Competition increases with abiotic stress and regulates the diversity of biological soil crusts

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Summary

1. The stress-gradient hypothesis (SGH) predicts that the frequency of facilitative and competitive interactions will vary inversely across abiotic stress gradients, with facilitation being more common when abiotic stress is high. The effect of competition intensity on species richness is generally thought to be negative, but tests along true stress gradients are lacking. This body of research has primarily focused on vascular plants and could be well informed by broadening to other communities.

2. We report the first regional-scale test of the SGH using biological soil crusts dominated by mosses and lichens, a key multi-functional community of arid and semi-arid ecosystems worldwide. We examined the intensity of facilitative or competitive interactions at the level of the community and among species pairs along an aridity gradient. Along this gradient we also examined the relationship between competition intensity and species richness.

3. All evidence strongly suggested that negative species interactions are prevalent in this study system and much more common than expected by chance. At the community scale, we found that abiotic stress associated with aridity was positively related to and explained 6–56% of the variance in indicators of facilitation or competition, dependent on the index and algorithm used. Despite this intriguing contradiction of the SGH at the whole community scale, we found scant dependency of species-level interactions upon abiotic stress. However, the sign and intensity of these interactions proved to be species-specific. We also found that the relationship between competition and species richness, usually negatively affected by competition, was positively related to richness at low abiotic stress, and negatively related to richness at high abiotic stress.

4. *Synthesis*. We propose that the response of species interactions to stress gradients may partially depend upon the particular modes of facilitation and competition, in addition to type of stressor and life-history strategies of species involved. We also hypothesize that because stress can act as a filter, a greater number of species interactions are possible under low stress conditions. We believe that this may render intransitivity dominant over niche segregation and expansion, potentially resulting in positive effects of competition on species richness in low stress situations.

Key-words: cryptogams, drylands, facilitation, intransitivity, lichens, mosses, niche expansion, niche segregation, semi-arid, stress-gradient hypothesis

Introduction

The stress-gradient hypothesis (SGH) proposes that the frequency of facilitative and competitive interactions will vary inversely across gradients of abiotic stress, with facilitation being the dominant interaction under high abiotic stress conditions (Bertness & Callaway 1994). This hypothesis, based upon the plant strategy theory of Grime (1977), began a reversal of the dominion of competition theory in ecological theory (e.g. Tilman 1977) and led to a proliferation of research on facilitation as a force structuring communities (Callaway 2007; Brooker *et al.* 2008). Several studies, conducted usually in alpine or water-limited environments, supported the SGH (e.g. Greenlee & Callaway 1996; Callaway *et al.* 2002; Maestre, Bautista & Cortina 2003), although recent syntheses (Maestre, Valladares & Reynolds 2005) and empirical work (Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Kawai & Tokeshi

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2007) casts some doubt as to whether the shape of the relationship was indeed monotonic and positive, or whether other relationships were possible. It has recently been suggested that much of the work supporting the SGH examined only high- and low-stress treatments using pair wise interactions, rather than true stress gradients and community-level interactions, which are a more ideal test of the SGH (Brooker *et al.* 2008; Maestre *et al.* 2009a).

One of the major reasons why competition has been such a prevalent topic in ecology is because it can potentially explain some aspects of community structure (Grime 1973). It has usually been assumed that competition intensity is a constraint upon the number of species which can occupy a habitat (Grime 1973), and competition has long been hypothesized to be the mechanism driving the downward limb of the hump-shaped productivity–diversity curve (Michalet *et al.* 2006). Despite the proliferation of research on the SGH, very few studies have empirically examined the influence of community-level biotic interactions as a driver of species richness at the entire community level along abiotic stress gradients (Hacker & Gaines 1997; Kikvidze *et al.* 2005; Cavieres & Badano 2009). Furthermore, none have been conducted using organisms other than vascular plants.

