

RESEARCH ARTICLE

Community-level natural selection modes: A quadratic framework to link multiple functional traits with competitive ability

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Abstract

1. Research linking functional traits to competitive ability of coexisting species has largely relied on rectilinear correlations, yielding inconsistent results. Based on concepts borrowed from natural selection theory, we propose that trait–competition relationships can generally correspond to three univariate selection modes: directional (a rectilinear relationship), stabilising (an n-shaped relationship), and disruptive (a u-shaped relationship). Moreover, correlational selection occurs when two traits interact in determining competitive ability and lead to an optimum trait combination (i.e., a bivariate nonlinear selection mode).
2. We tested our ideas using two independent datasets, each one characterising a group of species according to (a) their competitive effect on a target species in a pot experiment and (b) species-level values of well-known functional traits extracted from existing databases. The first dataset comprised 10 annual plant species frequent in a summer-rainfall desert in Argentina, while the second consisted of 37 herbaceous species from cool temperate vegetation types in Canada. Both experiments had a replacement design where the identity of neighbours was manipulated holding total plant density in pots constant. We modelled the competitive ability of neighbours (i.e., the log inverse of target plant biomass) as a function of traits using normal multiple regression.
3. Leaf dry matter content (LDMC) was consistently subjected to negative directional selection in both experiments as well as to stabilising selection among temperate species. Leaf size was subjected to stabilising selection among desert species while among temperate species, leaf size underwent correlational selection in combination with specific leaf area (SLA): selection on SLA was negative directional for large-leaved species, while it was slightly positive for small-leaved species.
4. *Synthesis.* Multiple quadratic regression adds functional flexibility to trait-based community ecology while providing a standardised basis for comparison among traits and environments. Our analyses of two datasets from contrasting environmental conditions indicate (a) that leaf dry matter content can capture an important component of plant competitive ability not accounted for by widely used

competitive traits, such as specific leaf area, leaf size, and plant height and (b) that optimum relationships (either univariate or bivariate) between competitive ability and plant traits may be more common than previously realised.

KEYWORDS

community assembly, competition experiment, correlational selection, leaf dry matter content, leaf size, phenotypic selection, plant–plant interactions, quadratic regression, specific leaf area, stabilising selection

1 | INTRODUCTION

Competition has long been considered a key biotic factor determining the structure of local communities (see reviews in Cahill, Kembel, Lamb, & Keddy, 2008; Webb, Ackerly, McPeck, & Donoghue, 2002). More recently, quantitative functional traits have also been recognised as important drivers of both community assembly and ecosystem processes (Keddy, 1992; Lavorel & Garnier, 2002; McGill, Enquist, Weiher, & Westoby, 2006). However, there is still a limited understanding of how plant traits relate to the outcome of competitive interactions between species (Kunstler et al., 2016), a link that has been a long-standing conundrum for ecologists (Grace, 1990). Most studies have related traits to competitive ability within a community or a group of selected interacting species via linear correlations (e.g., Freckleton & Watkinson, 2001; Gaudet & Keddy, 1988; Goldberg, 1996; Keddy, Nielsen, Weiher, & Lawson, 2002; Kunstler et al., 2016; Rosch, VanRooyen, & Theron, 1997; but see Gross et al., 2009). This approach, however, has yielded inconsistent results across studies and environments precluding generalisation and identification of traits that could be broadly linked with competitive ability (Craine, 2005; Goldberg, 1996; Leishman, 1999). Building on concepts borrowed from natural selection theory, we argue that rectilinear functions are not the only possible expectation for trait–competition relationships and that this realisation may help explain inconsistent results.

Competitive ability is understood here as the ability of an individual to limit the performance of a neighbouring individual (i.e., a competitive effect) and/or to withstand the competitive effect of neighbours (i.e., a competitive response; Goldberg & Landa, 1991). We define a functional trait as a measurable feature of plants that determines performance (e.g., growth) and, ultimately, fitness (McGill et al., 2006; Shipley et al., 2016; Violle et al., 2007). With these elements, we propose a framework based on the Darwinian principle stating that competition is a selective force in plant communities (see e.g., Aarssen, 1989 for a comprehensive review). Traditionally, natural selection has been thought to act in three basic ways or “modes” upon a functional trait within a population: directional, stabilising, and disruptive (Endler, 1986; Lande & Arnold, 1983). Directional selection is generally described by a monotonic relationship (e.g., a straight line) in which values at one end of a single functional trait axis are favoured (Mitchell-Olds & Shaw, 1987). Stabilising selection is an n-shaped, optimum relationship in which intermediate trait values are favoured, whereas disruptive selection is a u-shaped relationship

in which both ends of the functional trait are favoured. Directional selection can occur jointly with either stabilising or disruptive selection, shifting the maximum or minimum (respectively) towards one extreme of the range of observed phenotypes (Endler, 1986; Lande & Arnold, 1983). An important premise of our framework is that, since natural selection acts on individuals, the consequences are reflected at the population level but also at the community level (Shipley, 2010; Vellend, 2010). Therefore, trait values that determine an individuals' competitive ability would affect its fitness within a given community (Aarssen, 1989; Aerts, 1999; File, Murphy, & Dudley, 2012; Goldberg, 1996), and could be thus subjected to any of these three basic modes of selection and their combinations (Figure 1).

