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Vergnon, R., Ooi, M.K.J. and Freckleton, R.P. (2017) Complex Relationships between Competing Guilds along Large-Scale Environmental Gradients. American Naturalist, 189 (4). pp. 407-421. ISSN 0003-0147

https://doi.org/10.1086/690765

Title: Complex relationships between competing guilds along large-scale environmental gradients

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Dryad data: http://dx.doi.org/10.5061/dryad.1ns7n

Manuscript type: article

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

Manuscript elements that would appear in the online edition: appendixes

Online Appendix A: Existing spatial competition model

- Appendix A1: Model description
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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 counter-intuitive 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 grey 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 non-obvious 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' co-distribution can vary along environmental gradients.

1. Introduction

The question of how plant communities change with disturbance, habitat quality or climate is fundamental to plant ecology (Grime 2002; Keddy 2001; Tilman 1988), 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 determine 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 (Blois et al. 2013; Fukami and Wardle 2005). 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 (Olsen et al. 2016; Tylianakis et al. 2008).

The issue of how plant interactions vary along environmental gradients has been studied through at least three significant strands of the literature. First, Grime and Tilman (Grime 2002; Tilman 1988) 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 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 (Buckland and Grime 2000; Campbell and Grime 1992; Fargione and Tilman 2006; Grime et al. 1997; Shipley and Peters 1990). However there is little consensus emerging from this work (Craine 2005; Craine 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 has therefore an impact on diversity. An increasing body of literature now suggests that interactions can play a significant role in shaping diversity patterns (Brooker et al. 2008; Michalet et al. 2006; Xiao et al. 2009).

The Stress Gradient Hypothesis (SGH) 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 SGH 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 a same site (Doxford et al. 2012). A direct corollary of the SGH 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 as 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 gradient of environmental quality. The outcome of competition thus is 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 in 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 SGH (Armas et al. 2011; Callaway et al. 2002; Carlyle et al. 2010; Choler et al. 2001; Peltzer et al. 1998; Pugnaire and Luque 2001; Wilson and Keddy 1986). These studies have tended to consider a small number of levels for environmental quality ("good versus bad") (Brooker et al. 2008), whereas in reality gradients span wide ranges of conditions in a continuous way (Kawai and Tokeshi 2007; Maestre et al. 2005). 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 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.

2. Material and Methods

Model and model predictions

We formulate a simple competition model built upon concepts formulated by Vance (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:

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

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

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

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 i.e. 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 allows dispensing with a supply term in the equation for the resource (equation (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 resource such as light or airborne water) and pre-emptive 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 become 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} relatively to α_{21} or by allowing biomass B_2 to increase relatively 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 (equations (1) to (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 (see app. A) 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 describe the same mechanism where i) stable coexistence between two species competing for a limiting resource is possible and ii) 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 only focus here on the resource competition model described by equations (1) to (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 (because of a different growth form for instance). However to keep our simulation plan tractable we explore the two-dimensional parameter space [α_{12}, R] in two separate stages by simulating two scenarios in which only one of α_{12} or R increase 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 different levels of R (low, medium, high, fig. 1A) and 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, E). 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 i.e. 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 no assumption except that the two species compete to some degree. As expected, the spatial competition model presented in appendix (see app. 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 c.1500 km between northwest Portugal in the south and eastern England in the north (see Table B1). These sites were selected to contain comparable vegetation types and species composition. All belong to “grey dune” habitats, with similar sandy soils that are low in nutrients and organic matter, and retain little water (Rhind et al. 2006). On grey 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 UK dunes) and perennial herbs and grasses (Watkinson and Davy 1985).

At each site between two and four transects consisting of series of 1 metre by 1 metre contiguous quadrats were surveyed and revisited each year. Depending on site configuration and year the transect length varied between 10 and 200 metres, with an average sampled length across sites and years of 64 meters. 86% of transects were at least 30 meters long and 63% were at least 50 meters 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, % cover of perennial vegetation was also estimated, and mean height was measured (the latter for years 2009 to 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.1ns7n (Vergnon et al. 2016). It comprises a total of 8984 quadrats within 140 transect-by-year combinations and accounting for over 1.2 million annual plants.

Strong environmental gradients exist along the stretch of North-western 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 only co-occur and compete over 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 = 0.016) 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 < 0.001), mean monthly minimal temperatures (slope = -0.24, n = 9, P = 0.01) or mean daily temperatures (slope = -0.58, n = 9, P < 0.001). 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 (slope = -6.5, n = 8, P = 0.003 in autumn; slope = -4.9, n = 8, P = 0.001 in winter; slope = -0.36, n = 8, P = -0.36 in spring, 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 points clearly towards better conditions in the south: estimates of grazing by rabbits increase markedly and significantly (slope = 10.0, n = 9, P = 0.01) 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 = 0.78, see Fig. B1). 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 grey dune habitats (Crawley and May 1987; Pemadasa and Lovell 1974c; 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 hypothesised that taller perennials interfere more strongly with co-occurring annuals, and predicted that consequently there would be a negative relationship between the height of perennials and the abundance of annuals. We tested this hypothesis by analysing the relationship between perennial height and the abundance of annuals. For all sites and years we modelled 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:

$$\log N_{i,j,k} = a_{i,j} + b_{ij}P_{i,j,k} \qquad (4)$$

$a_{i,j}$ is the log density of annuals in the absence of perennials. $P_{i,j,k}$ is the height of perennial vegetation in plot *k* in year *i* and site *j*. $b_{i,j}$ 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:

$$C_{ij} = \max\left(b_{ij}P_{ijk}\right) - min\left(b_{ij}P_{ijk}\right) \qquad (5)$$

This measures the relative reduction (noting that equation (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 equation (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*).