Biological soil crusts (BSCs) are a key biotic community in drylands and other stressful systems and usually consist of some combination of bryophytes, lichens and cyanobacteria (reviewed in Belnap & Lange 2003). They are important multifunctional communities, which contribute to erosion resistance, influence hydrology and nutrient cycling and influence the establishment and performance of vascular plants (Belnap & Lange 2003). Generally speaking, BSC organisms are all stress tolerators because they must withstand UV exposure (Bowker *et al.* 2002), desiccation (Stark *et al.* 2004), high temperatures (Xu *et al.* 2009) and salinity (Chen *et al.* 2006). However, it is clear from four lines of evidence that the performance of most BSC species is hampered by abiotic stressors: (i) BSCs are more abundant in wetter, cooler climates and microclimates (Ponzetti & McCune 2001; Bowker *et al.* 2005); (ii) CO_2 exchange of soil lichens is steeply dependent upon water content up to saturation and strongly depressed at high temperatures (Lange *et al.* 1997); (iii) abundance of BSC organisms tracks intra- and inter-annual water availability (Belnap, Phillips & Smith 2007); and (iv) BSC performance is negatively impacted by experimentally increased frequency of small rain events, compared with fewer larger ones (Belnap, Phillips & Miller 2004).

Species interactions in BSC communities have only sparingly been examined. When a large number of stress-tolerant species overlap in distribution, the revised SGH predicts that there will be competition among them, even if they do not fit the competitor life strategy (Maestre *et al.* 2009a). To date, only two studies, conducted at a small scale at a single site, have actually documented the outcome of species interactions specifically using BSCs (Maestre *et al.* 2008, 2009b). These studies showed that competition is more intense than facilitation (Maestre *et al.* 2008) and that the intensity of competition decreases and increases when water or nutrients are limiting,

respectively (Maestre *et al.* 2009b). Thus, depending on the stressor examined, BSCs may support or contradict the SGH. Biological crusts are also intriguing in this context because the competition–facilitation mechanisms probably differ sharply from those of vascular plants. For example, competition for living space is of primary importance for BSCs rather than light competition or competition in the rhizosphere (Armstrong 2002). Facilitation may arise when interacting species pairs exhibit complementarity in resource acquisition strategies (Bowker, Maestre & Escolar 2010), or when a host lichen is an unwilling symbiont donor to a parasitic lichen (Schaper & Ott 2003).

In this study, we sought to test that biotic interactions in BSC communities follow the predictions of the SGH along a regional aridity gradient spanning from central to southern Spain. We also aimed to explore how these interactions drive species richness at the community level along this gradient. Evaluating the relative role of community-level biotic interactions and how it changes along environmental gradients is an important issue that has remained mostly overlooked by the facilitation–competition literature (Cavieres & Badano 2009). We examined community-scale indicators of the competition–facilitation continuum, as well as indicators at the scale of species pairs, using an observational approach, which has been put forward as a natural complement to the prevailing experimental studies and the only practical way to study the balance of species interactions at this observation scale (Brooker *et al.* 2008). Specifically, we asked the following questions: (i) At a large scale, is competition more prevalent than facilitation, as has been reported at small scales (Maestre *et al.* 2008)? (ii) As aridity increases, do facilitative species interactions increase monotonically (Bertness & Callaway 1994)? (iii) Is the correlation between biotic interactions and species richness dependent upon abiotic stress (Michalet *et al.* 2006)?

Materials and methods

STUDY REGION

This study was conducted at 18 sites located along an environmental stress gradient spanning about 112 400 km^2 over central, southern and eastern Spain (see Appendix S1 in Supporting Information). This gradient represents the range of conditions under which biological soil crusts are a prevalent type of ground cover in Spain. Among the sites, average annual precipitation and average annual temperatures ranged from 334 to 632 mm, and from 13 to 18 °C, respectively. Average minimum temperature ranged from 7 to 13 °C, and average maximum temperature from 20 to 22 °C. Vegetation in most cases was dominated by open steppes of *Stipa tenacissima*, whereas in three sites it was composed of open woodlands dominated by *Pinus halepensis* with an herbaceous or shrubby understorey. Eight sites were located on soils derived from limestones or calcareous marls, while the remaining 10 sites were located on gypsum-rich soils. All selected sites exhibited continuous, or more commonly, patchy biological crust cover in interspaces between plants, with sharp differences in community structure between the limestone-derived and gypsiferous soils. On gypsum soils, BSCs were dominated by lichens such as

Diploschistes diacapsis, *Squamarina lentigera*, *Fulgensia subbracteata* and *Psora decipiens*. On calcareous soils they were dominated by the mosses *Pleurochaete squarrosa*, *Didymodon* spp. and the lichen *Cladonia convoluta*. Despite their small stature and apparent niche overlap, many of these species differ strongly in chemical and morphological attributes in ways that probably strongly affect their function (see Appendix S2; Bowker, Maestre & Escolar 2010).

