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Abstract

Despite much research over the past 30 years, there is still little general understanding of how the outcomes of interactions vary along environmental gradients, particularly at large geographic scales. A simple expectation is that decreasing environmental quality should reduce densities of competitors and hence the effects of competition should weaken in poorer environments. A counterintuitive consequence is that associations between densities of competitors might change from negative to positive as environments decrease in quality. Here we test these predictions in a set of vascular plant communities where perennial species share space and resources with less competitive annuals. We surveyed nine gray dune communities annually for 5 years along a cross-European latitudinal gradient of habitat quality. We find that densities of annual and perennial species are negatively correlated at the high-quality end of the gradient, while at the low-quality end, guild densities are uncorrelated or positively correlated, consistent with a weakening of competition linked to increasing environmental limitations. Our results suggest that even simple interactions can give rise to nonobvious changes in species associations along environmental gradients. They highlight that understanding the outcome of species interactions may require explicit characterization of their changing intensity with environmental quality and that the factors limiting species' codistribution can vary along environmental gradients.

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Complex Relationships between Competing Guilds along Large-Scale Environmental Gradients

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ABSTRACT: Despite much research over the past 30 years, there is still little general understanding of how the outcomes of interactions vary along environmental gradients, particularly at large geographic scales. A simple expectation is that decreasing environmental quality should reduce densities of competitors and hence the effects of competition should weaken in poorer environments. A counterintuitive consequence is that associations between densities of competitors might change from negative to positive as environments decrease in quality. Here we test these predictions in a set of vascular plant communities where perennial species share space and resources with less competitive annuals. We surveyed nine gray dune communities annually for 5 years along a cross-European latitudinal gradient of habitat quality. We find that densities of annual and perennial species are negatively correlated at the high-quality end of the gradient, while at the low-quality end, guild densities are uncorrelated or positively correlated, consistent with a weakening of competition linked to increasing environmental limitations. Our results suggest that even simple interactions can give rise to nonobvious changes in species associations along environmental gradients. They highlight that understanding the outcome of species interactions may require explicit characterization of their changing intensity with environmental quality and that the factors limiting species' codistribution can vary along environmental gradients.

Keywords: competition, plant-plant interactions, environmental gradient, density patterns, species distribution, environmental change.

Introduction

The question of how plant communities change with disturbance, habitat quality, or climate is fundamental to plant ecology (Tilman 1988; Keddy 2001; Grime 2002) and has

recently come into sharp focus in the context of global environmental change. Many evolutionary, historical, and ecological factors determine whether a species will occur at a specific location (HilleRisLambers et al. 2012). At large scales, variation in environmental conditions determines the limits to the distributions of species or communities in two ways: either directly by filtering out unsuited species or indirectly via changing biotic interactions, which will in turn influence species abundances (Suttle et al. 2007). Interactions can play a dominant role in defining species spatial patterns (Gilman et al. 2010; Wisz et al. 2013), and recent studies have shown that including them in models for species distributions could generate significant departures from predictions yielded by models driven solely by environmental variables. (Araújo and Luoto 2007; Araújo and Rozenfeld 2014; Ockendon et al. 2014). However, routinely integrating species interactions into larger-scale predictions of the effects of environmental change is problematic, because the question of how interactions drive community structure in changing environments remains one of the thorniest in plant ecology (Tylianakis et al. 2008; Wisz et al. 2013).

A powerful approach to investigate the potential impact of changing environmental conditions on plant communities is to study their dynamics along gradients of environmental quality (Fukami and Wardle 2005; Blois et al. 2013). However, in general, the population-level outcomes of interactions in changing environmental conditions are not simple to predict and have been the subject of much study and discussion in ecology (Tylianakis et al. 2008; Olsen et al. 2016).

The issue of how plant interactions vary along environmental gradients has been studied through at least three significant strands of the literature. First, Tilman (1988) and Grime (2002) theorize how environmental constraints and competition determine the characteristics of co-occurring plant species. One of the main areas of disagreement between the two viewpoints concerns the role of competition in stressed, low-productivity habitats (Craine 2005). Grime

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posits that in those harsh environments, competition is unimportant and species presence depends on their ability to cope with disturbance. Conversely, Tilman suggests that it is primarily competition for nutrients that determines which species coexist in low-productivity habitats. These two views have sparked a long-lasting debate and have formed the basis for many empirical studies (Shipley and Peters 1990; Campbell and Grime 1992; Grime et al. 1997; Buckland and Grime 2000; Fargione and Tilman 2006). However, there is little consensus emerging from this work (Craine 2005, 2007; Grime 2007; Tilman 2007).

A second line of work has considered how diversity varies along environmental gradients, particularly productivity gradients resulting from varying environmental quality (Michalet et al. 2006). The underlying assumption is that the intensity of both facilitative and competitive processes varies with community biomass along the gradient of environmental quality. Whether positive or negative interactions dominate influences how frequently competitive exclusion occurs and therefore has an impact on diversity. An increasing body of literature now suggests that interactions can play a significant role in shaping diversity patterns (Michalet et al. 2006; Brooker et al. 2008; Xiao et al. 2009).

