

Directional, stabilizing, and disruptive trait selection as alternative mechanisms for plant community assembly

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Abstract. How plant functional traits (e.g., seed mass) drive species abundance within communities remains an unsolved question. Borrowing concepts from natural selection theory, we propose that trait–abundance relationships can generally correspond to one of three modes of trait selection: directional (a rectilinear relationship, where species at one end of a trait axis are most abundant), stabilizing (an n-shaped relationship), and disruptive (a u-shaped relationship). Stabilizing selection (i.e., the functional convergence of abundant species) would result from positive density-dependent interactions (e.g., facilitation) or due to generalized trade-offs in resource acquisition/use, while disruptive selection (i.e., the divergence of abundant species) would result from negative density-dependent interactions (e.g., competition) or due to environmental heterogeneity. These selection modes can be interpreted as proxies for community-level trait–fitness functions, which establish the degree to which traits are truly “functional”. We searched for selection modes in a desert annual-plant community in Argentina (which was divided into winter and summer guilds) to test the hypothesis that the relative importance of disruptive mechanisms (competition, disturbances) decreases with the increase of abiotic stress, a stabilizing agent. Average density was analyzed as a function of eight traits generally linked to resource acquisition and competitive ability (maximum plant height, leaf size, specific leaf area, specific root length), resource retention and stress tolerance (leaf dissection, leaf dry matter content, specific root volume), and regeneration (seed mass) using multiple quadratic-regression models. Trait selection was stabilizing and/or directional when the environment was harshest (winter) and disruptive and/or directional when conditions were milder (summer). Selection patterns differed between guilds for two important traits: plant height and seed mass. These results suggest that abiotic stress may drive within-community functional convergence independently of the trait considered, opposing the view that some traits may be inherently convergent while others divergent. Our quadratic model-based approach provides standardized metrics of both linear and nonlinear selection that may allow simple comparisons among communities subjected to contrasting environmental conditions. These concepts, rooted in natural selection theory, may clarify the functional link between traits and species abundance, and thus help untangle the contributions of deterministic and stochastic processes on community assembly.

Key words: *abiotic stress; community-level fitness function; environmental filtering; functional divergence; functional traits; limiting similarity; natural selection; phenotypic selection; plant strategies; trait–abundance relationship; Tweedie compound Poisson distribution.*

INTRODUCTION

Community assembly is generally thought to depend on the interplay between stochastic and deterministic niche-based processes, although debate persists on the conditions that determine their relative importance (Chase 2014). One particular point to further the debate is to increase our understanding of how functional traits affect species abundance in local communities (Cornwell and Ackerly 2010, Shipley 2014). Such an understanding

would arise from a framework that enables the formulation of general predictions on the functional relationship between traits and abundance. In particular for plants, an attempt in this direction has been made by Leishman and Murray (2001) who examined the predictions of four models of vegetation dynamics and species coexistence. However, resulting predictions were limited to rectilinear relationships and to the use of seed size as the sole predictor (Leishman and Murray 2001). Further, trait–abundance relationships are relevant to the evaluation of functional diversity and its link with assembly processes (Mason et al. 2005, Mouchet et al. 2010, de Bello 2012). In this case, only curvilinear relationships have been considered, the extremes being unimodal (or n-shaped) for a community showing trait convergence and low functional diversity, and bimodal (or u-shaped)

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for a community showing trait divergence and high functional diversity (Mason et al. 2005). Based on concepts borrowed from natural selection theory, we propose a framework applicable to any functional trait, and whose predictions include both rectilinear and curvilinear (n- and u-shaped) relationships.

Community-level selection modes: a quadratic approach to trait–abundance relationships

Natural selection is understood here as the differential probabilities of survival and reproduction of individuals (i.e., the components of individual fitness) that are associated to the phenotypic characteristics of those individuals (Lande and Arnold 1983, “phenotypic selection” sensu Endler 1986). Such phenotypic characteristics are the particular values taken by a “functional” trait, i.e., a measurable property of plants that determines fitness (McGill et al. 2006, Violle et al. 2007, Shipley et al. 2016), while “fitness” is an individual’s contribution to population growth (McGraw and Caswell 1996). Classical, population-level theory proposes that natural selection can act in three different ways or “modes” upon a functional trait: directional (individuals with values at one end of the functional trait are favored), stabilizing (individuals with intermediate trait values are favored), or disruptive (both ends are favored) (Endler 1986). Directional selection can occur jointly with either stabilizing or disruptive selection, shifting the maximum or minimum (respectively) away from the average trait value, while “pure” directional selection would be the particular case when such maxima/minima occur at the extremes or even outside the range of observed trait values (Endler 1986). Evolution is a possible (and the most studied) consequence of these processes at the population level (Endler 1986).