SAMPLING OF BIOLOGICAL CRUST COMMUNITIES

Within most sites ten 1.5-m line intercept transects were sampled for the assessment of community properties (one site is represented by seven transects, another by two due to curtailed sampling). Transects were non-randomly placed across multi-specific BSCs containing a minimum of 30 patches, which we considered necessary to calculate co-occurrence metrics. Within this constraint, we intentionally sampled transects with a wide variety in richness, cover, and dominance within each site. Transect placement was in all cases greater than 30 cm from the nearest perennial shrub or grass. In a few cases, small interspace size made it difficult to place 1.5-m transects, thus two parallel 75-cm long transects, spaced 30 cm apart, were sampled. Along the length of each transect the beginning and end of every interception of a BSC moss, lichen, rock or bare patch was recorded to a 1-mm resolution. Whenever possible, mosses and lichens were identified to species level in the field, otherwise they were ascribed to genera (*c*. 5% of taxa).

CHARACTERIZATION OF THE STRESS GRADIENT

Climatic attributes (annual radiation, temperature and rainfall) were collected for each site using available climatic interpolations for the Iberian Peninsula (Ninyerola, Pons & Roure 2005). In our study area, total annual precipitation, average annual temperature, average temperature minimum and average temperature maximum are all highly correlated. While temperatures can be high enough that they are a physiological stressor, they are so only during summer when the organisms are completely inactive due to desiccation. Rather, we view all of these variables as aspects of aridity. Precipitation of course increases water availability, and because higher temperatures drive potential evapotranspiration in times when BSC organisms are active, temperature decreases it. In keeping with this interpretation, we reduced the climate data to a single synthetic variable using principle components analysis (detailed below), and used it as a predictor of biotic interaction strength. The range of the stress gradient was similar in both soil types.

ESTIMATION OF BIOTIC INTERACTION INTENSITY

For the estimation of biotic interactions at the scale of the whole community, we used multiple community-level indices. In addition, we selected three species pairs common to all gypsum soils in the study area and examined pairwise interaction strength (detailed below).

Community-level comparisons

To estimate the outcome of biotic interactions at the community level, we carried out null model analyses of co-occurrence patterns (Gotelli 2000). This approach has often been employed to evaluate the importance of competitive interactions as a force structuring biotic communities (see Gotelli & Graves 1996 for a review), and in recent years it has been used to explore both competitive and facilitative interactions in vascular plant and BSC communities (Dullinger

et al. 2007; Maestre *et al.* 2008; Rooney 2008). We acknowledge that species co-occurrence can be affected by processes such as limited dispersal and habitat selection (Gotelli & Graves 1996). However, we believe that these aspects can only marginally affect co-occurrence in the studied communities because of the characteristics of the surveys employed (which minimized the sampling of non-suitable habitat) and the dispersal characteristics of the species studied (which make them quite unlikely to be dispersal-limited in the studied sites). We divided each transect into thirty 5-cm segments and for each the data were organized as a presence–absence matrix, where each row and column represents a different species and transect segment, respectively.

We estimated co-occurrence in each of the sampled transects (matrices) with two complementary co-occurrence indices: the C-score index and the number of species pairs. The C-score is calculated for each pair of species as $(R_i - S)(R_j - S)$, where R_i and R_j are the number of total occurrences for species i and j, and S is the number of squares in which both species occur; this score is then averaged over all possible pairs of species in the matrix (Gotelli 2000). The C-score is conceptually related to the concept of 'checkerboards', a species pair that never co-occurs in a sample. Checkerboards were viewed and enumerated as an index of competitive exclusion in classic ecology (Diamond 1975). The C-score determines the degree to which the spatial distribution of each species pair resembles a checkerboard and then finds an average value for the whole community. We selected the C-score among different available indices because it is relatively less sensitive to the presence of noise in the data and has good statistical properties (see Gotelli 2000 for a review). As the second complementary index, we used the number of species pairs, also considered originally by Diamond (1975). The logic underlying this index is that, at a fine scale, competitive exclusion should result in fewer species pairs co-occurring than expected by chance, given the number of possible pairings in the species pool (but see Kikvidze *et al.* 2005 and Hacker & Gaines 1997 for other views about the effects of species interactions upon diversity).