The stress gradient hypothesis drives a third strand of work on the interactions of species along gradients of environmental quality (Callaway et al. 2002; Lortie and Callaway 2006; Maestre et al. 2009). The stress gradient hypothesis posits that in poor-quality (high-stress) environments, interactions are frequently positive (facilitation), resulting from species' ameliorating effects on the environment. However, in high-quality (low-stress) environments, negative interactions become in turn more widespread and/or more intense as population sizes increase and competition becomes more significant (Bertness and Callaway 1994). Numerous examples of switches between competition and facilitation as environmental quality decreases have been reported (Brooker et al. 2008; He et al. 2013; Olsen et al. 2016), including at local scales, where the direction of interactions can change in successive years at the same site (Doxford et al. 2012). A direct corollary of the stress gradient hypothesis prediction is that more positive associations between species' densities at the low-quality end of environmental gradients should result from facilitation. One obvious question is whether positive interactions are always required for positive relationships between species' densities.

In the face of this complex ensemble of sometimes contradicting empirical and theoretical work, we argue that it is useful to consider some simple conceptual models of how we expect environments to affect interactions. For instance, imagine a situation in which a set of competing species exist at multiple sites along a gradient of environmental quality. At sites where environmental quality (e.g., resource availability) is low, species' abundances may not be large

enough to negatively affect the growth of their competitors (Grime 2002). In such a situation, species' abundances will be positively correlated because they respond in similar ways to opportunities in their environment. By contrast, at the high-quality end of the gradient, the greater growth and abundance of competitive species will impact on less competitive ones, leading to reductions in the abundance of the latter (e.g., Callaway et al. 2002). Consequently, the net effect of competition on co-occurring species may be different at opposite ends of the gradient of environmental quality. The outcome of competition is thus a balance between the positive effects of increasing habitat quality on all species in a community and the negative effects of increasing competition as densities increase. We explore the consequences of this tension between the two forces, using simple models below.

There have, of course, been a large number of studies that have explored how competition varies along gradients (Wisz et al. 2013), often in the context of the stress gradient hypothesis (Wilson and Keddy 1986; Peltzer et al. 1998; Choler et al. 2001; Pugnaire and Luque 2001; Callaway et al. 2002; Carlyle et al. 2010; Armas et al. 2011). These studies have tended to consider a small number of levels for environmental quality (good vs. bad; Brooker et al. 2008), whereas in reality, gradients span wide ranges of conditions in a continuous way (Maestre et al. 2005; Kawai and Tokeshi 2007). In addition, the study of competition along gradients commonly involves the use of spatially coarse measurements (i.e., average site biomass, gridded presence/absence data) to quantify the relative performances of coexisting plant species, particularly when concerned with large-scale gradients (Wisz et al. 2013). By contrast, observational studies that are both finely resolved and large scale are rare. Specifically, we are aware of no previous studies that have explored how competition and habitat suitability interact to determine local patterns in associations between species' abundances along large-scale environmental gradients. One of the key limitations is that in the many studies to have looked at competition along gradients, few have clearly demonstrated how competition intensity (in terms of either the per unit or net density effect) might vary with environmental quality and how this contributes to the overall outcomes (Freckleton et al. 2009).

Here we explore how changes in environmental quality drive the outcome of competitive interactions along large-scale environmental gradients. We specifically address two questions. First, is there evidence supporting variation in the intensity of competition along environmental gradients, and does this variation correlate with performance? Second, do we observe systematic variation in the outcome of competition, in terms of the strength and nature of the relationship between the densities of competing guilds, along the gradient? We begin by considering the outcome of competition

in simple models for resources, and we then show that empirically observed outcomes vary considerably both spatially and temporally. We discuss these results in the light of previous theories and argue that they are consistent with the effects on species densities of systematic changes in competitive intensity along the gradient of environmental quality.

Material and Methods

Model and Model Predictions

We formulate a simple competition model built on concepts formulated by Vance (1985) in which two types of species compete for a common resource at sites located along a gradient of environmental quality. Each site is made up of n plots (i.e., microsites). Resources are heterogeneously distributed within sites, so each plot has a different resource level. Each model run simulates the outcome of competition in terms of species densities within one plot. For each site, we therefore run a set of n simulations (one per plot) and aggregate results to obtain site-level patterns in species associations.

The system is described by the following equations:

$$\frac{dR}{dt} = -[cB_1(\beta - \gamma B_1 - \alpha_{12}B_2)R] - [cB_2(\beta - \gamma B_2 - \alpha_{21}B_1)R], \quad (1)$$

$$\frac{dB_1}{dt} = cB_1(\beta - \gamma B_1 - \alpha_{12}B_2)R, \quad (2)$$

$$\frac{dB_2}{dt} = cB_2(\beta - \gamma B_2 - \alpha_{21}B_1)R, \quad (3)$$

where B_1 and B_2 are the biomasses of the two competing species 1 and 2, β is the intrinsic growth rate of the two species, c is the resource to biomass conversion rate, R is the amount of available shared resource in a plot, γ is the intraspecific competition coefficient of the two species, and α_{12} and α_{21} are the coefficients quantifying interspecific competition of species 2 over species 1 and species 1 over species 2, respectively. Competition coefficients quantify the per unit effect of competition, that is, the negative effect exerted by one abundance unit of one competitor on the growth of the other. Here B_1 and B_2 are determined by a balance between the consumption of available resources and mortalities linked to intraspecific (quantified by coefficient γ) and interspecific (quantified by coefficients α_{12} and α_{21}) interference competition. In order for coexistence to be stable, intraspecific competition must be greater than interspecific competition for both species (Chesson 2000), and we set $\gamma > \alpha_{12}$ and $\gamma > \alpha_{21}$. The model assumes the existence of a finite pool of resource used by species and recycled back at a constant rate

into the system as individuals die. This simplifying assumption is particularly realistic if the shared resource is space, and it allows dispensing with a supply term in the equation for the resource (eq. [1]).