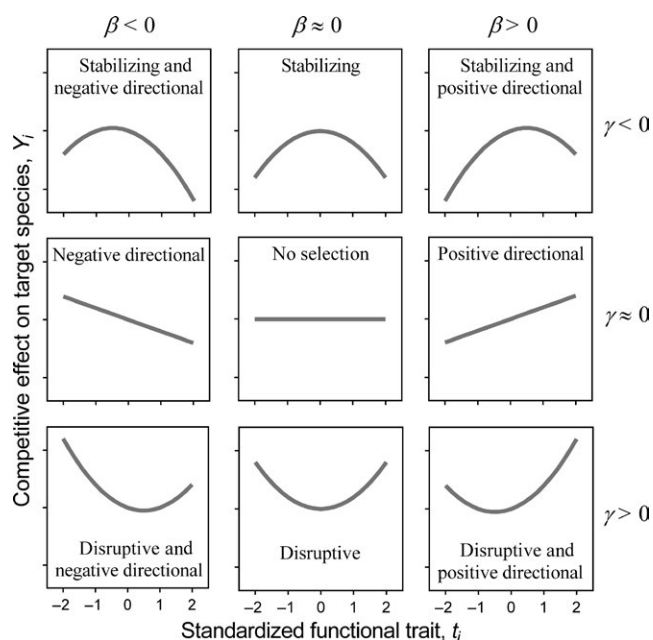


FIGURE 1 Trait–competition relationships according to the possible combinations of three univariate selection modes: stabilising, disruptive, and directional. Competitive ability (Y_i) can be quantified via inverse measures of target species' performance (e.g., mortality and the inverse of plant biomass) in the presence of neighbour species i , each one having a trait value t_i . Selection patterns are characterised using quadratic regression models of the form $Y_i = \alpha + \beta t_i + \gamma t_i^2$, where α is the y-intercept (set to zero in all panels), β is the linear selection gradient, and γ discriminates between stabilising (when negative, top row) and disruptive (when positive, bottom row) selection

The three basic selection modes described above consider single traits in isolation and, based on methods used by evolutionary biologists (Lande & Arnold, 1983), they can be characterised using quadratic regression models of the form $Y_i = \alpha + \beta t_i + \gamma t_i^2 + \varepsilon_i$ (Figure 1). Here, Y_i is the competitive ability of neighbour species i , each one having a value of the trait t ; α is the y -intercept, β is the linear selection gradient, and γ estimates the average curvature of the function and discriminates between stabilising (when negative) and disruptive (when positive) selection; ε is an error term associated to species i . These basic selection modes are also referred to as “univariate” in the evolutionary literature, in the sense that traits do not interact with each other to affect fitness (see e.g., Kingsolver, Diamond, Siepielski, & Carlson, 2012; Phillips & Arnold, 1989).

When considering multiple traits in pairs, the full quadratic regression model may take the following form

$$Y_i = \alpha + \sum_{j=1}^n \beta_j t_{ij} + \sum_{j=1}^n \gamma_j t_{ij}^2 + \sum_{j < k} \theta_{jk} t_{ij} t_{ik} + \varepsilon_i \quad (1)$$

Here, partial regression coefficients β_j and γ_j , respectively, measure univariate linear and nonlinear selection on trait j (see e.g., Phillips & Arnold, 1989). This multivariate approach allows for the estimation of direct selection on a given trait (β_j and γ_j) controlling statistically for indirect selection due to measured correlated traits (Lande & Arnold, 1983). Subscript k is used jointly with j to identify all possible two-way interactions between traits, giving $n(n-1)/2$ coefficients θ_{jk} to be estimated. Both subscripts assign the same labels to traits, from 1 to n , and estimated θ_{jk} 's are those where $j < k$ (cfr. equation 3 in Phillips & Arnold, 1989). For instance, in the case of four traits ($n = 4$), six interaction coefficients would be estimated, namely θ_{12} , θ_{13} , θ_{14} , θ_{23} , θ_{24} , and θ_{34} . Interaction coefficients (also known as cross-product terms) measure whether selection on one trait (j) depends on the values of another (k) and vice versa. This bivariate mode of selection has been referred to as “correlational selection” by evolutionary biologists (see e.g., Endler, 1986) since it would operate changing the covariance between two traits (Lande & Arnold, 1983). Correlational selection coefficients produce curved response surfaces (peaks, valleys, saddles, or ridges) and thus indicate nonlinear selection along axes that are not parallel to the axes represented by single traits (Phillips & Arnold, 1989). Regression on traits standardised to zero mean and unit variance yield standardised selection metrics that enable comparisons among different types of traits and organisms (Kingsolver et al., 2012; Lande & Arnold, 1983).

Underlying mechanisms of community-level selection modes have been recently discussed in the context of community assembly (Rolhauser & Pucheta, 2017). Here, we build on these ideas and on previous analyses of community-level trait-competition relationships. Directional selection would arise when traits determine a hierarchy of competitive ability (Goldberg, 1996; Goldberg & Landa, 1991; Keddy et al., 2002; Kunstler et al., 2012, 2016). For example, potential height in light-limited environments, where competition is clearly asymmetrical and the tallest species become the best competitors (Givnish, 1987; Kunstler et al., 2016; Westoby, Falster, Moles, Vesk, & Wright,

2002). Stabilising (optimum) selection may occur when two or more antagonistic agents determine a functional trade-off (Rolhauser & Pucheta, 2017), a process known as environmental filtering when such factors are abiotic (Kraft et al., 2015; see also Lasky, Sun, Su, Chen, & Keitt, 2013 who modelled environmental filtering using Gaussian, instead of quadratic functions). This may be particularly the case of productivity-related traits, assuming that determinants of productivity are homogeneous over the area occupied by a community (Grime, 2006). In contrast, within-site environmental heterogeneity would allow for niche partitioning and the functional divergence of competitive species (Adler, Fajardo, Kleinhesselink, & Kraft, 2013; Rolhauser & Pucheta, 2017), that is, a disruptive selection of competitive ability. Further, the importance of explicitly evaluating trait-trait interactions on individual fitness at the community level (referred to here as correlational selection) has been recently noted, although empirical evidence is largely scarce (Laughlin & Messier, 2015).