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 quasipoisson 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 data and varying the degree of smoothing until autocorrelation of model residuals was minimized. Selection of the simple linear or quadratic was done using analysis of variance.

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 Core Team 2014) using the mgcv library for GAMs (Wood 2011).

3. 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 = 0.004), mean maximum perennial height (slope = -9.923, n = 9, P = 0.009) (fig. 4A) and maximum perennial cover (slope = -3.691, n = 9, P = 0.006) (see fig. B2 panel A) 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 = 0.339) (see fig. B2 panel B).

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 = 7266, P < 2e-16, fig. 4B). At the level of individual sites the average value of *b* (see equation (1)), the per-unit effect of perennials, was negative across all sites (fig. 4C, and see Table C1) and only weakly associated with perennial height (slope = 0.11, n = 9, P = 0.25, 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 equation (5)) varied systematically, decreasing significantly with latitude (slope = -0.05, n = 9, P = 0.03, fig. 4E) and increasing significantly with perennial height (slope = 0.27, n = 9, P = 0.04, 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 = 0.03) and significantly more negative when mean maximum perennial height increased (slope = -0.002, n = 9, P = 0.02) (fig. 4G, H).

We found no evidence for a latitudinal pattern in the way bryophyte ground cover and mat thickness varied, nor 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 (see fig. 5 for detailed examples, and figs. 6 and B4 for overall patterns). As anticipated, relationships between the abundances of the groups were either positive (61 out of 140 cases, 44%), negative (52 of 140, 37%) or quadratic (27 of 140, 19%) (fig. B4, and see 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 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, E). 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) i.e. more competitive (slope = -1.03, n = 9, P = 0.01). Conversely quadratic relationships were statistically more frequent (slope = 1.24, n = 9, P = 0.02) where perennials were tallest (fig. 6D). A positive trend (slope = 0.22, n = 9, P = 0.39) also existed between the frequencies of negative relationships and perennial height (fig. 6F).

4. 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 and see app. A).

As a consequence predicting how the abundances of co-occurring species will covary under changing conditions may not only require systematically understanding 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, 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 (fig. 1B and fig. 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 (*Pers. Comm.* from second author) over the 5-year sampling period also pointed to greater height at southern sites, while there was no systematic change of mean densities with latitude (see Results and Fig. B2 panel B.

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-F and see 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; Freckleton and Watkinson 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 inter-specific interactions because most individuals removed are surrounded by intra-specific competitors. On the other hand non-manipulative 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 grey dune systems is already well documented (Pemadasa and Lovell 1974a; Pemadasa and Lovell 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-F). 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 micro-habitats. 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 (Armas et al. 2011; Bertness and Callaway 1994; Bowker et al. 2010; Callaway et al. 2002; He et al. 2013; Holzapfel et al. 2006; Le Bagousse-Pinguet et al. 2012). Alternatively the concepts formulated by Grime (Grime 2002) and Tilman (Tilman 1988) are frequently called upon when specifically measuring competition along productivity gradients (Campbell and Grime 1992; Carlyle et al. 2010; Sammul et al. 2006; Turkington et al. 1993; Wilson and Keddy 1986).

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 as we find no evidence of facilitation (fig. 4 and see 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 towards 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, F), 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 it cannot easily be used to assess Grime’s or Tilman’s models. 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 and Kikvidze 2008; Brooker et al. 2005). 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; Mingo 2014; Rees et al. 2012). In this study we have taken a pragmatic approach to measuring the impacts and outcomes of competition, and have used measures that allow us to distinguish per-unit impacts from net effects in the light of theoretical expectations (equations (1) to (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 i.e. the smaller area it actually occupies within its potential geographical distribution (Araujo and Peterson 2012; Pearson and Dawson 2003). The importance of integrating species interactions when considering realized niches has been recently discussed (Araújo 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 or not 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 both in terms of intensity and direction.