Interference competition is ubiquitous in natural plant communities and occurs when species have a direct negative impact on each other (Vance 1985). Overcrowding (i.e., the creation of physical barriers preventing access to otherwise available resources, such as light or airborne water) and preemptive use of space are common examples of interference competition in plant communities (Schoener 1983). Interference competition typically increases as the abundance and/or biomass of competitors becomes greater and direct physical interactions become more likely/intense. By contrast, exploitative competition involves indirect effects via differential depletion of the shared limiting resource. Because both species grow at the same rate β in our model, exploitative competition does not determine which species becomes dominant in the system.

Equations (2) and (3) show that in this model the net effect of competition between species is expressed by the term $\alpha_{ij}B_j$. Assuming that species 2 is a stronger competitor than species 1 (i.e., $\alpha_{12} > \alpha_{21}$), an increase in the strength of competition exerted by species 2 over species 1 along an environmental quality gradient can mathematically be implemented in two ways: either by increasing α_{12} relative to α_{21} or by allowing biomass B_2 to increase relative to B_1 . Because species 2 is a better competitor, this is achieved if the amount of available resources R increases along the gradient.

The notion of environmental quality encompasses multiple factors: gradients of improving conditions may be of increasing resources, as in the model described above (eqq. [1]–[3]), but also of decreasing mortalities. The exact nature of the gradient itself has no influence on the outcome of competition. To exemplify this, we include an existing spatial competition model in appendix A (apps. A–D are available online) that can be used to illustrate degrading environmental conditions for plant competitors as an increase in mortality (Crawley and May 1987). Potential real-life drivers of increases in mortality in plant communities are worsening climatic conditions or increasing disturbance, for example, increasing grazing intensity. Broadly speaking, our resource competition model and the spatial competition one shown in appendix A describe the same mechanism, where (1) stable coexistence between two species competing for a limiting resource is possible and (2) improving environmental conditions lead to a relative increase of the negative effect of the growing superior competitor that can depress the abundance of the inferior one. As a consequence of these fundamental similarities, we expect the different types of gradient they represent (available resource vs. mortality) to have no qualitative effect on the relationships they predict between competitors.

We focus here on only the resource competition model described by equations (1)–(3). In this model, either one of R or α_{12} changes along a gradient. Ecologically, both the amount of available resources R and the negative per unit effect of species 2 on species 1 α_{12} may increase along an environmental quality gradient at the same time. Indeed, better environmental quality will often signify more resources (greater R) and therefore higher vegetation biomass, and plants growing in a good-quality environment may also become more efficient in interfering with their weaker competitors (e.g., because of a different growth form). However, to keep our simulation plan tractable, we explore the two-dimensional parameter space $[\alpha_{12}, R]$ in two separate stages by simulating two scenarios in which only one of α_{12} or R increases independently along an environmental quality gradient (fig. 1). Such gradient simulations are designed to investigate the influence of the relative increase of either α_{21} or R on associations between competitors from one site to the next. To account for the absolute value of the competition term $\alpha_{ij}B_j$ as well as its relative value, we run three separate α_{12} gradient simulations corresponding to three differ-

ent levels of R (low, medium, high; fig. 1A); similarly, we run three R gradient simulations, each corresponding to a different, increasing level of α_{12} (fig. 1B).

We find that in both scenarios, a predictable sequence of three types of relationships between species' densities emerges when the net effect of competition increases along the environmental gradient: positive, quadratic (hump shaped), and negative (fig. 2). Both high R along increasing α_{12} gradients and high α_{12} along increasing R gradients accelerate transitions to negative associations by reducing the range of parameter values leading to positive or quadratic relationships (fig. 2D, 2E). The full set of relationships is observed in the subset of parameter space where competition is not so strong that relationships are always negative (high values of α_{12} and/or high values of R) or, conversely, so weak that relationships are always positive (low values of α_{12} and/or low values of R). In this resource competition model, all predicted relationships are symmetrical; that is, association patterns would be identical, regardless of what species is the best competitor or whether the identity of the best competitor changes along the gradient. The model therefore makes

Figure 1: Simulation plan. Two simulation types are envisaged, where the increasing gradient in environmental quality translates into either an increase in α_{12} (A) or an increase in the amount of available resources R (B). We set the intraspecific competition coefficient γ to 0.95. For coexistence to be stable, the condition $\alpha_{12} < \gamma$ must be met. When simulating α_{12} gradients (i.e., α_{12} varying between 0.05 and γ ; A), resource levels R are constant across sites and can be low (100 values ranging between 1 and 10; *bottom*), medium (100 values between 5 and 15; *middle*), or high (values between 45 and 55; *top*). Similarly, when simulating R gradients (B) ranging from 1 to 100, α_{12} is constant across sites and can be low (0.06; *bottom*), medium (0.25; *middle*), or high (0.7; *top*). In both A and B, R levels at sites are characterized by a mean value (circles) and an interplot variability bounded between lower and upper limits (bars). In all cases, α_{21} is kept constant along gradients and is always smaller than α_{12} ($\alpha_{21} = 0.05$). Throughout, the species growth rate β is set to 1, and the conversion rate c is set to $1e-4$; n (number of plots per site) is set at 100. Simulations are run for 1,000 time steps.