To determine the strength of co-occurrence in a sample, the co-occurrence indices are compared against a set of null models which serve as a baseline for what a community unstructured by species interactions would look like (Connor & Simberloff 1979). We used null models generated employing two different algorithms, 'fixed rows–equiprobable columns' and 'fixed rows–fixed columns'. The former retains species frequencies in the random matrices (i.e. rare species remain rare, common species remain common), but allows any number of species (from zero to the total number of species encountered) in each sample unit. The use of this null model has been recommended for standardized samples collected in homogenous habitats (Gotelli 2000). The latter algorithm retains both species frequencies in the random matrices and the number of species in each sample. The use of this null model has been recommended when each sample is a discrete entity, such as in the classic case of islands in an archipelago (Gotelli 2000). This is usually regarded as the most conservative null model comparison, as it allows the least deviation of a sample from its random expectation (Gotelli 2000). In our case − standardized samples collected in habitat patches that are somewhat discrete due to small-scale heterogeneity – there is no *a priori* method to determine which is the most appropriate null model. The best option in such instances is to use multiple null models and interpret them together. The indices obtained from each matrix were then compared with those derived from 5000 randomly assembled null matrices of both types.

Because the values of the C-score are dependent on the number of species and co-occurrences within each plot, we obtained a standardized effect size (SES) as $(I_{obs} - I_{sim})/S_{sim}$, where I_{obs} is the observed value of the C-score, and I_{sim} and S_{sim} are the mean and standard deviation, respectively, of this index obtained from the 5000 null communities (Gotelli & Entsminger 2006). In the case of the C-score, values of SES higher and lower than 0 indicate prevailing spatial segregation and aggregation among the species within a community, respectively, suggesting the dominance of competitive and facilitative interactions, respectively; in the case of the number of species pairs, these relationships are reversed. To obtain an estimate of overall prevalence of aggregation or segregation at the site level (co-occurrence patterns consistent with facilitation and competition, respectively), we averaged the SES values of each transect within sites. Null model analyses were conducted with Ecosim 7.22 (Gotelli & Entsminger 2006).

Analyses of species pairs

The co-occurrence metrics used above are useful for measuring the overall preponderance of aggregation or segregation in a community compared with a random expectation. Discrete samples often differ in species composition and therefore in which species pairs are present. To complement this information, we also calculated an interaction index for several species pairings which were present in enough samples (> 9) to analyse. We selected *Diploschistes diacapsis–Squamarina lentigera*, *Diploschistes diacapsis–Fulgensia subbracteata* and *Squamarina lentigera–Fulgensia subbraceata* as ubiquitous pairings at gypsiferous sites. The species composition and dominance varied widely among the sites with calcareous soils, thus there was no species pair which could be examined across all of them. For a given pair, we recorded the colony size of each species within each 5-cm segment of the transects and noted whether the species was growing in monoculture (in the absence of the other species) or in species mixtures (in the presence of the other species). We used interception length as a one-dimensional estimator of colony size. Unidimensional size measures have a history of use in lichenometry (Bradwell 2009); ours can be thought of as representing average diameter of a colony. The usage of 5-cm segments is based upon the observation that larger species such as *Diploschistes diacapsis* or *Pleurochaete squarrosa* could conceivably occupy the entire segment. However, as the average colony size was much smaller (0.94 cm) it was very frequent that multiple colonies of the same or different species occupied a given segment, thus with this segment size it was possible to observe either species aggregation or segregation. Because some transects had too few useful observations, we treated all transects within a site as segments of a single large (15-m) transect and pooled all of the observations within a site. To ensure an adequate number of monoculture and species mixture observations for each species of the pair, we ignored the presence or absence of other non-target species in the segment, and treated each segment as an independent observation. Thus, these analyses do not separate interactions among pairs from three-way or more complex interactions.

This pair-wise analysis had two advantages compared with the community-level approach: (i) the index of interaction was based upon suppression or facilitation of area, rather than on the frequency of complete exclusion, a more realistic scenario with lichen communities (Lawrey 1991); and (ii) the species being compared remained constant across the gradient, making this approach similar to most other tests of the stress-gradient hypothesis (Brooker *et al.* 2008). As an index of species interaction we used the Relative Interaction Index (RII; Armas, Ordiales & Pugnaire 2004), which compares colony size (or other performance measure) of species mixtures compared with monocultures. This index is positive when interactions are positive and negative when interactions are negative.

STATISTICAL ANALYSES

To reduce climate data to a single variable representing aridity, we conducted a principal component analysis based upon the correlation matrix (rotated to maximize correlation of variables with the axis) of our four climate variables. We extracted an axis with the following loadings, for use in the following analyses: mean annual precipitation $= -0.60$, mean annual temperature $= 0.92$, mean minimum annual temperature $= 0.92$ and mean maximum annual temperature $= 0.24$.