An important tenet for our framework is that natural selection acts on individuals’ phenotypes independently of their breeding relationship (i.e., whether they are from the same or from different species), so it can also have consequences at the community level (Shipley 2010, Vellend 2010). When individuals correspond to different species, natural selection modes may affect the abundance of trait values that correspond to those species, i.e., the dynamics of community assembly (Shipley 2010, Vellend 2010). It would thus be reasonable to expect trait–fitness relationships (or fitness functions) for the community level (Shipley et al. 2016), and we propose that these correspond to one of the possible selection modes. Nonetheless, linking individual fitness to species abundance requires assumptions about population dynamics (Shipley 2010). Following Shipley et al. (2016), we assume a positive relationship between individual fitness and population size, which holds as long as mass effects are limited (i.e., the immigration from other community types having different selecting mechanisms, see e.g., Shmida and Ellner 1984). Under these assumptions, the general shape of trait–fitness relationships

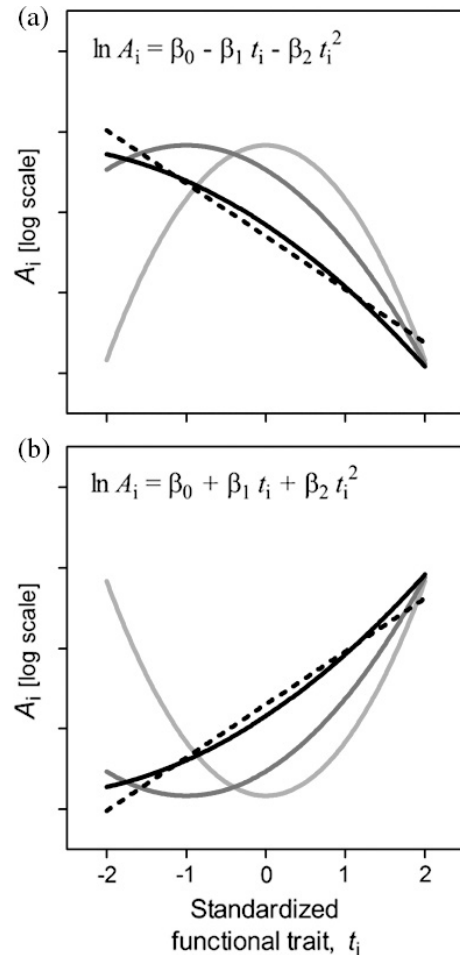


FIG. 1. Trait–abundance relationships according to three community-level natural selection modes: stabilizing, disruptive, and directional. Stabilizing (panel a) and disruptive (panel b) modes occur when intermediate trait values are either most or least favored, respectively. These patterns would be detected by either a negative or a positive quadratic coefficient (β_2) being significant in a linear regression model; equations are shown inside panels. Abundance (A_i) was modeled here as Poisson-Gamma distributed, and thus shown on a log scale. Directional selection (black lines) occurs when the optimum value lies at one extreme or even outside the range of observed phenotypes, and this may be best approximated statistically by a straight (dotted) line. Light grey curves illustrate “pure” stabilizing/disruptive patterns, i.e., when parameter β_1 is close to zero. Both β_1 and β_2 being significant would indicate a combination of directional and stabilizing or disruptive selection (dark grey lines).

characteristic of each selection mode would be respectively transferred into trait–abundance relationships (Fig. 1). Our log-linear approach would be analogous to maximum entropy models applied to community assembly (although they are not mathematically equivalent, see Warton et al. 2015). While maximum entropy models were primarily set to predict species relative abundance along environmental gradients (e.g., Shipley et al. 2011, Sonnier et al. 2012), the focus here lies on the particular shapes and possible causes of within-community trait–abundance relationships.

Underlying mechanisms: links to community assembly processes

Mechanisms leading to a particular community-level selection mode have not been explicitly addressed in the literature. Nonetheless, we can build on knowledge regarding the contrast between stabilizing and disruptive selection at the population level, and on ideas linking natural selection to community assembly. Within a population, stabilizing (or optimizing) selection can result from positive density-dependent interactions (e.g., facilitation) or when two or more antagonistic selecting agents determine trade-offs in resource acquisition and/or use (Travis 1989, Devaux and Lande 2010). Causes of disruptive (or divergent) selection include negative density-dependent interactions (e.g., competition) and environmental heterogeneity (Rueffler et al. 2006). Importantly, evolutionary biologists recognize that a single trait can be subjected to either stabilizing or disruptive selection, an outcome that depends on the particular ecological context of populations (Kingsolver and Pfennig 2007).