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Figures

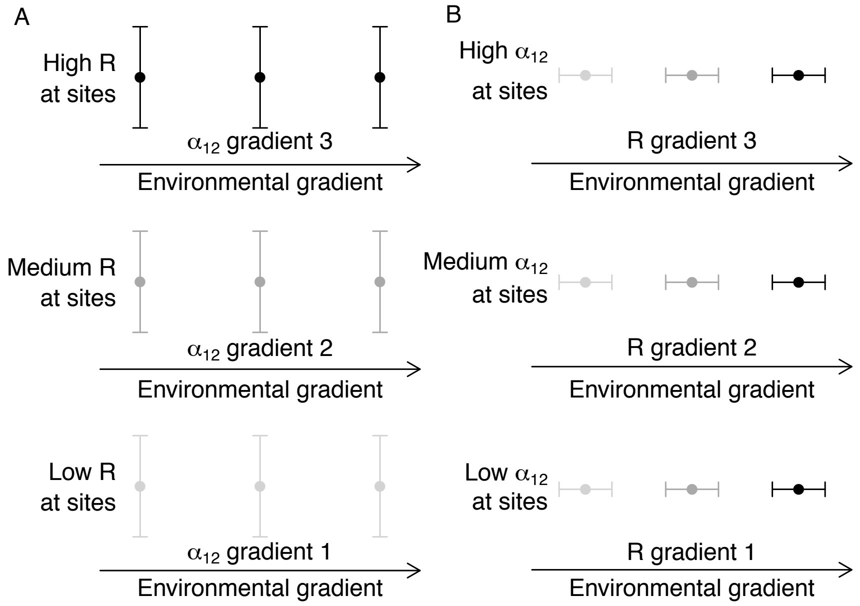

Figure 1. Simulation plan. Two simulation types are envisaged where the increasing gradient in environmental quality translates either in an increase in α_{12} (A) or in an increase in the amount of available resources R (B). We set the intraspecific competition coefficient γ to 0.95. For coexistence to be stable the condition $\alpha_{12} < \gamma$ must be met. When simulating α_{12} gradients (A) i.e. α_{12} varying between 0.05 and γ, resource levels R are constant across sites and can be low (100 values ranging between 1 and 10, bottom panel), medium (100 values between 5 and 15, middle panel) or high (values between 45 and 55, top panel). Similarly when simulating R gradients (B) ranging from 1 to 100, α_{12} is constant across sites and can be low (0.06, bottom panel), medium (0.25, middle panel) or high (0.7, top panel). In both A and B, R levels at sites are characterized by a mean value (indicated by dots) and an inter-plot variability bounded between lower and upper limits (indicated by 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* (the number of plots per site) is set at 100. Simulations are run for 1000 time steps.

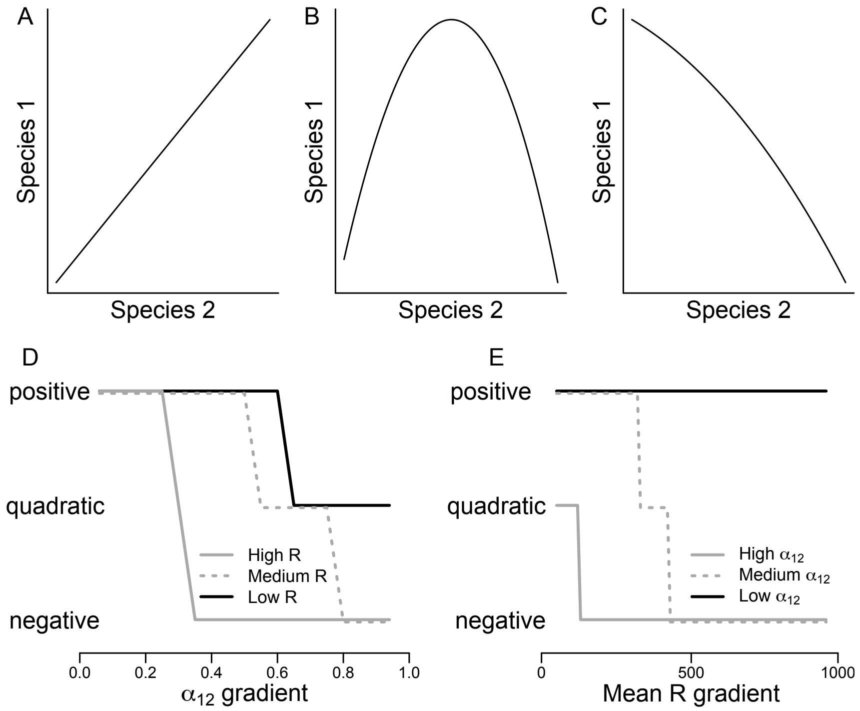

Figure 2. Model predictions. Panels A (positive), B (quadratic) and C (negative) show examples of the types of relationships between densities of competing species predicted by the model. Panels D and E show an exhaustive study of the range of predicted associations when parameters α_{12} and R vary,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

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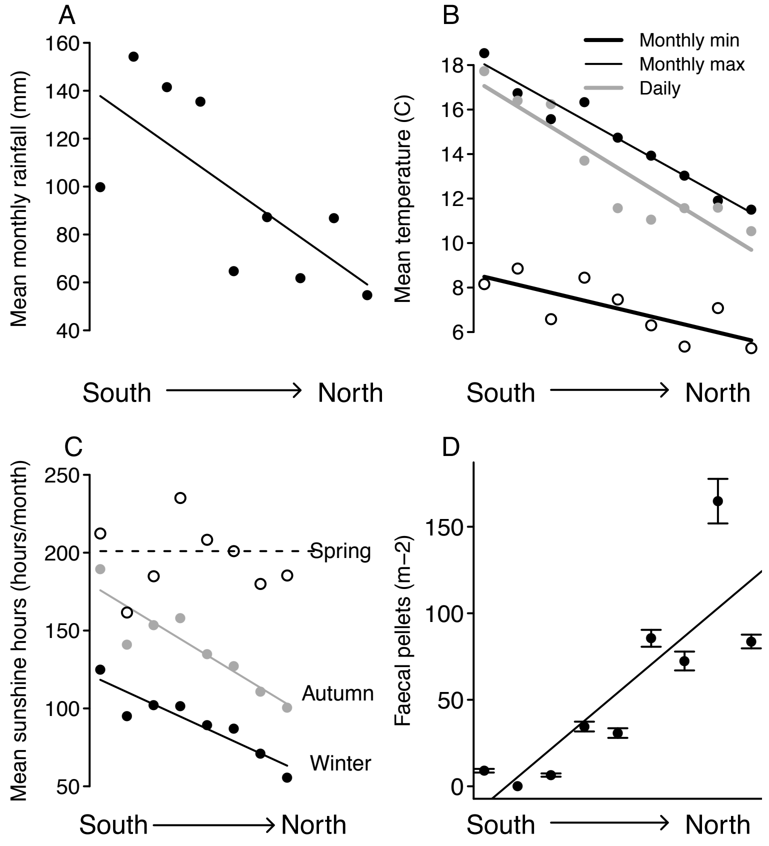

Figure 3: Latitudinal environmental gradients between autumn and spring (September to May). From south to north sampled sites experience a decline in mean monthly rainfall (A), mean temperatures (monthly minimum, monthly maximum and daily) (B) and mean monthly number of hours of sunshine (C). By contrast disturbance related to grazing pressure (estimated from counts of rabbit faecal pellets per m^2) increased going northward (D). Solid lines represent statistically significant relationships. Dashed lines are non-significant relationships and show the mean value for the variable across sites. Climate data was 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 IPMA (https://www.ipma.pt/en/index.html). Daily temperatures were measured at midday. Faecal pellet counts were recorded during the survey.