Based upon initial analyses (see Appendix S3), we excluded soil type as a factor and conducted the rest of our analyses on the pooled data set. To test the hypothesis that competitive interactions prevail in BSC communities, we conducted one-sample *t*-tests using the SES values of the various co-occurrence metrics and the RII indices from all of the species pairs. The set of values was tested against a null expectation of zero.

To provide an estimate of importance of competition or facilitation in community structure, we obtained correlation coefficients between one co-occurrence index (C-score using the fixed–fixed algorithm) and species richness for each site. One site with only two transects was excluded from this analysis.

To determine if the intensity of competition and its relationship with richness depend upon abiotic stress levels, we used a combination of Spearman rank statistics and linear regressions. The stress-gradient hypothesis suggests that under high abiotic stress species interactions will tend to be more facilitative, and under low abiotic stress they will tend to be more competitive (Bertness & Callaway 1994). However, it does not predict a linear relationship, or a particular curvilinear function. We adopted the Spearman rank test as our initial approach to testing for monotonic positive relationships between abiotic stressors and species interactions. More often than not we found that the relationship was approximately linear, thus we applied linear regression or Pearson's correlation as a better estimator of many of these relationships. All statistical analyses were conducted in JMP 4.0 (SAS Institute, Cary, NC, USA).

Results

COMMUNITY-LEVEL INTERACTION INTENSITY

Site means of SES of the C-score averaged 0.48 ($t = 4.6$, $P = 0.0003$) and 0.35 ($t = 3.5$, $P = 0.003$), using fixed–fixed and fixed–equiprobable algorithms, respectively. Results based upon the number of species pairs averaged -0.43 ($t = 4.6$, $P = 0.0003$) and -0.47 ($t = 5.6$, $P < 0.0001$), using fixed–fixed and fixed–equiprobable algorithms, respectively. Thus, regardless of the interaction index or algorithm being used, all t-tests indicated that net community-wide competition intensity was greater than would be expected by chance.

In general, the majority of evidence suggests that interactions in the BSC communities studied are well related to abiotic stress, but contradict the stress-gradient hypothesis; negative interactions become more prevalent as abiotic stress increases (Fig. 1). However, the strength of the evidence varies
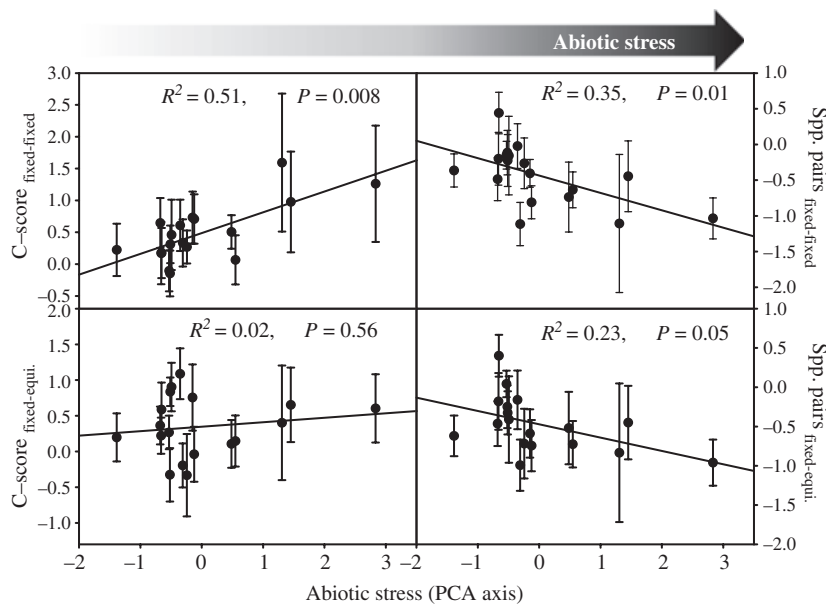
Fig. 1. Standardized effect sizes of mean co-occurrence statistics for each site as a function of abiotic stress. Each point represents one site and each error bar reflects the standard deviation among replicated transects within sites (usually 10). Linear regressions are fitted to site means.

based upon the null model algorithm used. Abiotic stress was strongly positive related to the C-score when using the fixed–fixed algorithm, accounting for 51% of the variance. We also recovered a positive slope using the fixed–equiprobable algorithm; however, the relationship was much weaker. The number of species combinations was also negatively related to the first PCA axis, explaining at least a fifth of the variance regardless of which algorithm was used.