Figure 2: Model predictions. A (positive), B (quadratic), and C (negative) show examples of the types of relationships between densities of competing species predicted by the model. D and E show an exhaustive study of the range of predicted associations when parameters α_{12} and R vary, respectively.

no assumption except that the two species compete to some degree. As expected, the spatial competition model presented in appendix A generates the same predictions of changing associations, despite representing the worsening of environmental conditions along the gradient in a different way.

Study System and Species

Model predictions were compared against data collected during a long-term, large-scale study of dune plant systems. The study was carried out on fixed sand dunes on the Atlantic coast of Western Europe and focused on the interaction between perennial species and a group of winter annuals that typically germinate in the autumn and set seed by spring (Pemadasa and Lovell 1974b).

Nine sites were surveyed each spring from 2008 to 2012 along a latitudinal range of ~1,500 km between northwest Portugal in the south and eastern England in the north (see table B1; tables B1, C1 are available online). These sites

were selected to contain comparable vegetation types and species composition. All belong to gray dune habitats with similar sandy soils that are low in nutrients and organic matter and retain little water (Rhind et al. 2006). On gray dunes, vascular plants typically grow within a matrix of moss and lichen and include a high diversity of winter annuals (20%–40% of the flora in dunes in the United Kingdom) and perennial herbs and grasses (Watkinson and Davy 1985).

At each site, between two and four transects consisting of a series of 1 × 1-m contiguous quadrats were surveyed and revisited each year. Depending on site configuration and year, the transect length varied between 10 and 200 m, with an average sampled length across sites and years of 64 m. Eighty-six percent of transects were at least 30 m long, and 63% were at least 50 m long. Transect positions were chosen to represent the range of conditions (aspect, slope) found at each site. A set of 16 native European winter annual species (see app. B1) were systematically and exhaustively counted in each quadrat. Those species represented the bulk

of annual abundances at sampled sites (approximately 60%–80% of all annual species recorded) and occurred frequently at multiple sites along the latitudinal range. In each quadrat, percent cover of perennial vegetation was also estimated, and mean height was measured (the latter for years 2009–2012). The 5-year survey resulted in an extremely large data set now deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.1ns7n2> (Vernon et al. 2017). It comprises a total of 8,984 quadrats within 140 transect $\times$ year combinations and accounts for more than 1.2 million annual plants.

Strong environmental gradients exist along the stretch of Northwestern European coast line surveyed in this study

(Doxford et al. 2012). At least two major sets of variables known to limit plant performance (e.g., individual size, growth, survival, fecundity) and competitive ability vary dramatically between Portugal and Great Britain (fig. 3). The first set of variables is climatic in nature. These factors display strong seasonal variations, and how this seasonality matches with periods of plant recruitment and growth is critical in determining which end of the latitudinal range is harshest. All annual species considered in this study are winter annuals that go through their entire life cycle between autumn and spring (with the exception of one occasionally biennial species; see app. B1). As a consequence, perennials and winter annual species co-occur and compete

Figure 3: Latitudinal environmental gradients between autumn and spring (September–May). From south to north, sampled sites experience a decline in mean monthly rainfall (A), mean temperatures (monthly minimum, monthly maximum, and daily; B), and mean monthly number of hours of sunshine (C). By contrast, disturbance related to grazing pressure (estimated from counts of rabbit fecal pellets m^{-2}) increased going northward (D). Solid lines represent statistically significant relationships. Dashed lines are nonsignificant relationships and show the mean value for the variable across sites. Climate data were sourced from the European Climate Assessment and Dataset (<http://eca.knmi.nl/>), the Met Office historical data portal (<http://www.metoffice.gov.uk/public/weather/climate-historic/#?tab=climateHistoric>), and the Instituto Português do Mar e da Atmosfera (<https://www.ipma.pt/en/index.html>). Daily temperatures were measured at midday. Fecal pellet counts were recorded during the survey.

over only part of the year, outside of the summer months. In this context, climatic data strongly suggest that southern sites benefit from a better environmental quality than their northern counterparts. From south to north, sites experience significant declines (slope = -6.7 , $n = 9$, $P = .016$) in mean monthly rainfall over the autumn-to-spring period (fig. 3A). As well as being wetter, southern sites are also much milder over the colder months of the year than locations at higher latitudes (fig. 3B). This is true whether considering mean monthly maximal temperatures (slope = -0.54 , $n = 9$, $P < .001$), mean monthly minimal temperatures (slope = -0.24 , $n = 9$, $P = .01$), or mean daily temperatures (slope = -0.58 , $n = 9$, $P < .001$). These milder temperatures between autumn and spring in the south typically translate into longer growing seasons (i.e., the period during which temperatures are above a base level that allows plant growth). Over the autumn-to-spring period, southern sites also benefit from more hours of sunshine (autumn: slope = -6.5 , $n = 8$, $P = .003$; winter: slope = -4.9 , $n = 8$, $P = .001$; spring: slope = -0.36 , $n = 8$, $P = .36$; fig. 3C). The second major variable likely to determine environmental quality for both perennial and annual species along the latitudinal range is grazing-related disturbance (Provoost et al. 2004). Again, variation in grazing intensity clearly points toward better conditions in the south: estimates of grazing by rabbits increase markedly and significantly (slope = 10.0 , $n = 9$, $P = .01$) going northward, meaning that growing seasons at southern sites are not only longer but also less perturbed (fig. 3D). Together these variables constitute a multifaceted gradient in environmental quality between mild, wet, low-disturbance sites in the south and colder, drier, more disturbed sites in the north.