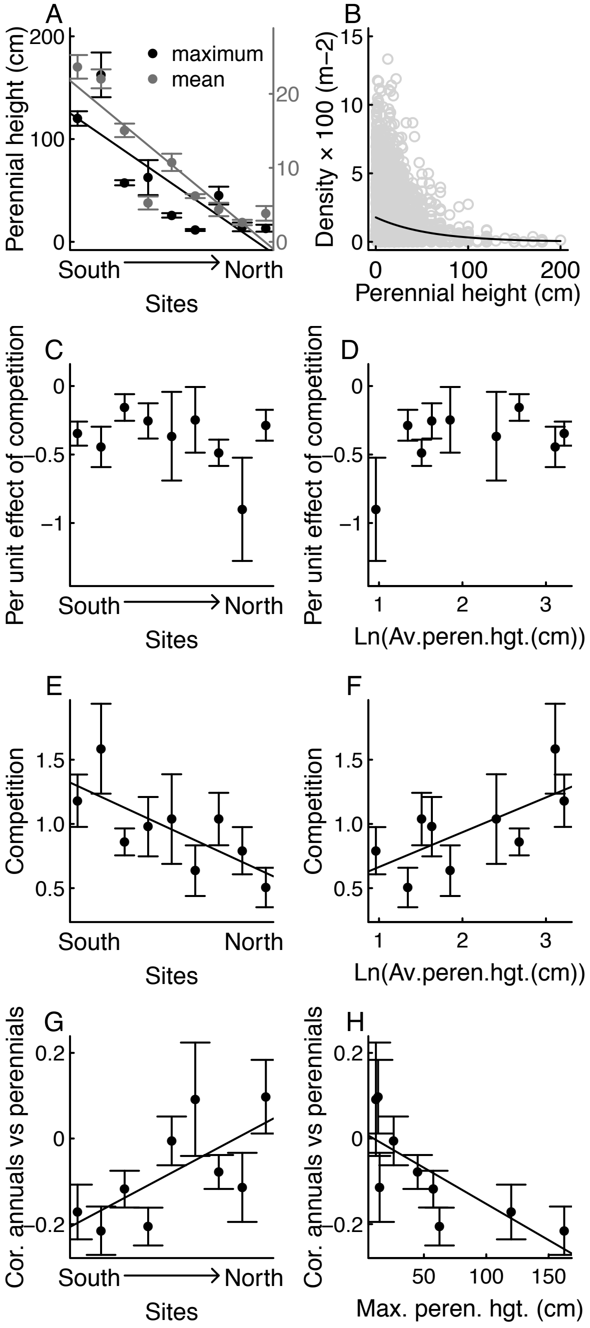

Figure 4. Changing perennial competitiveness along the sampled environmental gradient and corresponding correlations with annual species. Mean and maximum perennial height decrease significantly going from southern sites to northern ones (A). Across all sampled quadrats taller perennials are associated 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 heights (D). However estimates of the net effect of perennial competition on annuals (see Material and Methods) decrease 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.

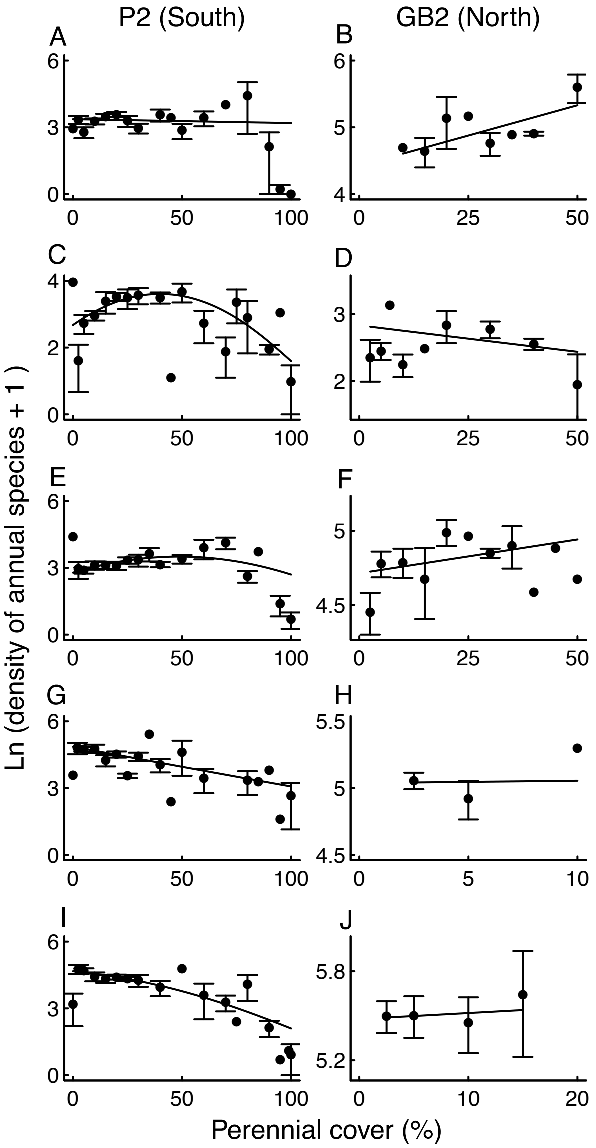

Figure 5. Examples of relationships between the densities of annual and perennial species for a southern transect (a single transect at site P2) and a northern one (single transect at site GB2), from 2008 (top) to 2012 (bottom). For each transect the logarithms of mean densities of annuals (m^{-2}) are shown for observed levels of perennial ground cover, with standard error bars. Solid 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.