INTERACTION INTENSITY AMONG SPECIES PAIRS

The *t*-tests revealed that species either had negative or neutral effects on one another's colony size, and effect sizes varied among the pairs (Fig. 2a). *Fulgensia subbracteata* exerted the strongest negative effect upon *D. diacapsis* ($t = -7.6$, $P < 0.0001$), whereas the effects of *D. diacapsis* on *F. subbracteata* were neutral ($t = 0.4$, $P = 0.65$). The pair *S. lentigera* and *D. diacapsis* exerted nearly symmetrical effects on one another ($t < -2.4$, $P < 0.02$). In contrast, the pair *F. subbracteata* and *S. lentigera* displayed no evidence of competitive or facilitative interactions ($t < 0.41$, $P > 0.58$). Correlation tests found scant evidence that pairwise species interactions are a function of abiotic stress (Fig. 2b). Correlations between the RII indices and abiotic stress were all fairly weak, with a high probability that any patterns were due to chance alone ($|\rho| < 0.41$, $P > 0.24$ in all cases).

EFFECT OF BIOTIC INTERACTIONS ON SPECIES RICHNESS

We found that the correlation between the SES of the C-score (using a fixed–fixed null model) and species richness is linearly and negatively dependent upon abiotic stress (Fig. 3). The most intriguing aspect of this result is that the sign of the direction switches from positive at low abiotic stress to negative at high abiotic stress.

Discussion

FACILITATIVE AND COMPETITIVE MECHANISMS

The majority of cases wherein the SGH is supported involves pairs of vascular plants and local facilitation brought about by buffering of abiotic stressors (usually climate-related), which offset the competition associated with proximity of another plant (Callaway 2007). Operating concurrently with these forces, plant competition generally manifests as competition for water and nutrients in the rhizosphere, or competition for light in the canopy (Grime 2001). The net balance of these opposing forces forms the basis of the SGH.

The lichens and mosses in most BSC communities are fundamentally different from vascular plants in terms of their facilitative and competitive mechanisms. Importantly, these organisms are primarily two-dimensional; therefore there is little canopy overlap as often seen with plants, and microclimatic buffering and light competition are probably unimportant forces in structuring BSCs. At high densities of BSC-forming organisms, competition for available living space is probably prevalent and an overlap is tantamount to a displacement in progress (Armstrong 2002). In rock lichen communities, which share these properties, it has been suggested that species with the fastest radial growth rates will tend to be the best competitors for space (Armstrong 1991). When morphology precludes spatial sharing, living space can become a surrogate resource which species may compete for (Crowley, Stieha & McLetchie 2004). Because BSC constituents do not have roots to transport water and nutrients, most resource uptake is thought to be accomplished by interception from the atmosphere or direct contact with the substrate (St. Clair *et al.* 2002). For this reason, the plant-centric mechanisms of competition and facilitation are not applicable, and occupation of more living space becomes even more important, because it also secures access to more resources.
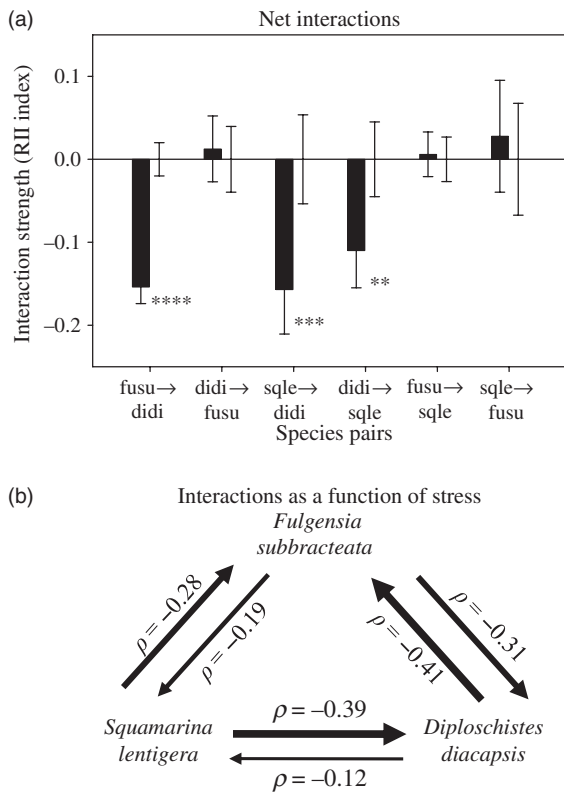
(a)