Natural selection has been thought to underlie assembly rules and the resulting trait convergence or divergence in communities (Keddy 1992, Weiher and Keddy 1995, Shipley 2010, Grime and Pierce 2012). Abiotic factors are generally accepted to filter out maladapted species and consequently drive trait convergence (see Kraft et al. 2015 for a recent review). Moreover, Weiher and Keddy (1995) proposed that competitive traits should diverge in productive environments; such “limiting similarity” would be the result of competitive exclusion among pairs of similar species. Further, Vellend (2010) recognized that selection among co-occurring species can be density dependent, either positive or negative. Echoing population-level mechanisms, competition may therefore lead to the divergence of the most abundant species in a community, i.e., community-level disruptive selection (see also Moullot et al. 2007 for a similar prediction based on the concept of limiting similarity).

In contrast, Grime (2006) proposed that competitive, productivity-related plant traits (leaf longevity, specific leaf area) should converge towards optimum values in communities, while regenerative, disturbance-related traits (such as seed size and shape) should diverge (see also Shmida and Ellner 1984). A key assumption behind this idea is that determinants of productivity (e.g., soil fertility and topography) are homogeneous over the area occupied by a community, while disturbances would generate heterogeneity at a finer scale (Grime 2006). Supporting both contrasting views, recent applications of coexistence theory pointed out that competition may cause either functional convergence (through “fitness differences”) or divergence (through “niche differences”, Mayfield and Levine 2010), although this conflict may be scale-dependent since, for instance, the divergent view of

competition implies resource partitioning in a heterogeneous habitat (Adler et al. 2013).

Hypothesis and predictions for a desert annual-plant community

We searched for patterns of stabilizing, disruptive, and directional trait selection in an annual-plant community located in central-northern Monte Desert, Argentina. The community can be divided into winter and summer guilds, and water deficit appears to be larger for the former (Rolhauser and Pucheta 2016). Although mass effects from different community types could occur towards the site (mostly from neighboring hills), such events involve only a few very rare annual species which were not considered in this study (Rolhauser 2015). Within this community, we have measured eight functional traits generally linked to resource acquisition and competitive ability (maximum plant height, leaf size, specific leaf area, specific root length), resource retention and stress tolerance (leaf dissection, leaf dry matter content, specific root volume), and regeneration (seed mass; see e.g., Pérez-Harguindeguy et al. 2013). Based on the ideas listed previously, we hypothesize that the relative importance of disruptive mechanisms (competition and/or disturbances) decreases with the increase of abiotic stress, which is a stabilizing agent independently of the trait considered. Here we imply that competition would be less important under higher abiotic stress, which would hold if water is the limiting resource (likely in our study site) and when the observed response is related to community structure (Goldberg and Novoplansky 1997). This predicts that stabilizing patterns will be more evident in winter (the harshest season), while disruptive patterns may occur in summer, particularly for competitive and/or disturbance-related traits.

Functional diversity indices have been proposed as tools for detecting community assembly patterns (Mouchet et al. 2010, de Bello 2012, Spasojevic and Suding 2012). In a simulation exercise, functional divergence (FDiv) was found to be particularly appropriate when abundance data are available (Mouchet et al. 2010). FDiv measures the degree to which the most abundant species possess extreme trait values, an indication of diversified ecosystem functions (de Bello et al. 2010, Mouchet et al. 2010). Stabilizing, directional, and disruptive selection modes should be respectively associated with low, intermediate, and high FDiv. We thus expect FDiv to be lower in winter than in summer.

Adding complexity, evolutionary biologists have long recognized that natural selection may often act upon sets of related traits (Lande and Arnold 1983, Schluter and Nychka 1994). Following the basic approach proposed by Lande and Arnold (1983), we evaluated whether multivariate trait axes were subjected to community-level selection modes, and whether these were better descriptors of species abundance than single functional traits.

MATERIALS AND METHODS

Study site

Our study was conducted in Médanos Grandes sand field, San Juan, Argentina (31°43'18" S, 68°08'17" W; 576 m of elevation), which is one of the driest areas of the Monte Desert (see e.g., Roig et al. 2009). Details of the study site (~20 ha) are described in depth in Rolhauser and Pucheta (2016). Briefly, mean temperature is 27.0°C in January and 7.9°C in July, and mean annual precipitation is 92 mm, peaking in summer. Water balance, calculated from rainfall, temperature, and solar irradiance data, appears to be more favorable in summer than in winter (Rolhauser and Pucheta 2016). Topography is nearly flat, and soil is sandy. Land use comprises extensive goat farming with very low effective stock density. The vegetation is an open shrubland dominated by *Bulnesia retama* (Zygophyllaceae), which covers about 15% of the study site. Winter annuals grow mostly underneath shrub canopies, whereas summer annuals can also be abundant in the open spaces among shrubs (Rolhauser and Pucheta 2016). Both soil characteristics and vegetation are fairly homogeneous across the site.