Note that nutrient levels are broadly similar along the sampled latitudinal range (e.g., Doxford et al. 2012) and that existing variations do not correlate significantly with latitude (slope = 0.11 , $n = 7$, $P = .78$; see fig. B1; figs. A1, B1–B4 are available online). Hence, observed differences between communities across sites are unlikely to be related to differences in soil nutrient content. This is not surprising because sites were selected to be as similar as possible in terms of their underlying species composition, which is closely related to nutrient composition in such systems (Rodwell 2000).

As indicated above, the predictions of varying species associations generated by the resource competition model hold whether or not the identity of the best competitor changes along the environmental quality gradient. However, the literature does suggest that perennial species are competitively superior to winter annual species in gray dune habitats (Pemadasa and Lovell 1974c; Crawley and May 1987; Rees and Long 1992; Turnbull et al. 2004). As a result of this asymmetric competition, it is thought that winter annuals persist in the face of perennial competition

by making the most of opportunities created by disturbance (Provoost et al. 2004). The spatial competition model shown in appendix A integrates the assumption of asymmetry.

Data Analysis

We tested the predictions made by the simple competition models described in figure 1, namely that the competitiveness of perennials influences the type of relationship (i.e., positive, quadratic, or negative) they form with their inferior annual competitors. To do so, we estimated perennial competitiveness from data and described the nature of corresponding associations between annual and perennial plant species.

Under the assumption that perennial species are better competitors than annuals, we hypothesized that taller perennials interfere more strongly with co-occurring annuals, and we predicted that consequently there would be a negative relationship between the height of perennials and the abundance of annuals. We tested this hypothesis by analyzing the relationship between perennial height and the abundance of annuals. For all sites and years, we modeled this relationship at transect level using a generalized linear model with a negative binomial error structure and a log link.

According to this model, the predicted number of annuals in year i , site j , and plot k is given by

$$\log N_{ijk} = a_{ij} + b_{ij}P_{ijk}, \quad (4)$$

where a_{ij} is the log density of annuals in the absence of perennials, P_{ijk} is the height of perennial vegetation in plot k in year i and site j , and b_{ij} is the slope that relates annual density to the height of perennials. In order to estimate the overall impact of competition from perennials, for each transect within year, we calculated

$$C_{ij} = \max(b_{ij}P_{ijk}) - \min(b_{ij}P_{ijk}). \quad (5)$$

This measures the relative reduction (noting that eq. [4] predicts log density) in annual density along a transect resulting from variation in perennial height.

The rationale for using these two measures is as follows: along a gradient of habitat quality, competition could vary in two respects relating to its intensity and the overall amount of competitors. In our system, the per unit effect of competition (b in eq. [4]) might vary as a consequence of an increase in the relative competitiveness of the perennials (increasing intensity per unit of vegetation). Alternatively, increasing the quality of habitat might increase the range of densities and heights of competitors, particularly the maximum height of perennials leading to increased impacts on annuals (measured by C).

Parameters b and C are empirical estimates of per unit and net effects of competition, respectively. As such, they relate to the mathematical formulation of competition underlying the competition model presented in figures 1 and 2. On the one hand, b relates to the competition coefficient α_{12} in equation (2), while on the other hand, C is linked with the net effect of competition $\alpha_{12}B_2$. An empirical assessment of model assumptions (i.e., that the per unit and/or net effects of competition increase with environmental quality) can therefore be implemented by testing separately whether the two metrics b and C correlate with observed variation in environmental quality.

If competition occurs, then we expect one of three types of relationships between dune annual and perennial densities (as in fig. 2): positive, quadratic, or negative. Relationships may be more frequently quadratic or negative at sites where empirical estimates of competition C and/or b are higher. This is because as perennial density increases, the negative impact on the density of annuals will be comparatively greater where perennials are more competitive. For a given transect at a given year, the relationship between dune annual counts and perennial cover (expressed as a percentage) was described by a simple linear model or, alternatively, by a model allowing for dune annual abundances to peak at intermediate perennial cover (i.e., a hump-shaped relationship including a quadratic term as part of the linear predictor). To determine which model type best describes observations, we fitted both models to the data using a generalized additive model (GAM) with a quasi-Poisson error structure. We accounted for the potential influence of spatial autocorrelation by systematically including a smooth function of quadrat position in both model types. The level of smoothing to be used was determined by fitting the linear model to the data and varying the degree of smoothing until autocorrelation of model residuals was minimized. Selection of the simple linear or quadratic was done using ANOVA.

Rather than interactions with perennial species, confounding factors may in fact be responsible for observed changes in the way annual species perform along the environment gradient. In particular, bryophytes (i.e., mosses and lichens) form mats that can affect annual species either negatively by preventing their seeds from settling on to a suitable substrate or positively by improving the environmental conditions (i.e., moisture and temperature) experienced by their seedlings (Doxford et al. 2012). We assessed the influence of mosses and lichens on annuals by monitoring the change in bryophyte ground cover and mat thickness along the environmental gradient as well as the change in correlation between those variables and the abundance of annuals. All analyses performed in this study were implemented using the statistical software R (R Development Core Team 2014), using the *mgcv* library for GAMs (Wood 2011).