(b)

Fig. 2. Interactions among biological soil crust species pairs. (a) One-sample *t*-test results, testing the hypothesis that RII values (a facilitation index) for each site differ from zero. In all cases, the interaction strength appears in the left bar and the null model (mean = 0) on the right; error bars indicate one standard error. fusu, *Fulgensia subbracteata*; didi, *Diploschistes diacapsis*; sqle, *Squamarina lentigera*. (b) Spearman correlations between RII values for a pairwise species interaction and abiotic stress. Positive correlations would support the stress-gradient hypothesis; *ρ* is provided in all cases, arrow width is proportional to *ρ* statistics.

The relative unimportance of 'typical' facilitation mechanisms does not imply that facilitation does not occur among BSC constituents. Lichens and bryophytes exhibit an impressive chemical complexity. Some chemicals have a role in nutrient uptake (Hauck *et al.* 2009), and others may function in pathogen defence (Tay *et al.* 2004), thus species with complementary chemical arsenals may mutually benefit by association with one another. This chemical complexity also has a negative side in that there could well be a large number of allelopathic compounds (Tay *et al.* 2004). Differences in morphology may also strongly influence the redistribution of water resources (see Appendix S2), which could lead to facilitative species combinations (Spitale 2009). For example: (i) an unbroken crustose lichen is likely to shed water like a patch of exposed bedrock (Alexander & Calvo 1990), (ii) a thick moss colony might retain water like a sponge, and after saturation promote infiltration into underlying soil (Brotherson & Rushforth 1983). These features would suggest the existence of beneficial and detrimental combinations, but it has never been demonstrated that a benefactor moss or lichen can enhance water availability to a neighbouring beneficiary. Finally, much more so than in
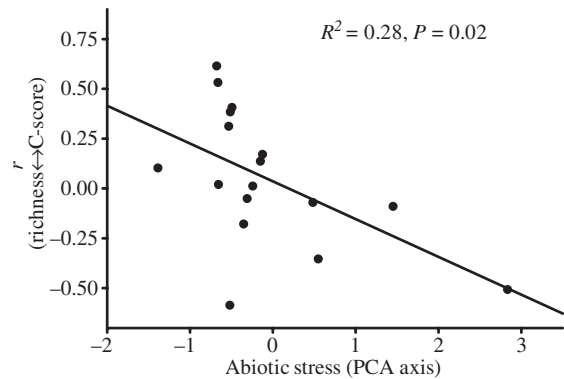

Fig. 3. The effect of competition–facilitation (indicated by the SES of the C-score calculated using the fixed–fixed null model) upon species richness changes along a stress gradient. At low stress, greater prevalence of competition is positively related to richness, whereas at high stress there are negative correlations. *r* = Pearson's correlation coefficient.

vascular plants, parasitism prevails in lichen communities. It is common for a lichen mycobiont to parasitize another lichen species, eventually stealing its photobiont and overtopping the original lichen (Schaper & Ott 2003); under this scenario, functioning as a host is a type of facilitation. The net balance of observed competition–facilitation probably depends on the degree to which the cumulative effects of these facilitative mechanisms offset the formidable effect of competition for living space and resource access.

The relative prevalence of competition among pairs observed in this study might be explained by the degree to which a particular species pair possesses complementary attributes. For example, we saw complete offset in the pair *F. subbracteata–S. lentigera*. This may have resulted from the complementary combination of parietins (*Fulgensia* spp.) and usnic acid (*Squamarina* spp.), chemicals which affect nutrient uptake under different pH optima (Hauck *et al.* 2009). On the other hand, *S. lentigera–D. diacapsis* have large colonies, exhibit aggressive lateral growth and are both probably water shedders (Cantón, Solé-Benet & Domingo 2004). Thus, competition for space and surface area to intercept rainfall probably accounts for the symmetrical negative interaction among this pair. The highly asymmetrical relationship among *F. subbracteata* and *D. diacapsis* is counterintuitive because we might expect the large, fast-growing and aggressive *D. diacapsis* to simply overgrow *F. subbracteata* (Armstrong 2002). That the opposite is closer to the truth is suggestive of a parasite–host relationship, but this possibility has not been reported and the reasons for this interaction outcome remain enigmatic.