In this work, we are particularly focused on the competitive effects of neighbours on a target species (or “phytometer”). We thus measure competitive ability (Y_i) as an inverse function of target species performance (Sackville Hamilton, 1994). We test our ideas using two datasets from contrasting environmental conditions, each one characterising a set of neighbour species according to (a) their competitive effects against a target species in a pot experiment and (b) species-level values of well-known and widely used functional traits (see e.g., Pérez-Harguindeguy et al., 2013). The first dataset comprised annual plant species frequent in a summer-rainfall desert in Argentina (Rolhauser & Pucheta, 2016), while the second consisted of herbaceous species living in a range of temperate vegetation types in Canada (Keddy et al., 2002). On top of serving as independent examples, we used these datasets to explore different aspects of trait-based competition. While linking species-level trait values to species-level competitive effects has been a widely used approach (e.g., Freckleton & Watkinson, 2001; Gaudet & Keddy, 1988; Goldberg, 1996; Keddy et al., 2002; Rosch et al., 1997), it is important to acknowledge that competition operates at the individual level where stochastic processes may obscure the deterministic role of trait-based mechanisms (Chase, 2014). We thus used our desert annual plants dataset to explore the extent to which the three univariate selection modes (directional, stabilising and disruptive) based on species-level trait values can explain individual-level competitive effects. Further, the temperate herbaceous plants dataset contained a relatively large number of species characterised by a small number of traits providing us the necessary degrees of freedom to fit the full quadratic regression (Equation 1) and evaluate the relative strength of correlational selection of species-level competitive effects.

2 | MATERIALS AND METHODS

2.1 | Desert annual plants dataset

This dataset contained species-level trait values and individual-level quantifications of competitive effects. The latter were obtained

from a pot experiment specially designed to test our ideas on the three basic, univariate selection modes. The experiment had a “replacement” design where the identity of neighbours within experimental units was manipulated holding total plant density constant. This design is particularly suitable for questions based on the functional similarity of competing species (Sackville Hamilton, 1994). The experimental units were 1.5 L black plastic (nursery) pots, where one target-species individual coexisted for ~60 days with one individual of a neighbour species. We used 10 different neighbour species (see list in Table S1 in Appendix S1) which were all warm season annuals frequent in an open shrubland (31°43′18″S, 68°08′17″W) located in the central-northern Monte Desert, Argentina (hereafter called “the study site,” Rolhauser & Pucheta, 2016). The target species was *Tribulus terrestris* (Zygophyllaceae; hereinafter referred to as *Tribulus*), an abundant exotic species in our study site (Rolhauser & Pucheta, 2016, 2017). *Tribulus* was also included as a neighbour species to explore how intraspecific competition mapped onto the trait-competition scenario.

The pot experiment was conducted in the experimental field of the Universidad Nacional de San Juan (~46 km away from the study site) during the summer of 2013–2014. All plants involved in this experiment (i.e., both target and neighbour plants in each pot) originated from seeds contained in soil and debris (see below) collected in the study site. Water sheet flow in the field accumulates large amounts of non-dormant seeds of desert annuals in naturally occurring obstructions or dams (Rolhauser, 2015). In these dams, seeds are mixed with soil and other coarse material transported by water such as twigs and dry leaves, and we call this “debris mixture.” In November 2013, we collected seed-rich debris mixture and topsoil from open areas among shrubs to fill the pots. In late January 2014, we filled each pot with five parts of topsoil and topped them with one part of debris mixture. Pots were placed in a large garden bed of 1.5 m by 10 m built on the ground and arranged EW. The bed allowed us to water the pots relatively easily by pulses of submersion and capillary rise. In each pulse, we filled the bed with water up to half the height of the pots and maintained this level for about 30 minutes to allow the entire substrate in each pot to imbibe. During germination and establishment stages, we watered the pots every second day to prevent topsoil desiccation (mimicking field conditions after a large rain event that would trigger massive germination). After this stage (see below), we watered the pots whenever the superficial substrate of at least one pot lightened (a sign of water deficit), resulting in a watering frequency that ranged between 3 and 7 per days. This watering method reflected to some extent the restricted and pulsating nature of resource supply in deserts (Reynolds, Kemp, Ogle, & Fernandez, 2004).

Seedling emergence started 4 days after the first watering, and we surveyed species diversity of seedlings in each pot. A month later (late February), we considered the establishment phase completed, and we thinned plants to obtain the desired combinations of species. When possible (i.e., when more than one individual of the necessary species were present), thinning was carried out so that both individuals were placed centred on either side of an imaginary line

dividing the pots in half (maximum distance between individuals was constrained by the diameter of pots, ~12 cm). We managed to obtain at least 12 replicates for all neighbour species except for *Solanum euacanthum*, for which only six replicates were available (Appendix S1). At this stage, larger plants started shading those in adjacent pots. We thus rearranged pots to form blocks in order to homogenise conditions among experimental units. Blocks were formed according to the height of the tallest individual in each pot, so that block one contained pots with the tallest plants, and so on; the position of pots within each block was randomised. This resulted in a randomised incomplete block design since the number of replicates was not equal across neighbour species (see the resulting assignment of pots into blocks in Table S3 in Appendix S1). Towards the end of April 2014, all remaining individuals had seeded and many of them had already begun to senesce, therefore we decided to terminate the experiment. The duration of the experiment largely coincided with the length of the growing season of naturally occurring plants in the field, of about 3 months. Harvest of above-ground plant biomass was carried out in blocks, except for those individuals that died during the experiment and were immediately harvested. Both target and neighbour plants within a pot were harvested simultaneously. As a result, from the 146 *Tribulus* plants used (30 and 116, respectively, from pots with conspecific and heterospecific neighbours), 79 were harvested following mortality patterns during the experiment (~54%) and the remaining 64 were harvested following the blocking design at the end of the experiment. Harvested plants were oven-dried at 60°C for at least 72 hours and then weighed.