Plant density and functional traits data

Our approach consisted of relating average trait values of annual species to their site-average density (i.e., a measure of population size). Plant-density data were collected from a livestock-exclusion experiment installed in autumn 2009 (Rolhauser and Pucheta 2016). This experiment had a split-plot design, in which the presence of livestock (fenced and unfenced) was the main factor, and microsite type (shrub understory and open spaces) was the subordinate factor, with 20 replicates for each combination of factors (for a total of 80 selected microsites). Each fenced and unfenced plot (10 × 10 m) included an adult of *Bulnesia retama* (i.e., shrub microsite) and a surrounding area without shrubs (i.e., open microsite; see details in Appendix S1). In each selected microsite, we laid out a 50 × 50 cm permanent frame where we counted the number of plants per annual species. We visited the frames 18 times between August 2010 and April 2013 (2010: August, September, November, December; 2011: February, April, June, August, November, December; 2012: February, April, September, October, November, December; 2013: February, April), i.e., covering three complete growing seasons hereafter referred to as “years”.

We collected functional traits data for all species following standardized protocols (Pérez-Harguindeguy et al. 2013). For foliar and root traits, we collected 10 healthy individuals per species. 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. For each species, we looked for individuals of similar size across the whole study area; all individuals of each species were

collected on the same day. Individuals were collected with most of their roots and were processed within 24 h after adequate rehydration. All intact leaves from each individual were weighed fresh and immediately scanned using a flatbed scanner under 300-dpi resolution. All roots with diameters between approximately 0.01 and 0.1 mm were collected from each individual and scanned. After scanning, roots and leaves were oven-dried at 60°C for at least 72 h and then weighed. We took morphometric measurements of fresh roots and leaves (length, width, perimeter, and area) using ImageJ (Schneider et al. 2012). With these quantities, we obtained individual values of leaf size (LS, area), leaf dissection (LD, perimeter/√area), specific leaf area (SLA, area/dry weight), leaf dry matter content (LDMC, fresh weight/dry weight), specific root length (SRL, length/dry weight), and specific root volume (SRV, volume/dry weight).

To estimate seed dry mass (SM), we harvested seeds from at least 8 individuals per species. Harvested seeds were oven-dried at 60°C for at least 96 h and then weighed. We also obtained data on maximum plant height (*H*) from field measurements. Overall, we compiled information of eight functional traits that characterized 14 winter and 18 summer species. For the analyses below, individual trait values were averaged to obtain a single trait value per species (see data table in Appendix S2).

Data analysis

We calculated a single average density for each species in each year on record. Previous results showed negligible effects of livestock on plant density (Rolhauser and Pucheta 2016), so we did not distinguish between levels of livestock exclusion. Thus, average density (*D*, number of individuals per frame) for species *i* and year *j* was calculated as

$$D_{ij} = \frac{\sum_{s=1}^m \sum_{v=1}^n d_{sv}}{mn} 0.15 + \frac{\sum_{o=1}^m \sum_{v=1}^n d_{ov}}{mn} 0.85$$

where d_{sv} and d_{ov} are the number of individuals under shrub *s* and in open space *o* at visit *v*, 0.15 and 0.85 are relative weights given to observations of shrub and open microsities respectively (accounting for their overall cover); *m* is the total number of frames surveyed for each microsite type (i.e., 40) and *n* is the total number of visits within a year.

Based on methods used by evolutionary biologists (Lande and Arnold 1983), we evaluated patterns of trait selection (Fig. 1) using quadratic multiple regression implemented as mixed Poisson-Gamma models, i.e., a type of generalized linear mixed model (Zhang 2013). The Poisson-Gamma distribution (also known as Tweedie compound Poisson, Zhang 2013) is a subclass of the exponential dispersion family in which the power (or “index parameter”, *p*) of the mean-variance relationship (Variance function_(mean) = mean^{*p*}) lies in the interval (1; 2); *p* = 1 corresponds to the Poisson distribution, and *p* = 2 to the Gamma distribution (Dunn and Smyth

2005). This compound distribution has mass at zero and support on the non-negative reals (Dunn and Smyth 2005). It is thus suitable for modeling our response variable (D_{ij}), which has non-integer positive values and exact zeros.