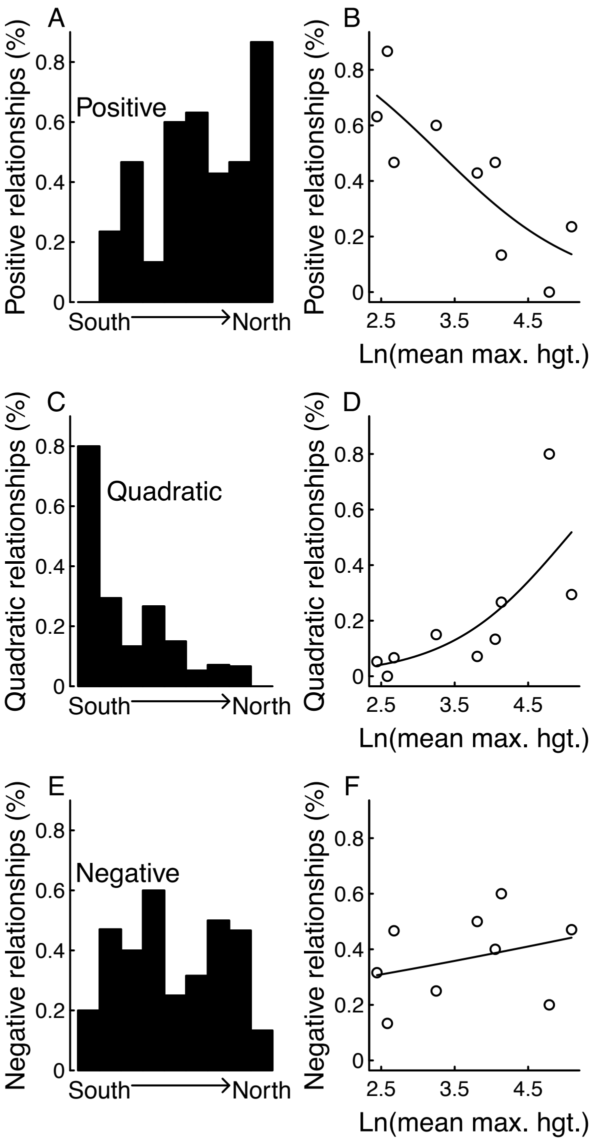

Figure 6. Frequency of the different types of relationship (positive, negative and quadratic) observed between perennial cover and dune annual density along the environmental gradient. Panels A, C, E show the proportions of transects across years where each relationship was found, for all nine sites.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

Online Appendixes

Online Appendix A. Existing spatial competition model (*Crawley and May 1987, Population dynamics and plant community structure: competition between annuals and perennials. Journal of Theoretical Biology 15:475-489*)

Appendix A1 Model description

In the main body of text we present a detailed exploration of a resource competition model where the gradient of environmental quality is represented either by a change in the per-unit negative effect of competition α_{12}, or by a change in resource availability R. In order to show that our model predictions are both realistic in dune annual/perennial plant systems and robust to the way worsening conditions are simulated along the environmental gradient, we include here the outputs of an existing spatial competition model fully described in Crawley and May (1987). We provide here a brief description of the model and of its outputs in the context of a gradient of environmental quality driven by changes in mortality (rather than resource availability).

The spatial competition model presented below was developed by Crawley and May (1987) and specifically simulates competition between perennial and annual species in a dune environment. As such it includes a number of assumptions known to be realistic for these particular systems. Briefly these are that i) perennials outcompete annuals when sharing space, ii) annuals have no impact on the demography of perennials, iii) perennials grow by lateral spreading to their immediate surroundings only (i.e. there is no long distance colonization) and iv) annuals disperse by seeds and this dispersal is not distance limited. Although perennials are better competitors than annuals, coexistence can still be achieved because annuals are in turn better dispersers than perennials and can reach any open space in the simulated habitat. Perennials and annuals exist on n by n lattice in which each cell can be occupied by a single individual annual plant or single perennial ramet. Death and birth events occur in a specific order in the model: at each time step some perennial ramets die then new perennial growth occurs. After these steps are completed annuals have the opportunity to settle within remaining empty spaces. This order reflects the fact that annuals can only settle if and when gaps open in the perennial vegetation cover. The model was initially used to explore the range of parameters (birth and death rates) that would allow stable coexistence between the superior perennial competitor and the inferior annual one. In the original version of the model only perennials experienced death events. Here we allow annuals to experience death events as well, and we use this modified version of the model to simulate competition along a gradient of increasing mortality. Realistic drivers of such a gradient in our study systems are worsening climatic conditions and increasing disturbance linked to grazing, both of which would affect equally annual and perennial species.

From this the dynamics of empty cells that open in the perennial vegetation cover can be described by the following equation:

$$E_{t+1} = \left(E_t(1-d)+d\right)\left(1-b(1-d)(1-E_t)\right)^6$$

E_t is the proportion of empty cells at time t, b is the birth rate of perennial ramets, d is the death rate of perennial ramets linked to disturbance. The exponent comes from the number of first order perennial neighbours that can theoretically colonize an empty cell.