Results

Perennial Competitiveness along the Gradient

There was considerable variation in the growth and abundance of perennial species along the environmental gradient. Their performance—as quantified by mean perennial height (slope = -1.597 , $n = 9$, $P = .004$), mean maximum perennial height (slope = -9.923 , $n = 9$, $P = .009$; fig. 4A), and maximum perennial cover (slope = -3.691 , $n = 9$, $P = .006$; see fig. B2A)—decreased drastically with increasing latitude. Abundances of annuals varied greatly in space and in time within single sites, but mean densities did not change significantly with latitude (slope = 5.46 , $n = 9$, $P = .339$; see fig. B2B).

We found widespread evidence supporting competition between the two sets of perennial and annual species, with a clear and significant negative relationship between the height of the perennial vegetation and the density of annuals across all sites and years (slope = -0.017 , $n = 7,266$, $P < 2e-16$; fig. 4B). At the level of individual sites, the average value of b (see eq. [1]), the per unit effect of perennials, was negative across all sites (fig. 4C; table C1) and only weakly associated with perennial height (slope = 0.11 , $n = 9$, $P = .25$; fig. 4D). This indicates that the impacts of competition per unit of perennial height were not variable across sites or affected by changing environmental quality along the latitudinal range. However, in contrast, the net effect of competition (C in eq. [5]) varied systematically, decreasing significantly with latitude (slope = -0.05 , $n = 9$, $P = .03$; fig. 4E) and increasing significantly with perennial height (slope = 0.27 , $n = 9$, $P = .04$; fig. 4F).

Changes in the height and ground cover of perennials along the environmental gradient were associated with clear changes in correlation with annual species' abundances. Mean annual correlation between annual abundances and perennial cover became significantly less negative with increasing latitude (slope = 0.02 , $n = 9$, $P = .03$) and significantly more negative when mean maximum perennial height increased (slope = -0.002 , $n = 9$, $P = .02$; fig. 4G, 4H). We found no evidence for a latitudinal pattern in the way bryophyte ground cover and mat thickness varied or in their effect on annual species (see fig. B3).

Relationships between the Densities of Annual and Perennial Species

The shape of the relationship between dune annual abundance and perennial cover varied greatly along the environmental gradient (for detailed examples, see fig. 5; for overall patterns, see figs. 6, B4). As anticipated, relationships between the abundances of the groups were either positive (61 out of 140 cases, 44%), negative (52 of 140, 37%) or qua-

Figure 4: Changing perennial competitiveness along the sampled environmental gradient and corresponding correlations with annual species. Mean and maximum perennial heights decrease significantly going from southern sites to northern ones (A). Across all sampled quadrats, taller perennials are associated with lower densities of annual species (B). The mean per unit effect of competition is negative for all sites and does not vary significantly with latitude (C) or perennial height (D). However, estimates of the net effect of perennial competition on annuals (see “Material and Methods”) decrease

dratic (27 of 140, 19%; fig. B4; app. D). For a given site and at a given year, more than one type of relationship was found across transects in 30 of all 45 (67%) year-site combinations. At the transect level, relationships also frequently changed (44% of cases) from one year to the next.

Despite this variability, there were clear trends in the occurrences of the different types of relationship along the environmental gradient, apparent from visual examination (fig. B4) and summarized in figure 6. The proportion of positive relationships was larger among transects at northern sites (fig. 6A), while antagonistic (i.e., negative and quadratic relationships) became more common going southward (fig. 6C, 6E). When plotting the proportion of each type of relationship against the logarithm of maximum perennial height, we found that positive relationships became significantly less represented as perennials grew taller (fig. 6B), that is, more competitive (slope = -1.03 , $n = 9$, $P = .01$). Conversely, quadratic relationships were statistically more frequent (slope = 1.24 , $n = 9$, $P = .02$) where perennials were tallest (fig. 6D). A positive trend (slope = 0.22 , $n = 9$, $P = .39$) also existed between the frequencies of negative relationships and perennial height (fig. 6F).

Discussion

One might expect that the abundances of co-occurring competitors should be negatively correlated. However, in our analysis, we have revealed a striking diversity of associations between the members of two competing guilds. Specifically, we show that there is a distinct shift from negative and quadratic relationships to positive ones along an environmental gradient. Moving northward along this gradient, standing perennial biomass strongly decreases, and the negative correlation between the densities of competitors weakens. Empirical estimates for the net effects of competition exerted by perennials on annuals decrease from south to north, while per unit effects are uncorrelated with latitude. Simple models predict that such a decrease in the net effects of competition along gradients can explain a shift from negative to positive associations between the densities of superior and inferior competitors (fig. 2E; app. A). As a consequence, predicting how the abundances of co-occurring species will covary under changing conditions may require systematically understand-

clearly and significantly going northward (E) and increase with the logarithm of mean perennial height (Ln(Av. peren. hgt.); F). In parallel, mean correlation (Cor. annuals vs perennials) between annual species' abundances and perennial ground cover goes from negative to positive when latitude increases (G) and maximum perennial height (Max. peren. hgt.) decreases (H). Solid lines represent statistically significant relationships.

Figure 5: Examples of relationships between the densities of annual and perennial species for a southern transect (single transect at site P2) and a northern one (single transect at site GB2) from 2008 (*top*) to 2012 (*bottom*). For each transect, the logarithms of mean densities of annuals (m^{-2}) are shown for observed levels of perennial ground cover, with standard error bars. Lines show the type of relationship (negative, positive, or quadratic) best fitting the data. Only quadratic and negative relationships are found at the southern transect, whereas positive relationships dominate in the north. The best-fitting relationships are determined using generalized additive models (GAMs) integrating a smooth function of quadrat position to account for spatial autocorrelation (see “Material and Methods”). Note that in all but one of the cases pictured here (D), spatial autocorrelation has no influence on the type of relationship best fitting the data. In these cases, regression lines are obtained from simpler GAMs that do not contain a smoothing term.

ing not only what types of interaction exist between them but also how the intensity of these interactions changes with the environment.