All neighbour species were characterised in terms of eight functional traits: leaf size (LS, area), leaf dissection index (LD, perimeter/√area), specific leaf area (SLA, area/dry weight), leaf dry matter content (LDMC, dry weight/fresh weight), specific root length (SRL, length/dry weight), specific root volume (SRV, volume/dry weight), maximum plant height (H), and seed mass (SM, dry weight). Species-level trait values for these species were extracted from our local database (published in Rolhauser & Pucheta, 2017). Briefly, 10 healthy individuals per species were collected to characterise leaf and root traits, whereas at least eight individuals per species were used to estimate seed dry mass values (Rolhauser & Pucheta, 2017). Collection timing (between November 2010 and March 2014) and place (in shrub understories or in open spaces) depended on the temporal and spatial distribution of species; field measurements of maximum plant height were also carried out within this time frame (Rolhauser & Pucheta, 2017). Using the individual-level trait values from which these species averages were obtained, we show here that variation among species included in this experiment is much greater than variation within species, which justifies the use of species average values (Appendix S1).

2.2 | Temperate herbaceous plants dataset

This dataset contained species-level estimates of both trait values and competitive effects. Data on the competitive effects of temperate herbaceous species living in eastern Ontario, Canada, were

obtained from Keddy et al. (2002). The plants used in this experiment were collected from a range of vegetation types in eastern Ontario, including old fields with either deep clay or shallow sandy soils over Precambrian gneiss, old fields with shallow soils over limestone, rock barrens over Precambrian gneiss, and alvars, which are environments characterised by shallow soils over flat limestone (Nielsen, 1993). All collection sites were located within the cool temperate ecoclimatic province of Canada (Strong, Zoltai, & Ironside, 1989).

The experiment had a replacement design similar to ours, where *Trichostema brachiatum* (Lamiaceae; hereinafter referred to as *Trichostema*) was the target species. The experiment included 63 neighbour species and two environmental treatments: stress (using 0.5 L pots) and control (using 1 L pots). Data on widely used functional traits for these species were not available in the original paper and were extracted from the TRY database (Kattge et al., 2011). Trait data were not available for all species used in Keddy et al. experiment, and the resulting dataset was limited to 37 species characterised in terms of plant height, LDMC, LS, and SLA (see list of species in Appendix S2; references for these data include Aubin, Beaudet, & Messier, 2000; Aubin et al., 2012; Aubin, Messier, & Kneeshaw, 2005; Aubin & Ricard, 2000; Masse, Prescott, Müller, & Grayston, 2016; Morris, 2014; Wiebe, Morris, Luckai, & Reid, 2013). The TRY database provided several trait values for most of these species. We thus estimated maximum plant height for each species as the 99% quantile of observed values. For the remaining traits, we computed “typical” trait values for each species as the arithmetic mean of observed values.

2.3 | Data analysis

Data analysis was performed on each dataset independently. Based on a quadratic regression framework (Equation 1), our general approach consisted of using stepwise variable selection to find the best combination of traits to explain neighbours' competitive effects. Competitive effects of neighbour species i were calculated as the log inverse of the above-ground dry biomass of target-species individuals, denoted as $\ln(1/B_i)$. In the case of the conspecific treatment in the desert-annuals experiment, two values of *Tribulus* $\ln(1/B_i)$ were obtained from each pot, which were averaged to obtain a single measure per pot. Backward elimination was conducted when available degrees of freedom allowed fitting a full initial model, while forward addition was performed when this was not possible (see below). The importance of model terms was assessed based on the small sample (or second-order) Akaike information criterion (AIC_c), which decreases with model fit and sample size, and increases with the number of parameters (Burnham & Anderson, 2003). It is thus a useful measure for variable selection; for example, the removal of the least important term in a model would generate the largest decrease (or the smallest increase) in AIC_c . AIC_c was calculated using the package $AICCMODAVG$ in R (Mazerolle, 2016). In general, quadratic terms were considered for all continuous predictors, that is, traits and other covariates (see below). Quadratic terms were always evaluated in the presence of the corresponding linear term (see e.g., Lande & Arnold,

1983). Thus, linear terms were removed only if the corresponding quadratic term had been previously removed during backward elimination, while quadratic terms were added only if the corresponding linear term had been previously added during a forward procedure. The degree of collinearity (i.e., the correlation among predictors) in the resulting best models was diagnosed using variance-inflation factors (VIF) calculated with the function `vif` of the package `car` in R (Fox & Weisberg, 2011). Predictors with $VIF > 10$ may be seriously affected by collinearity and the simplest remedial measure is to drop them from the model (Kutner, Nachtsheim, Neter, & Li, 2005).

For the desert annual plants dataset, *Tribulus* $\ln(1/B_i)$ was modelled as a function of neighbour traits using multiple Gaussian linear mixed-effects models (i.e., assuming normal errors) using the function `lme` of the package `nlme` in R (Pinheiro & Bates, 2000). Functional traits (standardised to zero mean and unit variance) and harvest date (centred) were modelled as fixed effect predictors, whereas blocks were included in all models as random effects. Harvest date was included to account for the effect of individual age on growth. The relatively small number of species prevented a backward elimination of traits, so we carried out a forward selection process instead (Appendix S3). Models were fitted by the maximum likelihood method to allow for meaningful comparisons during variable selection (Mazerolle, 2016; Pinheiro & Bates, 2000). We refer to these models as “trait-based.”