We fitted quadratic multiple mixed Poisson-Gamma models separately for winter and summer species using the function `cplmm` of the package `cplm` in R (Zhang 2013). D_{ij} was modeled (through a log link function) as a function of standardized traits (to zero mean and unit variance, ln-transformed prior to analyses) included as fixed effects, while species identity and year were included as normally distributed random intercepts. We performed a backward selection process (similarly to Sonnier et al. 2012) in which the least important fixed term was removed at each step from a full, initial model, until no terms remained (except for the intercept; the random part was the same for all models). Initial models contained both linear and quadratic terms of functional traits, and linear terms were removed only if the corresponding quadratic term was previously removed (because quadratic terms need to be evaluated in the presence of the corresponding linear term, see e.g., Lande and Arnold 1983). Importance of model terms was evaluated according to marginal likelihood ratio tests (Zhang 2013), i.e., when the effects of the remaining terms in the model were already accounted for. The resulting models were ranked using the second-order Akaike information criterion (AIC_c) which is recommended for small samples such as ours; the best model would be the one with the smallest AIC_c (Burnham and Anderson 2002). AIC_c values were calculated using the package `AICcmodavg` in R (Mazerolle 2016). Further details on methods and results of the backward processes can be found in Appendix S4.

Trait-abundance relationships were illustrated using component-plus-residual plots, also known as partial residual plots (e.g., Fox and Weisberg 2011). Partial residuals for trait t were formed by adding the fitted linear component for this predictor (i.e., $\exp[\beta_0 + \beta_1 t + \beta_2 t^2]$, Fig. 1) to the residuals of the full model. These plots allowed us illustrating inter-annual variation of average density around fitted values while conserving the original (standardized) variation of functional traits.

We described multivariate functional variation of winter and summer species using principal component analyses based on the eight ln-transformed traits. Resembling Lande and Arnold (1983)'s approach, we used the first four principal components (hereafter referred to as "composite traits") as predictors of average density in quadratic multiple mixed Poisson-Gamma models (retained axes had eigenvalues larger than one, according to the Kaiser-Guttman criterion (see e.g., Borcard et al. 2011), except for the fourth principal component of summer species, see Appendix S3). Together, these composite traits accounted for 86% and 83% of total variation, respectively, for winter and summer species (Appendix S3: Table S2). Model selection was performed as noted previously (see details in Appendix S4).

We calculated FDiv modifying the method proposed by Vileger et al. (2008), which is generalized for a multi-dimensional trait space. Because we aim to provide a measure of FDiv for each partial regression curve (i.e., a selection pattern for a given trait), we need to consider that each regression curve is found after the effects of the remaining traits in the model were already accounted for. Thus, two modifications were needed (see full details in Appendix S5): (1) we calculated FDiv separately for each trait in the model, (2) for which we used, instead of observed abundances, the abundances predicted by each trait while holding the remaining traits constant. These predicted abundances are the same fitted linear components used to construct the component-plus-residual plots (i.e., the predicted abundance of species i considering trait t was calculated as $\exp[\beta_0 + \beta_1 t_i + \beta_2 t_i^2]$). We refer to this measure as predicted functional divergence, pFDiv.

RESULTS

Within winter species, the best model built on single functional traits combined H , SM, SLA, and LDMC, in decreasing order of importance (Table 1). Trait-abundance relationship for H was consistent with a combination of stabilizing and positive directional selection, while a combination of stabilizing and negative directional selection was found for SM (Fig. 2). In addition, selection for winter species appeared to be directional towards lower SLA and higher LDMC (Fig. 2). By contrast, composite traits were not significantly related to winter species average density (Appendix S4: Fig. S1).

The best model explaining average density of summer species combined SM, LDMC, LS, SRL, and SLA, in decreasing order of importance (Table 1). Trait-abundance relationships for both SM and SLA were consistent with disruptive selection (Fig. 2). Selection patterns of LDMC, LS, and SRL were directional towards higher values (Fig. 2). The best model built on composite traits did not provide a better description of average density than that built on single functional traits; hence, details of the former will not be discussed further (Appendix S4: Fig. S2).

Predicted functional divergence (pFDiv) was lowest for the most intense stabilizing pattern, i.e., H of winter species, for which the quadratic coefficient (β_2) was -1.379 and pFDiv was 0.370 (Table 1; Fig. 2). Concomitantly, pFDiv was highest for the most intense disruptive pattern, i.e., SM of summer species, for which $\beta_2 = 1.737$ and pFDiv = 0.988 (Table 1; Fig. 2). For those traits showing pure directional patterns, there was a positive relationship between the linear coefficient (β_1) and pFDiv (Pearson's correlation = 0.94 , $p = 0.06$, $n = 4$); the largest β_1 (1.653), corresponding to LS of summer species, was associated with a relatively high pFDiv (0.911 ; Table 1; Fig. 2).