We note that the agreement found between model predictions and observations does not in itself constitute formal proof that competition varying with environmental quality is the mechanism at play in the communities we surveyed. However, a strong case for this interpretation can be made even in the absence of complementary experimental tests. Our interpretation relies on two assumptions: first, that the gradient is such that northern sites are less suited to plant growth and survival than the ones further south, and second, that the underlying relationship between the species is a competitive one.

The assumption of a south-to-north decreasing gradient in environmental quality is very strongly supported by data (fig. 3). Southern sites are milder and wetter and benefit from more sunshine and more daylight than those further north over the time of the year where perennial and annual species actually co-occur, compete, and grow. In addition, southern sites experience very little grazing, while it is a significant source of disturbance for plant communities at northern locations. The way our competition models represent the worsening of growing conditions along gradients can be interpreted in the context of these real-life drivers of environmental quality. Given the differential in precipitation along the latitudinal range between autumn and spring, water availability is a realistic candidate for a limiting resource that decreases going northward and a direct match for the gradient in available resources R simulated in our resource competition model (figs. 1B, 2E). Each climatic and consumer-related factor discussed above is also likely to lead to increasing mortality rates for both guilds going northward, as in the mortality gradient we simulated in the spatial competition model shown in appendix A. The robustness of model predictions to the type of simulated gradients combined with the uniform direction of change of major factors of environmental quality provides justification for linking observed patterns to the competition process. Differences in the size and biomass of individual plants growing in the south and in the north further strengthen this view. As would be expected if growing conditions worsened with increasing latitude, the standing biomass (the combination of abundance; i.e., ground cover and height) of perennials is very clearly greater in the south than in the north. It is less obvious what the relationship should be between environmental quality and the abundance or height of annual species, whose dynamics are thought to be primarily driven by their superior competitors (Rees and Long 1992; Turnbull et al. 2004). Although we did not routinely measure dune annual heights, observations on the ground (M. K. J. Ooi, personal communication) over the 5-year sampling period also pointed to greater height at southern sites, while

Figure 6: Frequency of the different types of relationships (positive, negative, and quadratic) observed between perennial cover and dune annual density along the environmental gradient. A, C, and E show the proportions of transects across years where each relationship was found for all nine sites. For each site, those proportions add up to 1. B, D, and F show the same proportions against the natural logarithm of the mean maximum height ($\text{Ln}(\text{mean max. hgt.})$) of perennials at each site, averaged across years and transects. Regression lines given by generalized linear models with a quasi-binomial error structure are shown.

there was no systematic change of mean densities with latitude (see “Results”; fig. B2B).

The second assumption of negative interactions made by our simple models finds direct support in our data. Although we do show that positive associations exist between

the densities of co-occurring annual and perennial species, the underlying interactions appear to be always competitive (fig. 4C–4F; table C1).

The question may arise whether it is appropriate to use observational data to make inferences over processes in the absence of experimental tests. Simulations suggest that in spatially structured plant communities, observational data may actually outperform experimental approaches in terms of measuring the effects of competition (Freckleton and Watkinson 2000, 2001). This is a consequence of the spatial structure that develops within natural communities in which competitive interactions are strong (Pacala 1996; Pacala and Levin 1997): when competition is strong, spatial segregation of species occurs. Simple experimental approaches, such as removal, are then ineffective in demonstrating or measuring interspecific interactions because most individuals removed are surrounded by intraspecific competitors. On the other hand, nonmanipulative regression approaches are more robust because they use all variance in densities, including small proportions of sites in which species densities are mixed (Freckleton and Watkinson 2001). An alternative methodology would be to combine approaches, although experimental manipulation is time consuming, and there is a trade-off with extent of data coverage. The approach we took instead was to maximize the extent of our data collection.

Our empirical findings on the outcome of competition between annuals and perennials are also well supported in the literature: the asymmetric nature of competition between superior perennials and inferior annuals in gray dune systems is already well documented (Pemadasa and Lovell 1974a, 1974c; Rees and Long 1992; Turnbull et al. 2004), as is the importance of this competition in influencing the population dynamics of annuals.

Alternative mechanisms to competition could lead to the patterns observed along the latitudinal range. For instance, the positive relationships found at northern sites between annuals and perennials could theoretically stem from positive interactions between the two guilds. However, the occurrence of positive interactions is not substantiated in our data (see fig. 4C–4F). One may also imagine a mechanism by which interactions have no effect at all and increasingly positive correlations between guilds going northward are linked to perennials and annuals occupying increasingly dissimilar microhabitats. However, this also seems unlikely, given the evidence for negative effects of perennials on annuals in all communities, including those at northern locations in which densities are positively correlated (fig. 4C). From the existing data and literature, changing competition along an environmental gradient appears as the most likely explanation for the transitions in guild associations highlighted here.