Having accounted for perennial deaths and births in calculating the proportion of empty cells, annuals have the opportunity to colonize some of the remaining free space as described by the equation below.

$$A_{t+1} = \left(1 - exp^{(-cA_tE_t)}\right)(1 - d)$$

Where A_t is the proportion of total space used by annuals, c is the number of surviving seeds produced by each annual plant, E_t is the free space that can be colonized by annuals after accounting for death and birth events among perennials and d is the mortality rate linked to disturbance. The gradient of environmental quality is represented by running a succession of simulations with increasing mortality rates d (between 0.5 and 0.75). Throughout we use $c = 20$ and $b = 0.5$. We run the model for 1000 time steps. Note that there is no parameter that quantifies the per-unit effect of perennials on annuals in this set of equations and it is the net effect of competition by perennials as they cover a greater proportion of the lattice that increases with decreasing mortality. This type of competition can be thought of as interference competition since perennials pre-emptively occupy space rather than simultaneously exploit it alongside annuals (see Schoener 1983).

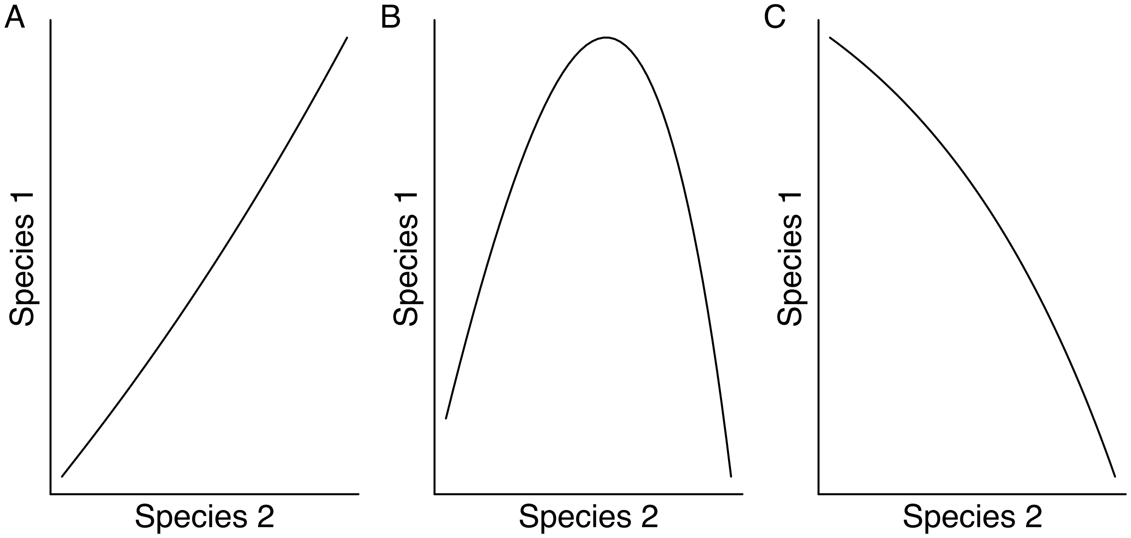

Figure A1 Predicted outcomes of Crawley and May's spatial competition model for dune perennials and annuals in the context of a gradient of disturbance-related mortality. As environmental quality increases and mortality decreases (A: *d* ranges from 0.7 to 0.75; B: *d* ranges from 0.58 to 0.63; C: *d* ranges from 0.5 to 0.55) relationships between species of the two guilds go from positive, to quadratic, to negative.

Online Appendix B. Study sites and species

Table B1 Geographical positions of all sampled sites.

Site	Lat.	Long.
P2 (Praia do Tocha, Aveiro, Portugal)	40.32	-8.85
P3 (Praia do Amorosa, Viana do castelo, Portugal)	41.65	-8.82
S1 (Monte Blanco, Galicia, Spain)	43.23	-8.93
F1 (Ondres Plage, Aquitaine, France)	43.58	-1.48
F2 (Les Conches, Vendee, France)	46.39	-1.49
F3 (Sainte Barbe, Bretagne, France)	47.60	-3.15
F4 (Hatainville, Normandie, France)	49.40	-1.82
GB1 (Penhale, Cornwall, UK)	50.22	-5.01
GB2 (Holkham, Norfolk, UK)	52.98	0.77

Appendix B1 Species of winter annuals included in the study and dominant perennial species along the sampled latitudinal range

The winter annual species included in the study were: *Arenaria serpyllifolia* (L.), *Asterolinon linum-stellatum* (L.)*, Cerastium diffusum* (L.)*, Cerastium semidecandrum* (L.), *Erodium cicutarium* (L.), *Geranium molle* (L.), *Mibora minima* (L.), *Myosotis ramosissima* (Rochel)*, Phleum arenarium* (L.), *Polycarpon tetraphyllum* (L.), *Saxifraga tridactylites* (L.)*, Senecio vulgaris* (L.)*, Veronica arvensis* (L.), *Viola tricolor* (L.)*, Viola kitaibeliana* (Schultes) and *Vulpia fasciculata* (Forskal). All those species germinate in the autumn or early spring and complete their life cycle by early summer, with the exception of *E. cicutarium*, which is occasionally biennial. From south to north and for each site, the dominant perennial species were *Corema album* (L.), *Sedum sediforme* (Jacq.), *Crucianella maritima* (L.) at P2; *Anthyllis vulneraria* ssp. *Iberica* (L.), *Artemisia crithmifolia* (L.), *Medicago marina* (L.), *Cistus salvifolius* (L.) at P3; *Daphne gnidium* (L.), *A. crithmifolia*, at S1; *Erica scoparia* (L.), *C. salvifolius* at F1, *Ephedra distachya* (L.), *Eryngium campestre* (L.) at F2; *Rosa pimpinellifolia* (L.), *Sedum acre* (L.)*, E. distachya* at F3, *Hypochaeris radicata* (L.), *Galium verum* (L.), *Festuca arenaria* (Osbeck), *Carex arenaria* (L.), *Leontodon taraxacoides* ((Vill.) Merat), *Plantago lanceolata* (L.) at F4; *Lotus corniculatus* (L.), *Thymus polytrichus* (A. Kern. ex Borbás) at GB1; *Festuca rubra* (L.), *G. verum*, *C. arenaria* at GB2.