For the temperate herbaceous plants dataset, the response variable was proportional to *Trichostema* $\ln(1/B_i)$. Originally, Keddy et al. (2002) published their results in terms of average neighbour species “relative competitive performance.” This was calculated as $RCP_i = B_0 - B_i/B_0$, where B_0 was the average above-ground biomass of *Trichostema* when grown alone, and B_i when grown with neighbour species i (Keddy et al., 2002). Since the value of B_0 was not provided in the original paper, we assumed it to be 1g (which would suffice for comparative purposes) and calculated B_i as $(1 - RCP_i) * 1g$. Given the absence of individual-level observations, competitive effects were related to traits using fixed-effects Gaussian linear models, for which we used the function `lm` in R (Fox & Weisberg, 2011). In this case, plant traits were log-transformed to control for extreme values and then standardised. The initial model contained both linear and quadratic terms of all four traits, all possible cross-products terms, and all possible interactions between stress treatment and trait-related terms. This model was simplified through backward elimination (Appendix S3).

We also described the multivariate functional variation across the species in each dataset using principal component analysis based on standardised single functional traits (see Appendix S2). We used the resulting principal components (PCs) as predictors of neighbours' competitive ability the same way we did for single traits, and we refer to these models as “PC-based.” Retained PCs (the first three in the case of desert annuals, and the first two in the case of temperate species) were meaningful in terms of the Kaiser–Guttman criterion, that is, their eigenvalues were larger than one (Borcard, Gillet, & Legendre, 2011, see full results in Appendix S2). The best PC-based models were selected through backward elimination (Appendix S3).

TABLE 1 Statistical summaries of the best trait-based and PC-based models explaining the competitive effects in a pot experiment of 10 annual species that are frequent in a site within the Monte Desert (Argentina)

Model	Variable	Estimate	SE	df	t value	p value	VIF
Best trait-based, AIC _c = 251.9	Harvest date	-0.028	0.003	1/110	-10.78	<0.0001	1.02
	Leaf dry matter content	-0.387	0.099	1/110	-3.92	0.0002	3.80
	Leaf size	-0.141	0.113	1/110	-1.25	0.2133	5.16
	Leaf size ²	-0.223	0.062	1/110	-3.59	0.0005	1.91
	Plant height	0.413	0.132	1/110	3.12	0.0023	7.11
	Specific root length	-0.304	0.118	1/110	-2.57	0.0115	5.79
Best PC-based, AIC _c = 261.8	Harvest date	0.142	0.062	1/112	-10.04	<0.0001	1.02
	PC1	-0.142	0.125	1/112	2.28	0.0244	4.35
	PC3	-0.131	0.069	1/112	-1.14	0.2582	7.23
	PC3 ²	-0.027	0.003	1/112	-1.89	0.0616	10.19

Estimated parameters are shown along with their standard errors. Significance of model terms was evaluated using marginal tests based on the t-distribution. AIC_c: small sample Akaike information criterion; df: numerator/denominator degrees of freedom; VIF: variance-inflation factor; PC: principal component. See Figure 2 for a graphical representation of the trait-based model.

Univariate trait-competition relationships described by the best model for each dataset were illustrated using component-plus-residual plots, also called partial residual plots (Fox & Weisberg, 2011). In general, a partial residual associated with observation i in response to predictor j , denoted $e_{\text{partial},ij}$, is calculated by adding the fitted linear component corresponding to this predictor (i.e., the prediction made by j for observation i keeping all other covariates at their average value, ρ_{ij}) to the corresponding residual of the full model (e_i), that is, $e_{\text{partial},ij} = \rho_{ij} + e_i$ (Fox & Weisberg, 2011). Partial residuals $e_{\text{partial},ij}$ are then plotted against predictor j . In our case, ρ_{ij} for trait t_j equals $\alpha + \beta_j t_{ij} + \gamma_j t_{ij}^2$ (see Equation 1) since all remaining traits in models have zero mean. In addition, we used two-dimensional filled contour plots (Mittal, 2011) to illustrate predicted trait-competition relationships where correlational selection was detected.

3 | RESULTS

3.1 | Desert annual plants

The best trait-based model explaining neighbour competitive effect on *Tribulus* -quantified as $\ln(1/B_i)$ - included LDMC, LS, potential plant height (H) and SRL, along with harvest date (Table 1). Trait-competition relationship for LS was consistent with stabilising selection, without a significant directional component (Table 1; Figure 2). Relationships for LDMC and SRL were negative directional and positive directional for H (Table 1; Figure 2). In addition, *Tribulus* $\ln(1/B_i)$ decreased linearly with harvest date, which reflects that individuals that died earlier were smaller (Figure 2). All VIFs in this model were <7.2, indicating tolerable collinearity.

The best PC-based model included the first and third PCs (Table 1). Traits most strongly related with PC1 were SLA (positively) and LDMC (negatively), whereas SRL and H were most strongly related (positively) with PC3 (Appendix S2). This model showed lower performance (i.e., both higher AICc and VIFs) compared to the best

trait-based model (Table 1). Hence, we will not look into the details of interpreting the PC-based model, although it is noteworthy that trait-competition relationships were negative directional for PC1 and stabilising for PC3 (Table 1).

3.2 | Temperate herbaceous plants

The best trait-based model fitted to these data combined LDMC, SLA, and LS (Table 2). There was a combination of negative directional and stabilising selection on LDMC (Figure 3a). We also found correlational selection on SLA and LS (Table 2). Selection on SLA was negative directional within large-leaved species, while it was slightly positive within small-leaved species (Figure 3b). Furthermore, selection on LS was positive directional for low-SLA species and negative for high-SLA species (Figure 3c). The resulting selection surface is represented by a saddle with an off-centred saddle point. Competitive ability peaks at low SLA and large LS and decreases steeply towards either high SLA or small LS (Figure 3d). The stress treatment resulted in a relatively small (and marginally significant) decrease in the overall competitive ability of neighbours (Table 2). There were no significant interactions between stress treatment and traits (Table 2; Appendix S3), implying that none of the functional patterns listed above were affected by this factor. All VIFs in this model were <1.6, indicating very low collinearity. PCs were not significantly related to the competitive ability of these species (Appendix S3).