Many empirical studies have measured competition and/or facilitation among plant species along environmental

gradients. Results have generally been interpreted in one of two contexts. The stress gradient hypothesis (Maestre et al. 2006) or models of productivity/diversity relationships (Michalet et al. 2006) are often used as theoretical frameworks when measuring the relative strength of negative/positive interactions along environmental gradients (Bertness and Callaway 1994; Callaway et al. 2002; Holzapfel et al. 2006; Bowker et al. 2010; Armas et al. 2011; Le Bagousse-Pinguet et al. 2012; He et al. 2013). Alternatively, the concepts formulated by Tilman (1988) and Grime (2002) are frequently called upon when specifically measuring competition along productivity gradients (Wilson and Keddy 1986; Campbell and Grime 1992; Turkington et al. 1993; Sammul et al. 2006; Carlyle et al. 2010).

Our analyses suggest that the mechanisms explaining density patterns in our data differ from those anticipated by both the stress gradient hypothesis and recent productivity/diversity models, because we find no evidence of facilitation (fig. 4; table C1). Although our results do not contradict these theories—indeed, it may be that facilitation occurs beyond the northern edge of the latitudinal range we have studied—they show that transitions from negative to positive associations do not necessarily involve positive interactions. Our data and model predictions together point toward the following interpretation. The clear negative impact of the perennial vegetation on the abundance of annuals varies systematically with the height of the perennials (fig. 4B, 4F), which is maximum at high-biomass, low-disturbance southern sites and minimum at the less productive and more perturbed northern sites. This decreasing intensity of competition suggests that the main drivers of community structure differ at opposite ends of the environmental gradient. In the south, indirect effects of the environment dominate via intense asymmetric competition. As a result and despite being adapted to the same habitat and using common resources, the densities of the two guilds mainly change in opposite direction. Conversely, in the north—where environmental quality is lower and competition is weak—direct effects of the environment prevail, and the abundances of both species groups tend to increase and decrease together. We show that the change in the way annual species perform along the environmental gradient cannot be explained by the influence of bryophytes, whose performance and associations with annuals do not change systematically with latitude. Although bryophytes are very likely to have an important influence on annual species, they may be responsible for within-site temporal variation rather than for a consistent, predictable latitudinal change (Doxford et al. 2012).

Our results are outwardly consistent with Grime's prediction that the role of competition in structuring communities becomes negligible in unproductive and perturbed sites. However, the fine-scale resolution of our data means

that it cannot easily be used to assess Grime's or Tilman's model. Indeed, both theories make broad predictions of how different habitats may be dominated by different species types characterized by different sets of traits. By contrast, our study monitors changes in the abundance of the same suite of species within a single habitat type, and our results may not be directly relevant in this particular context (Rees 2013).

There has been considerable debate about how the importance of competition may be measured. Several concepts and indices of competition have been proposed and used to explore how interactions vary along gradients or in different environments (Brooker et al. 2005; Brooker and Kikvidze 2008). A criticism of this approach to understanding competition is that there is often a reliance on defining importance without clearly stating what the importance is with respect to (Freckleton et al. 2009). There is also a problem in that indices can have unwanted behavior, such as varying in a trivial way with measures of performance (Freckleton et al. 2009; Rees et al. 2012; Mingo 2014). In this study, we have taken a pragmatic approach to measuring the impacts and outcomes of competition, and we have used measures that allow us to distinguish per unit impacts from net effects in the light of theoretical expectations (eqq. [1]–[3]). The outcomes we have considered are the correlation and shape of the relationship between species' densities. This was chosen as the basis for the analysis because of the theoretical prediction that these measures should be sensitive to changing environmental conditions and strength of competition. In general, there is no "one size fits all" for studies on competition and other interactions, and as we have previously emphasized, the measures should be tailored to the question in hand.

Recent work on multispecies competition has highlighted that in more diverse communities, both the way interactions change and their outcomes may be more difficult to predict. For example, Martorell and Freckleton (2014) found that in a large plant community, interactions were weak among established individuals. In such cases, changing environmental conditions might be expected to impact primarily through species-specific individual responses to climate. However, in the establishment phase, interactions had significant effects on population sizes, with little predictability to the structure of the network of interactions.

Climate models are useful tools when attempting to describe the changes in a species' fundamental niche (i.e., the area where it can occur) in the face of global change. However, they are less appropriate when describing a species' realized niche, that is, the smaller area it actually occupies within its potential geographical distribution (Pearson and Dawson 2003; Araujo and Peterson 2012). The importance of integrating species interactions when considering realized niches has been recently discussed (Araujo and Luoto

2007; Gilman et al. 2010; Ockendon et al. 2014). The results presented here illustrate the major impact interactions can have on the abundance of species within their climate range but also the variety of outcomes they can produce when interplaying with a changing environment, in line with recent experimental results (Kraft et al. 2015). They suggest that parsimonious models of simple, purely competitive interactions can be sufficient to generate the sets of changing associations observed along natural gradients. Specifically, they show that positive associations between guilds or species are not necessary consequences of facilitative interactions and that whether it is possible to infer one from the other (Xu et al. 2015) will change depending on the system studied. Our study highlights that environmental change may affect species large-scale distributions in complex ways and that better forecasting must explicitly integrate the mechanisms of interaction change in terms of both intensity and direction.

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"Thus are the seaward slopes washed into gullies and ravines, which are left obstructed by fallen trees and branches. Over these active nature soon spreads a mantle of greenness and bloom, by means of rapidly growing creeping vines, forming almost inaccessible fastnesses. In these secluded haunts the Lyre Bird hides itself from the gaze of man. It is found over a large extent of country, but is peculiar to the mountain districts of Australia, and especially to those on the southeastern face of the continent." From "The Lyre Bird" by Grace Anna Lewis (*The American Naturalist*, 1870, 4:321–331).