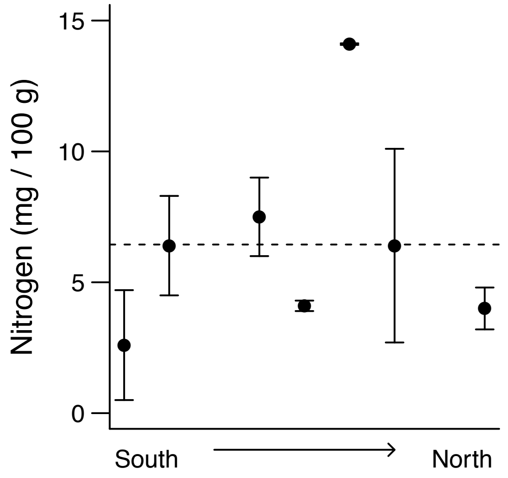

Figure B1 Soil nutrient concentrations along the latitudinal range. Variations in nitrogen soil concentrations were uncorrelated with latitude (slope = 0.11, n = 7, P = 0.78). Error bars represent standard deviations. Data taken from Doxford *et al.* 2012 (see full reference in main text).

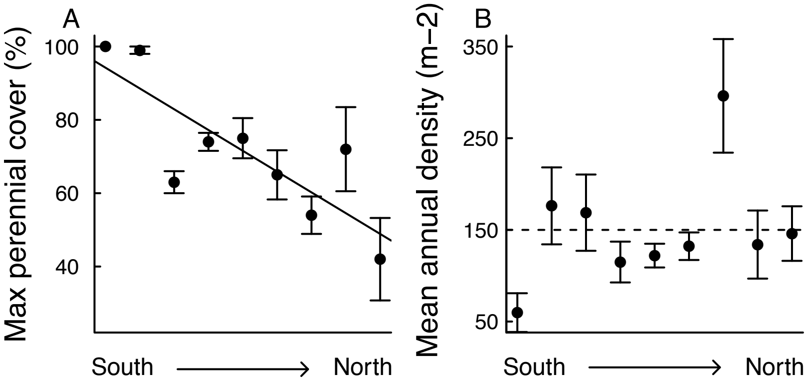

Figure B2: Additional figures documenting the variations in the densities of both perennial and annual species along the environmental gradient. The mean maximum perennial cover (slope = -3.691, n = 9, P = 0.006, (A)) decreases significantly with latitude. On the other hand mean density of annual species does not change continuously with latitude (slope = 5.46, n = 9, P = 0.339, (B)). Standard error bars are represented.

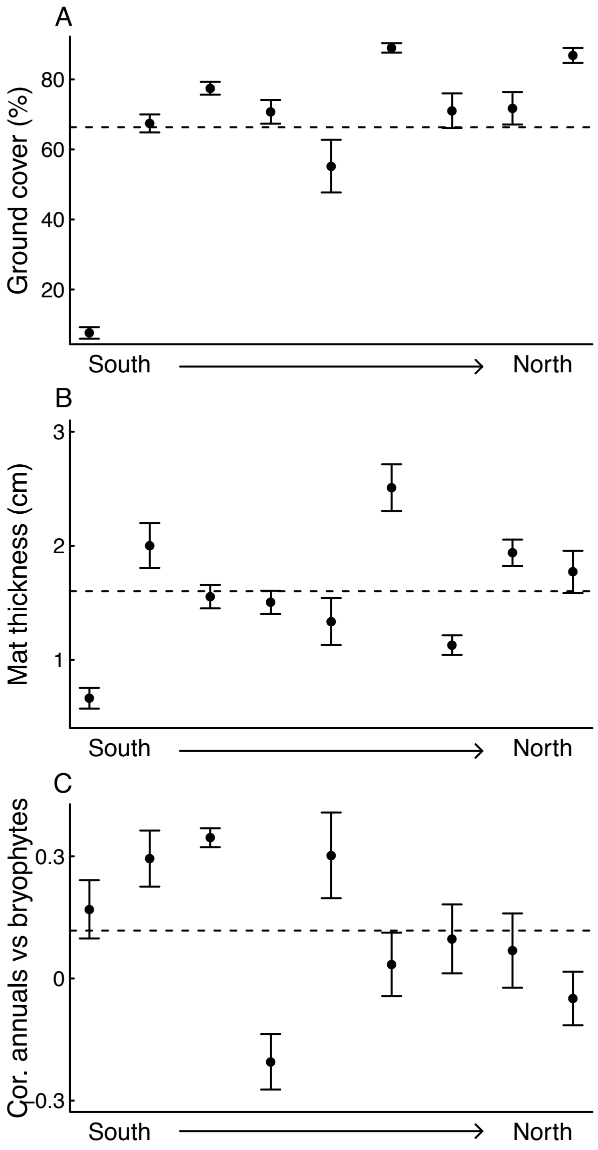

Figure B3 Changes in the ground cover and mat thickness of bryophytes along the sampled latitudinal range, and correlation with annual species. Ground cover and mat thickness (panels A and B) did not change systematically with latitude (slope = 3.45, n = 9, P = 0.08; slope = 0.04, n = 9, P = 0.365, respectively). Associations (correlation between annual species density and bryophyte ground cover) between annuals and bryophytes also did not vary linearly with latitude (slope = -0.02, n = 9, P = 0.296) and were generally positive (C). Dashed lines represent mean values across sites.

