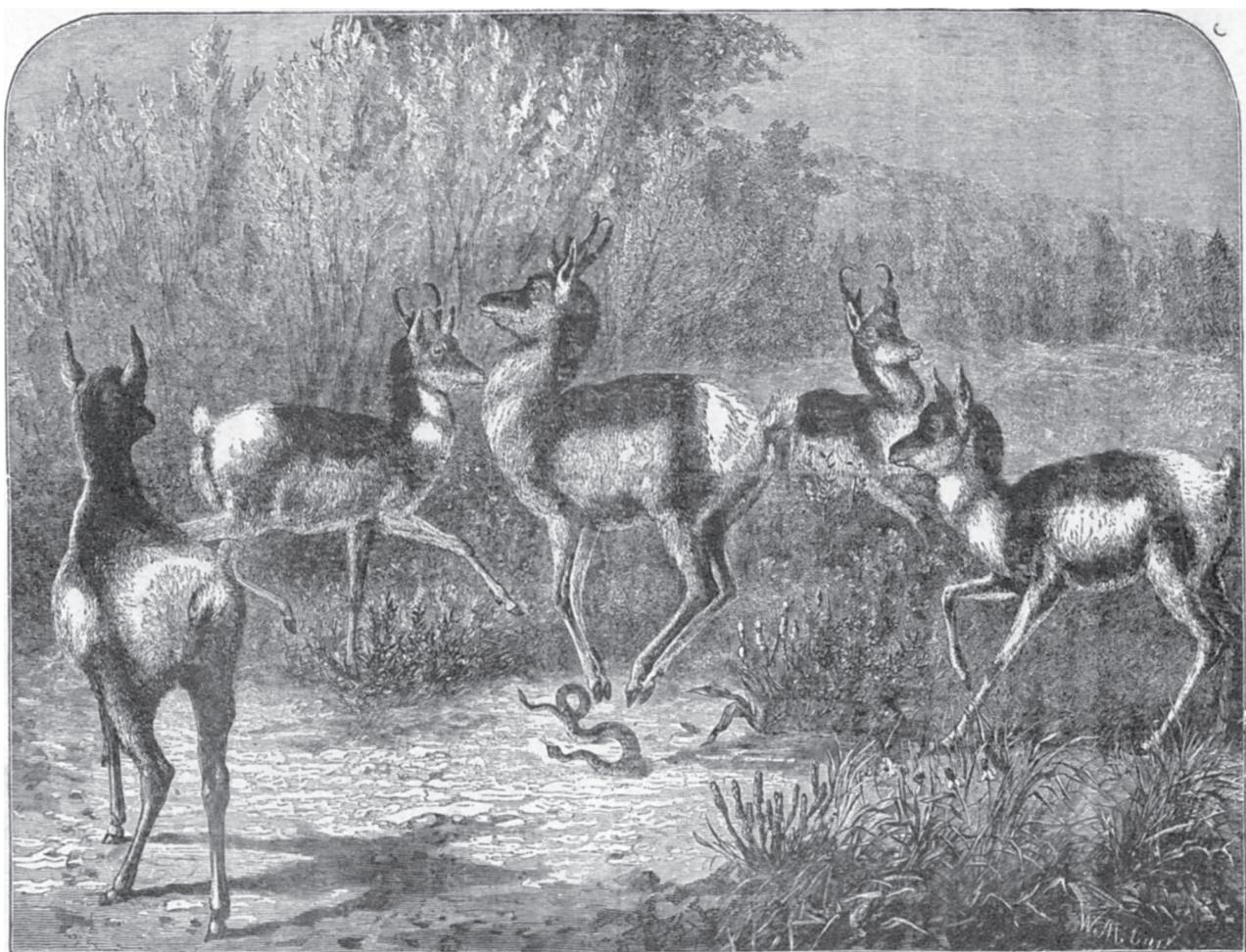
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