DISCUSSION

Significant trait-abundance relationships found here support the view that non-random trait-based processes

TABLE 1. Statistical summaries of the best multiple mixed Poisson-Gamma models linking functional traits to species abundance (average number of individuals per 50 × 50 cm frame) for winter and summer annual species registered in a site within the Monte Desert (Argentina).

Guild	Trait	χ^2	df	P value	Coefficient	Estimate	SE	χ^2	P value
Winter species	<i>H</i>	26.20	2	<0.0001	Linear	0.780	0.207	11.66	0.0006
					Quadratic	-1.379	0.190	26.20	<0.0001
	SM	16.99	2	0.0002	Linear	-0.632	0.186	9.89	0.0017
					Quadratic	-0.718	0.162	15.65	0.0001
					SLA	7.22	1	0.0072	Linear
LDMC	4.72	1	0.0298	Linear	0.384	0.167	4.72	0.0298	
Summer species	SM	14.37	2	0.0008	Linear	-0.552	0.537	0.96	0.3261
					Quadratic	1.737	0.462	10.87	0.0010
	LDMC	8.93	1	0.0028	Linear	1.217	0.360	8.93	0.0028
					LS	8.08	1	0.0045	Linear
	SRL	7.86	1	0.0051	Linear	1.373	0.446	7.86	0.0051
	SLA	8.46	2	0.0146	Linear	-0.653	0.391	2.62	0.1053
					Quadratic	1.251	0.409	7.86	0.0051

Notes: *H*, plant height; SM, seed mass; SLA, specific leaf area; LDMC, leaf dry matter content; SRL, specific root length; SRV, specific root volume; LS, leaf size. Functional traits in each model appear in decreasing order of significance (according to Chi-Square likelihood ratio tests, LRT), pooling the effects of both linear and quadratic terms if applicable. Estimates, SE, and LRT are also shown for each coefficient (Fig. 1).

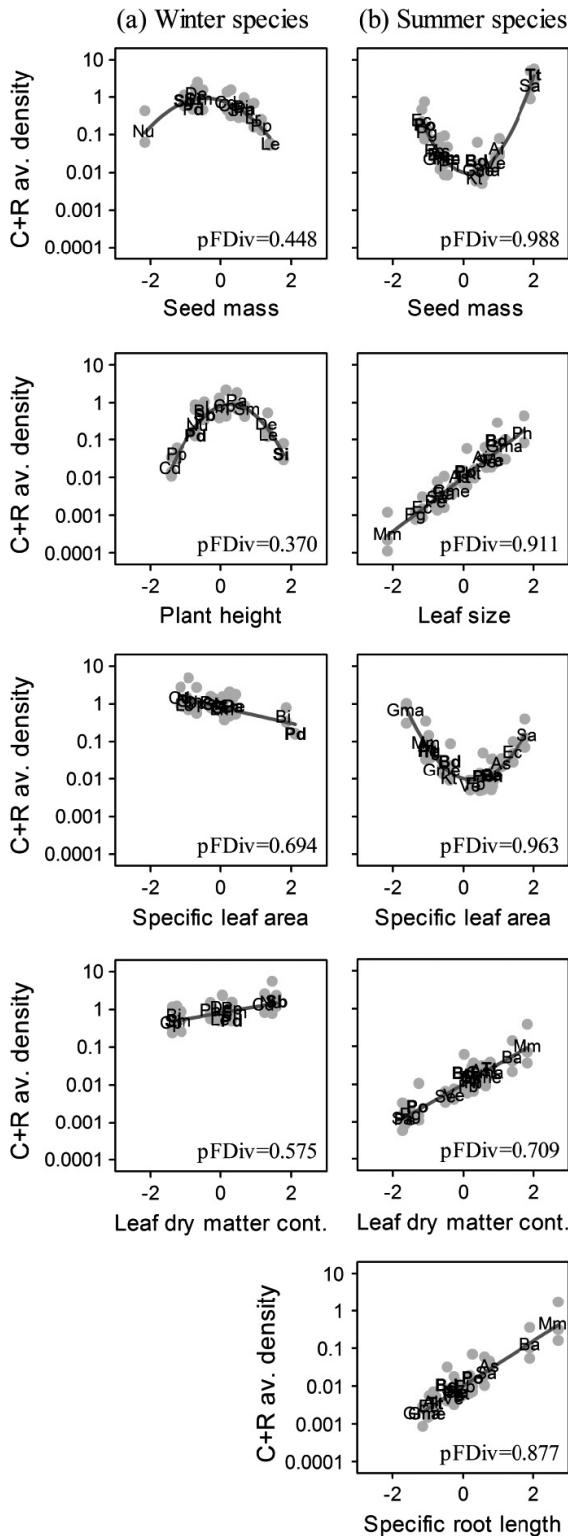
affect species abundance at a local scale (Cornwell and Ackerly 2010). Overall, single functional traits were better descriptors of species abundance than composite traits. Possibly, composite traits may be masking the effects of single traits, which may be more tightly related to plant performance (see also Spasojevic and Suding 2012, and see e.g., Angert et al. 2009 for an example of opposite results). Further, the shift in selection patterns between winter and summer guilds found for SM and SLA opposes the view that some traits may be inherently convergent while others divergent in communities (see also Bernard-Verdier et al. 2012, Adler et al. 2013). Instead, our results support the general premise of Weiher and Keddy (1995)’s model, in that severe environments (in our case, winter) would promote within-community functional convergence, while less severe environments (in our case, summer) may allow for strategy divergence. These results also agree with those of evolutionary studies (summarized by, for instance, Kingsolver and Pfennig 2007) in that a single trait can be subjected to either stabilizing or disruptive selection, and we propose that this outcome may depend on the level of abiotic stress. While some studies arrived to similar conclusions (e.g., Mason et al. 2012), others claim that patterns are strongly contingent on both trait and environment (Bernard-Verdier et al. 2012). Given the great diversity of plant species and habitats and the scarcity of empirical evidence on trait functionality, we support the quest for more data on trait-abundance relationships to develop general trait-based predictions (Shipley et al. 2016).