4 | DISCUSSION

4.1 | Competitive trait selection in desert annual plants

Two traits related with the quality of plant tissues were retained in the best model, that is, LDMC and SRL. High LDMC could result from small cells with thick walls which would confer leaf elasticity and

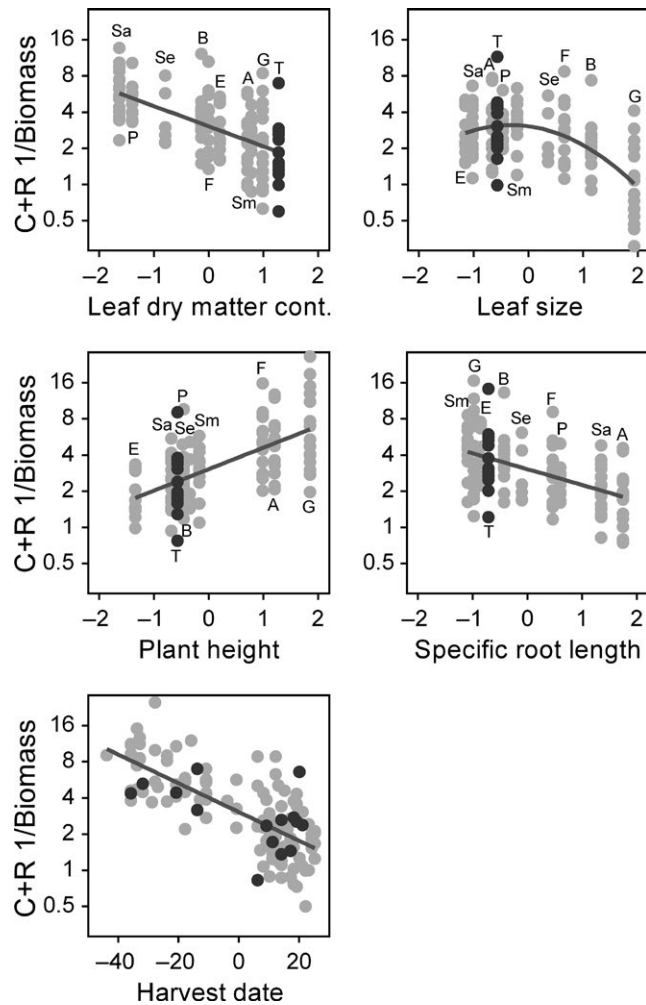


FIGURE 2 Component-plus-residual (C+R) plots illustrating the estimated relationships between trait values and competitive effects on a target species (1/biomass, in log scale) of 10 desert annual species in a pot experiment (see model summary statistics in Table 1). Lines show predicted values (the linear components) while each grey dot (dark grey dots for the target species, *Tribulus terrestris*, T) shows the sum of the component and the residual corresponding to each observation. Other species codes are A: *Amaranthus standleyanus*; B: *Boerhavia diffusa* (exotic); E: *Euphorbia catamarcensis*; F: *Flaveria bidentis*; G: *Gomphrena martiana*; P: *Portulaca oleracea* (exotic); Sa: *Sclerophylax arnotii*, Se: *Solanum euacanthum*; Sm: *Sphaeralcea miniata*. Species codes are placed above or below the corresponding data points in panels with stacked observations

allow tolerance to water limitation, but would limit photosynthesis under moist conditions (Niinemets, 2001). We would thus expect a negative directional pattern in the absence of water stress, where species with low LDMC are most competitive. Our results coincide with this expectation and further suggest that the experimental conditions (full sunlight and 1.5 L pots) may have been generally benign for these desert species.

Specific root length represents a trade-off between resource acquisition and the associated dry mass costs of building and maintaining roots (see Pérez-Harguindeguy et al., 2013 and references

therein). High SRL can result from having a low diameter or low tissue density and may be beneficial in disturbed soils with high resource availability (Eissenstat, 1991). However, thick roots exert more penetrative force on soil and transport more water, while those with high tissue density tend to have higher longevity (Pérez-Harguindeguy et al., 2013). Our results showed a negative directional selection on SRL. Given our pulsating watering system, we speculate that the higher competitive ability of low- vs. high-SRL species may have been the result of (a) faster water extraction from the soil during pulses via thicker roots and/or (b) the maintenance of active root systems during inter-pulses via more resistant roots. Overall, these results indicate that a seemingly conservative strategy underground (i.e., low-SRL) may be coupled with an acquisitive strategy above-ground (i.e., low-LDMC) to confer plants high competitive ability. They thus support the recent view that selective pressures may differ between above- and belowground organs (Bergmann, Ryo, Prati, Hempel, & Rillig, 2017).

The best trait-based model also included two traits related to the size of individuals and their organs, that is, potential plant height (H), on which selection was positive directional, and LS, on which selection was stabilising. In general, both H and LS are positively related with competitive ability when light is the limiting resource, but tall plants and large leaves are energetically costly and would be inefficient if light is not limiting (Givnish, 1987; Westoby et al., 2002). In addition, small leaves create a thinner boundary layer favouring both gas exchange and heat dissipation (Givnish, 1987; Westoby et al., 2002). Our results indicate that taller plants may have outcompeted target-species individuals through better access to direct sunlight. In contrast, the optimum LS found here suggests opposite selecting forces perhaps associated to a trade-off between light interception vs. gas exchange and heat dissipation. Overall, these results suggest that selective pressures on LS and H were at least partially uncoupled and support the stance that they may be associated with different aspects of the ecological strategies of coexisting species (Falster & Westoby, 2003).