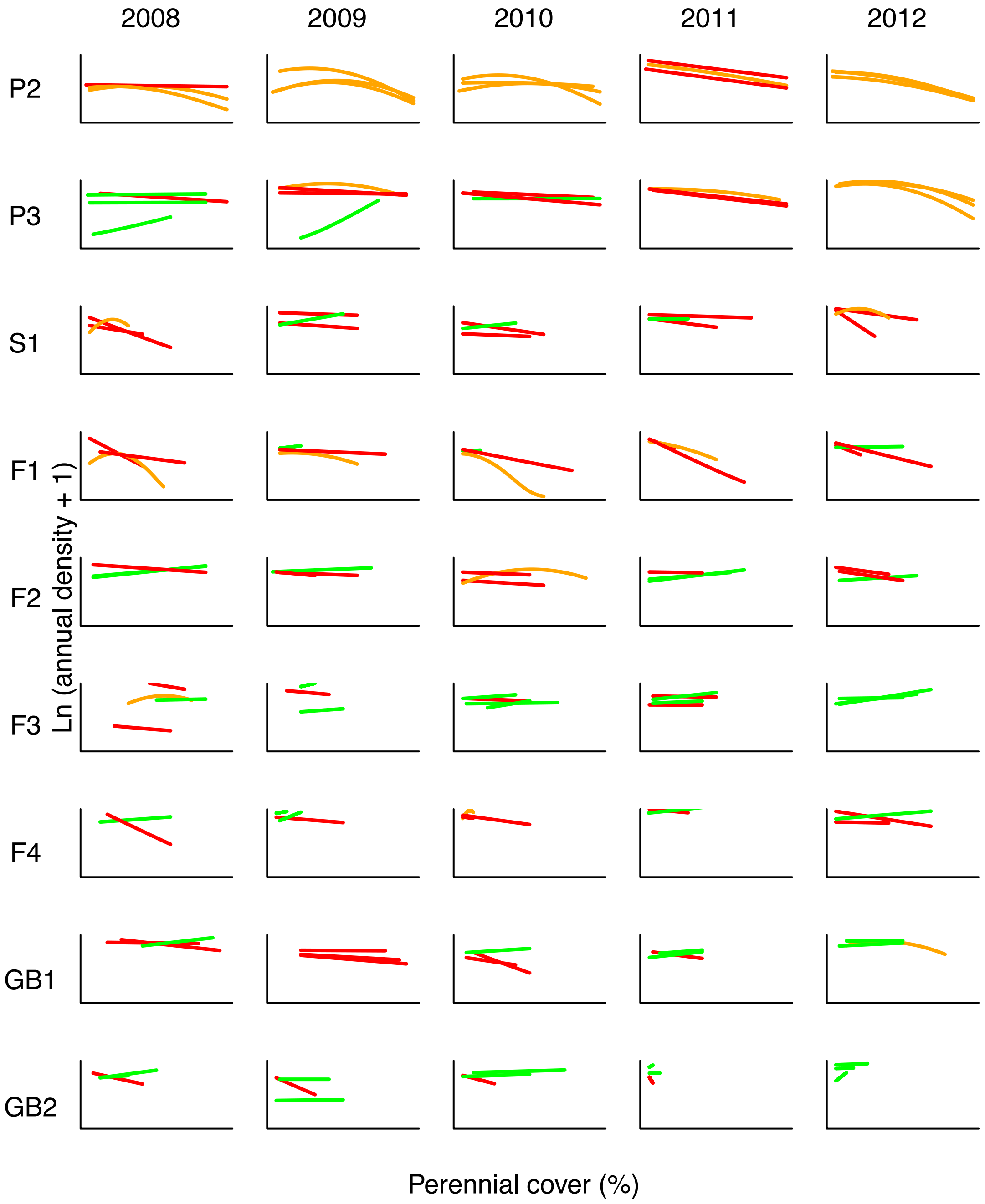

Figure 6. All 140 transect-level relationships between perennial cover and densities of annual species (m^{-2}) across all years and all sites. The types of relationship are color-coded: red for negative, amber for quadratic and green for positive.

Online Appendix C

Table C1 Mean per-unit effects of perennial competition on annual species (across transects and years for a given site).

Site	Mean slope estimates	Standard errors	One-sided t-test p value
P2	-0.35	0.09	0.001
P3	-0.44	0.15	0.005
S1	-0.16	0.10	0.068
F1	-0.25	0.13	0.037
F2	-0.37	0.32	0.141
F3	-0.25	0.24	0.160
F4	-0.49	0.10	0.001
GB1	-0.90	0.38	0.018
GB2	-0.29	0.11	0.014

All mean effects are negative (significantly so at 0.05 in the case of P2, P3, F1, F4, GB1 and GB2) suggesting that interactions between the two guilds are systematically competitive at all sampled sites.

Online Appendix D. Additional details on the method used to identify the type of relationships between the densities of annual and perennials species

In a very small number (2 cases) of transect-level relationships between perennial cover and annual abundance a “U-shaped” quadratic (rather than the much more frequently observed hump-shaped curve) best fitted the data. We tested the robustness of those relationships by re-fitting the data after discarding observations with excessive leverage i.e. data points that had a disproportionate influence on model parameter values. Leverages are the diagonal elements of the “Hat matrix”, which describes the influence of each observation on each fitted value. We excluded points with excessive leverage, which is generally defined as leverage greater than 2×(p/n), with *n* the number of observations and *p* the number of model parameters. Upon re-running the analysis on the new data subsets we found that both U-shaped relationships were not robust and were best described by the basic linear model. We therefore re-categorized them as basic linear and used the corresponding parameter estimates.