Traits explaining annual-plant species abundance

Four traits characterizing whole plants, seeds, and leaves were required to explain species abundance in

winter (i.e., *H*, SM, SLA, and LDMC), while five traits characterizing seeds, leaves, and roots were required in summer (i.e., SM, LDMC, LS, SLA, and SRL). A recent review showed that 4–8 traits were sufficient to predict plant community structure, and that traits from multiple organs were usually required (Laughlin 2014). In our study, the occurrence of succulence (i.e., species with low SLA and LDMC) weakens the correlation between SLA and LDMC (Appendix S3: Table S1), and this allowed both variables to have significant unique contributions. Further, the high correlation between *H* and LS in summer species determined the exclusion of the former from the best model. These results illustrate that measuring traits from multiple organs does not necessarily ensure explanatory dividends and that some degree of organ related redundancy may be needed.

The most abundant winter species were characterized by intermediate-to-high *H*, intermediate-to-low SM, and sclerophyllous leaves (i.e., low SLA and high LDMC). Seed mass trades off with seed output and may thus reflect a compromise between patch occupation and successful establishment in the face of hazards, such as drought and competition (Westoby et al. 2002). Also, large seeds would be more prone to predation (Thompson et al. 1993). Further, maximum height may confer competitive ability as light becomes limiting (e.g., Westoby et al. 2002), while a prostrate growth can benefit desert annual plants in winter by keeping aerial parts near the ground, where air temperature is higher (Mulroy and Rundel 1977). Annual plants in our study site concentrate under the shade of *Bulnesia* shrubs during winter, when freezing temperatures are frequent (Rolhauser and Pucheta 2016). Our results would thus suggest that forces selecting for small or large seeds (possibly granivory and drought, respectively) and for high or low stature



(possibly competition under shaded conditions and cold stress, respectively) may have roughly balanced one another. Such harsh environmental conditions may also explain the relative success of sclerophyllous species.

FIG. 2. Component-plus-residual (C + R) plots illustrating the estimated relationships between traits and average density (number of individuals per 50×50 cm frame; see Table 1) for 14 winter- (a) and 18 summer- (b) annual species registered in a site within the Monte Desert (Argentina). Lines show predicted values (the linear components) while each grey dot shows the sum of the component and the residual corresponding to each observation (i.e., there were three annual average density values for each species); species codes are plotted at the average of the three values. Height and leaf size panels were matched since they were highly correlated. Species codes are the first letters of the genus and the specific epithet (Appendix S2). Exotic species are shown in bold. The corresponding predicted functional divergence (pFDiv) is shown inside each panel.