At our study site, both tough-leaved and succulent annuals can dominate the open spaces among shrubs (Rolhauser & Pucheta, 2016). This is at odds with our experimental results and suggests that the success of species in the field may not be entirely dictated by their competitive ability. Other factors, such as the ability to respond to seasonal precipitation and drought (e.g., Angert, Huxman, Chesson, & Venable, 2009) may also be important for these annual plants. Interspecific differences in such responses across years (Angert et al., 2009), coupled with limited seed dispersal (Venable, Flores-Martinez, Muller-Landau, Barron-Gafford, & Becerra, 2008) might counterbalance the competitive differences found here and possibly explain annual species coexistence at our study site.

4.2 | Competitive trait selection in temperate herbaceous plants

All three leaf traits available in this dataset were retained in the best model, that is, LDMC, SLA, and LS. The environmental conditions in

Variable	Estimate	SE	df	t value	p value	VIF
Leaf dry matter content	-0.692	0.131	1/67	-5.27	<0.0001	1.44
Leaf dry matter content ²	-0.277	0.110	1/67	-2.52	0.0140	1.57
Specific leaf area	-0.420	0.119	1/67	-3.54	0.0007	1.18
Leaf size	0.160	0.114	1/67	1.41	0.1637	1.08
Specific leaf area * leaf size	-0.315	0.138	1/67	-2.28	0.0260	1.18
Stress	-0.390	0.217	1/67	-1.80	0.0770	1.00

Estimated parameters are shown along with their standard errors. Significance of model terms was evaluated using marginal tests based on the *t*-distribution. The R^2 of this model was 0.39. Other abbreviations as in Table 1. See Figure 3 for a graphical representation of these results.

the temperate species experiment were aimed to provide plants with ample moisture, nutrients, and space in the control treatment, but a restricted offer in the stress treatment (Keddy et al., 2002), although we found a marginal effect of the treatment. The negative selection gradient observed here on LDMC suggests that these relatively benign conditions may have generally favoured low- over high-LDMC species. Nonetheless, the presence of an optimum LDMC (skewed towards low values) suggests that water availability may have somewhat limited the performance of species with extremely low LDMC even in the 1 L control pots.

Specific leaf area represents the trade-off between potential growth (maximised in high-SLA leaves) vs. leaf longevity (maximised in low-SLA leaves; Westoby et al., 2002). In addition, low-SLA leaves tend to have higher photosynthetic rates per unit area at high irradiation levels (via higher leaf thickness) but would be inefficient in the shade (Niinemets, 2001). Kunstler et al. (2016) found a negative linear relationship between SLA and competitive effects among trees worldwide and attributed the pattern to the benefits that low SLA provides in terms of light interception. Notably, we found support for this negative relationship within large-leaved species but not within small-leaved species. Here, large-leaved, low-SLA species were the most competitive possibly because they maximised both light interception and assimilation. Keddy et al. (2002) arrived at a similar conclusion based on the observed positive correlation between neighbour plant biomass and competitive effects. When leaves are small, however, increasing SLA was not associated with a decrease in competitive ability but instead with a slight increase. This suggests that species investing in small and thin leaves (possibly cheaper) may have somewhat compensated the overall loss in light interception. That is, plants with high SLA and low LS may have managed to achieve intermediate levels of competitive ability not because they overtopped and shaded target-species individuals but due to a rapid use of soil resources in pots.

Overall, these results seem to agree with what might be expected from the distribution of species across environments in the field. The most competitive species appear to be adapted to productive environments (via low LDMC, low SLA, and large leaves, such as *Cirsium arvense*) while those with low competitive ability

TABLE 2 Statistical summaries of the best trait-based model explaining the competitive effects in a pot experiment of 37 herbaceous species from different temperate vegetation types in Canada (Keddy et al., 2002)

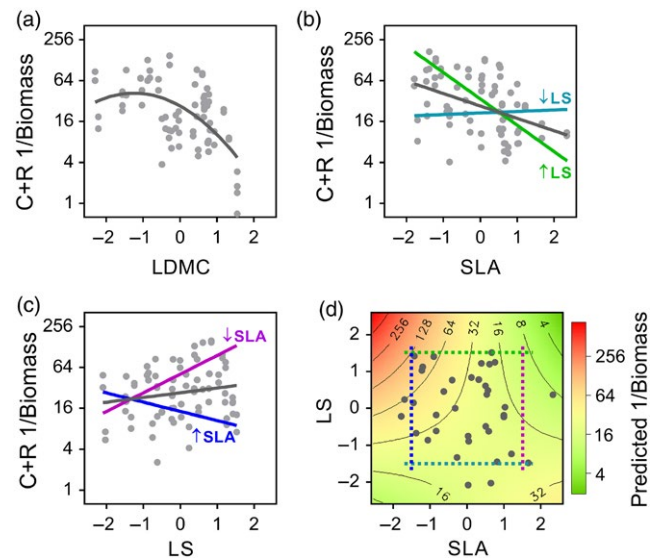


FIGURE 3 Component-plus-residual (C+R) plots illustrating the estimated relationships between trait values and competitive effects on a target species (1/biomass, in log scale) of 37 temperate species in a pot experiment carried out by Keddy et al. (2002) (see model summary statistics in Table 2). Grey lines show predicted values (the linear components) for each of the three traits included in the model (a–c) keeping the remaining traits at their mean standardised value (i.e., zero); grey dots show the sum of the component and the residual corresponding to each of the 37 species. Predictions were averaged across stress treatments since these effects were relatively small and marginally significant. In specific leaf area (SLA) and leaf size (LS) panels (which showed interacting effects), colour lines show predicted values for either high (↑) or low (↓) values of the other trait (i.e., 1.5 standard deviations above or below the mean, respectively). (d) Background colour and contour lines indicate predicted values for SLA–LS combinations; grey dots represent species' trait values and dotted lines are placed at 1.5 standard deviations above or below the mean using the same colour code as in b, c

(characterised by high LDMC, high SLA and large leaves, such as *Carex pensylvanica*) may be better adapted to more restrictive environments. Consistently, the former were mostly collected in open

fields with deep soils whereas the latter were mostly collected in shallow-soils environments (Nielsen, 1993).