Within summer annuals, selection patterns of SM and SLA changed to disruptive. Unlike winter, soil surface during summer can be completely covered by annuals, making space occupancy and competition more important. In these conditions, if SM and SLA are somehow correlated with competitive ability (see e.g., Pérez-Harguindeguy et al. 2013), the co-dominance of such contrasting strategies (i.e., small- vs. large-seeded species, and low- vs. high-SLA species) would require them to be spatially or temporally segregated (Shmida and Ellner 1984). For instance, *Allionia incarnata* (large-seeded) appears to be restricted to soil depressions and ephemeral streams, while *Bouteloua aristoides* (small-seeded) can be abundant in higher (likely dryer) microtopographic positions, although these patterns still need to be explicitly quantified. Our results also suggest that possessing larger leaves (which maximize light interception efficiency, see e.g., Westoby et al. 2002), higher SRL (i.e., fine, likely fast-growing roots, Eissenstat 1997), or higher LDMC (i.e., tougher leaves) may be alternative strategies that yield high abundance in crowded and hot summer conditions.

Strengths, limitations and future directions

Our framework and results stress that curvilinear relationships need to be considered when relating functional traits to species abundance. Perhaps, this contributes to explain the lack of strength in linear correlations between seed size and abundance found in the literature by Leishman and Murray (2001). Further, we showed that steep linear selection gradients, i.e., the dominance of a single extreme strategy, can determine a high FDIV. We thus suggest that FDIV should not be directly taken as a measure of diversified ecosystem functions when communities are subjected to strong directional selection.

Our quadratic regression approach has several limitations, many of which were intensively discussed in the field of evolutionary biology. For instance, interactions among traits were not considered in our models due to insufficient degrees of freedom. Interactions between linear terms (i.e., the cross-product regression coefficients) are particularly interesting for evolutionary biologists because they measure nonlinear selection acting on trait pairs, which is known as correlational selection (Brodie et al. 1995, Blows and Brooks 2003, Kingsolver et al. 2012). Thus, we did not

detect whether community-level selection on one trait depended on the values of other traits, while we underestimated the overall strength of nonlinear selection (see Blows and Brooks 2003). Since the number of cross-product coefficients grows quadratically with the number of traits, achieving such goals would require collecting an adequate sample size (which would be limited by local species richness) as well as minimizing the number of traits without compromising trait-space dimensionality (see Laughlin 2014). Yet, as we discussed above, it may be difficult to anticipate which traits will explain species abundance despite the correlations among them.

Fitting quadratic functions provides standardized metrics of selection strength, i.e., linear and quadratic coefficients (Lande and Arnold 1983, Brodie et al. 1995). However, such interpretability comes at the expense of lack of flexibility in fitting observed data; true fitness functions (and surfaces) may be much more complex, with multiple “peaks” and “valleys” (Brodie et al. 1995, Kingsolver et al. 2012). As suggested for population-level fitness functions, complexities in trait–abundance relationships may be better fitted using smoothing techniques, such as nonparametric generalized additive models (Schluter and Nychka 1994). Perhaps, future community-level studies may benefit from reporting both selection coefficients and nonparametric fitness functions; the former may allow simple comparisons among communities (e.g., along environmental gradients) while the latter may help account for the specific subtleties of study cases (see also Kingsolver et al. 2001).

By providing a framework for trait–abundance relationships, our approach may help reinforce one of the loose foundation stones in trait-based plant ecology, i.e., the degree to which traits determine individual fitness (Shipley et al. 2016). As we did here following Shipley et al. (2016), trait functionality could be judged using density as a proxy for average individual fitness assuming that mass effects are limited. This assumption could be relaxed by broadening the scale of the study and including landscape-scale species abundances into log-linear models as a meta-community “prior” (Warton et al. 2015).

Most importantly, our framework has an implication that can be crucial in the search for trait functionality. Although it is now widely accepted that functional traits are those that influence individual performance and fitness (following definitions by McGill et al. 2006, Violle et al. 2007), it is not entirely clear which shapes such functional relationships could take. Handbooks for standardized measurements (see Pérez-Harguindeguy et al. 2013 for the most recent version) interpret functional traits as “indicators” of plant function, i.e., whether they are positively or negatively correlated with a fitness component. Since these handbooks are comprehensive summaries of traits’ ecological significance, this may suggest a common implicit directional assumption of trait functionality in the literature. For instance, Gibert et al. (2016) used more than 500 linear correlations (carried out at various scales, in observational and manipulative

studies) to look for generalities in the relationship between traits and plant growth. Conversely, a recent model-based approach to plant community assembly found that conceiving within-community multimodal trait distributions can improve predictions of species abundances along environmental gradients (Laughlin et al. 2015). Concordantly, our framework stresses that traits need not be linearly correlated with individual fitness to be functional; nonlinear relationships should also be expected. This novel framework, rooted in natural selection theory, may clarify the functional link between traits and species abundance in communities and thus help untangle the contributions of deterministic and stochastic processes on community assembly.

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