4.3 | Strengths, limitations, and future directions

Our approach provides standardised metrics of both univariate and bivariate nonlinear selection, along with widely used estimates of linear selection. We believe this functional flexibility will improve descriptions of trait–performance relationships that may help reveal the “function” in functional traits (McGill et al., 2006; Rolhauser & Pucheta, 2017). Further, standardisation may allow simple comparisons of selection patterns across environments. The homologous research line at the population level has been prolific and has enabled useful meta-analyses describing spatial and temporal patterns of phenotypic selection (Kingsolver et al., 2012). Here, we analysed data from a desert and from a temperate system (which included resource manipulation) and detected important similarities.

First, we found a prevalence of stabilising over disruptive selection. Stabilising selection of competitive ability is largely concordant with the view that traits related to plant competitive ability and productivity should converge towards optimum values in homogeneous environments (Grime, 2006). This stance can be mechanistically sustained on the fundamental morpho-physiological constraints and trade-offs that shape individuals' ability to acquire and retain resources and thus make competitive ability environment-dependent (Aerts, 1999; Austin & Smith, 1989; Tilman, 1990). On the contrary, disruptive selection, and more generally community-level multimodal trait–fitness relationships (Laughlin et al., 2015), require within-site environmental heterogeneity and niche differentiation (Rolhauser & Pucheta, 2017). We thus argue that stabilising trait–competition relationships may be more common than previously realised, particularly in environmentally homogenous sites.

Second, LDMC consistently captured an important component of plant competitive ability that was not accounted for by other traits included in the best models, such as SLA, LS, and plant height. This result seems particularly relevant since LDMC has seldom been considered in studies focused on trait–competition relationships (e.g., Freckleton & Watkinson, 2001; Gaudet & Keddy, 1988; Goldberg, 1996; Gross et al., 2009; Keddy et al., 2002; Kunstler et al., 2016; Rosch et al., 1997; but see Liancourt, Tielborger, Bangerter, & Prasse, 2009). Our findings thus support the notion that different traits measured in the same organ, such as LDMC and SLA, may reflect different ecological functions (Hodgson et al., 2011). Echoing Lande and Arnold (1983), we stress the importance of multiple regression since patterns of explanatory complementarity among traits, like the ones shown here, may go unnoticed in studies that fit models for each trait separately.

Further, considering correlational selection in the temperate species experiment uncovered changes in the functionality of SLA that depended on LS. This pattern may deserve further examination and could as well inspire the revision of other functional relationships. For instance, the linear decomposition of relative growth rate into the effects of SLA, LDMC, leaf thickness, and leaf mass fraction

(Hodgson et al., 2011) could be further refined by allowing for trait–trait interactions. Perhaps, these notions help identify under which circumstances SLA reflects fast plant growth or, alternatively, an adaptation to light deficient conditions (Hodgson et al., 2011).

Our results from the desert-annuals experiment showed that species-level functional traits were useful predictors of individual-level competitive effects and agreed with results from a global study where rectilinear functions were used (Kunstler et al., 2016). These findings illustrate the utility of database-retrieved trait values to explain individual performance in a competitive context, despite the scatter introduced when analysing individuals instead of species. Theoretically, a better understanding of individual-level competitive ability would be achieved using trait values of interacting individuals. However, studies at the individual level might be somewhat limited since many important traits (such as LDMC and SLA) require destructive measurements that may affect individual performance, which may be particularly restrictive for small-sized individuals.

As originally acknowledged by Lande and Arnold (1983), the multiple regression approach “helps to reveal the target(s) of selection, and to quantify its intensity, without identifying the selective agent(s).” Part of the problems that arise when inferring the functional role of traits stem from their natural covariation (Lande & Arnold, 1983; Mitchell-Olds & Shaw, 1987). Trait collinearity results in regression coefficients that are not truly estimated while all other variables remain constant and are thus contingent to the observed structure of phenotypic covariation (Mitchell-Olds & Shaw, 1987). Such contingency would be particularly important for correlative studies if fitness peaks in adaptive landscapes change across environments and in time (see Laughlin & Messier, 2015). Conclusive evidence on the causation of selection needs the addition of experimental manipulations (Mitchell-Olds & Shaw, 1987; Wade & Kalisz, 1990). Manipulations of trait distributions should be aimed at generating uncorrelated phenotypic distributions across all traits, although this may be increasingly difficult as the number of traits increases. Environmental manipulations would help uncover the agent of selection through the analysis of environmental effects on the shape of fitness functions (Wade & Kalisz, 1990). Our analysis of the temperate species experiment showed that the stress treatment did not significantly change the shape of trait–competition relationships, but much more data are needed on this regard. It would be important to bear in mind that experimental manipulations can either be impractical or overly unrealistic, so that research programmes combining both observational and manipulative studies may be most constructive (Keddy, 1989; Kraft et al., 2015; Mitchell-Olds & Shaw, 1987; Tilman, 1989). We propose that selection patterns in such studies can be captured and interpreted using the tools and concepts presented here.

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AUTHORS' CONTRIBUTIONS

A.G.R. conceived the ideas and designed the experiment with input from E.P. and M.R.A.; A.G.R. and M.N. conducted the experiment and collected the data; A.G.R. analysed the data and led the writing of the manuscript. All the authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Mean trait values of desert annuals were published by Rolhauser and Pucheta (2017) and are also available in Appendix S1. Biomass data of *Tribulus* individuals are in Appendix S1. Traits data of temperate herbaceous species are deposited and accessible at the TRY database <https://www.try-db.org/TryWeb/Home.php> (Kattge et al., 2011), while the competitive effects of these species were published by Keddy et al. (2002).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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