TESTING THE STRESS-GRADIENT HYPOTHESIS

Maestre *et al.* (2009a) highlight the paucity of tests of the SGH which take into account all community members. The observational co-occurrence approach applied here has been criticized for assuming that detecting a pattern, e.g. species aggregation or segregation, is the same as the underlying process, e.g.

facilitation or competition (summarized in Gotelli & Graves 1996; Gotelli 2000). We maintain that pattern and process are related (e.g. Kikvidze *et al.* 2005; Tirado & Pugnaire 2005), rendering our approach useful but imperfect. Furthermore, there is no fully satisfactory alternative to testing the SGH using the whole community along true stress gradients, because the complexity of communities functionally precludes the traditional experimental approach except in the simplest of communities. Thus, we propose that our approach is appropriate for the questions we are asking and that it is a fundamental way to advance this body of research and a necessary complement to experimental approaches (Brooker *et al.* 2008).

The SGH has been recently revised to account for some of the inconsistencies in pairwise empirical tests, particularly the disagreement of results from some arid versus alpine zones (Maestre *et al.* 2009a). These authors proposed that whether or not the SGH is supported may depend on life-history strategies (stress tolerators versus competitors *sensu* Grime 1977) of the interacting species, and whether the stressor is a consumable resource or not. They predict that: (i) when a pair or group of interacting species fall into the same life-history strategy, competition will be more prevalent, and (ii) a positive relationship between abiotic stress and facilitation when the stressor is a resource which can feasibly be enhanced by one of the interacting species. The first part of this assertion is clearly supported in our work, both at the whole-community scale (Fig. 1) and among two of the three observed species pairings (Fig. 2). In this way, our work agrees remarkably well with the only other co-occurrence data on BSC lichens from a single site in central Spain (Maestre *et al.* 2008). A look at the sparse available literature of lichen and/or bryophyte communities suggests that either competitive interactions prevail [rock lichens (Armstrong & Welch 2007); *Sphagnum* bogs (Rydin 1993); heathland bryophytes (Scandrett & Gimingham 1989)], or net interactions are neutral [log-inhabiting bryophytes (McAlister 1995)]. Only two articles report an important role for facilitation in a bryophyte community (Mulder, Uliassi & Doak 2001; Spitale 2009). This broad pattern may arise because lichens and bryophytes tend to occupy stressful environments (as they cannot compete for light with taller vascular plants in less stressful environments) and because of the previously mentioned special importance of inhibition for living space (Armstrong 1991; Rydin 1993). Different results may be observed in bryophyte–lichen communities characterized by less abiotic stress or greater space sharing due to variation in growth form.

Competition intensity is predicted to decrease with increasing stress (Bertness & Callaway 1994), but we found the opposite in three of the four null models. What might account for this response? The primary abiotic stressor is undoubtedly water availability, which is affected both by rainfall and temperature. Thus, we must ask if it is possible for the considered organisms to enhance access to this resource for neighbours and reduce the relative prevalence of competition for space. We might hypothesize that the answer is related to the frequency of larger rain events, a variable that is probably related to both total annual precipitation and average annual temperature, and whether the species involved tend to be a run-off generators or water retainers. We do not have enough data to test this assertion across our entire gradient, but a comparison of rainfall event sizes in Madrid (central Spain, similar and close to sites at the least stressful part of the gradient) and Almería (SE Spain, similar and close to sites at the most stressful part of the gradient) during the pre-sampling period of 2007–08 revealed that Madrid received 45% more rain events, sufficient to saturate crustose lichens (*c.* 1.25 mm, Lange *et al.* 1997; daily climate data obtained from http://www.tutiempo.net). During a large rain event, a runoff generator will absorb water until its smaller capacity is satisfied and then create runoff from its surface which might be intercepted by neighbours with greater water requirements. A water retainer, such as a large moss, will absorb rainfall intercepted from above like a sponge, but when fully hydrated, will allow water to infiltrate into the soil. The moisture may be available to neighbours over multiple days *via* capillary action. The deeply infiltrated water will be less susceptible to evaporation from the surface, a temperature-linked process and available for a longer period of time. In this way, at lower abiotic stress levels, we can envision a scenario where facilitative effects on water availability may nearly balance competition for living space. On the contrary, if rain events tend to provide insufficient water to satisfy the needs of a runoff-generating species, no runoff will be generated and no excess water will infiltrate underneath a water retainer. Any infiltrated water will be retained very near the surface, where its evaporation will probably occur very quickly at warm temperatures. A closer examination of the functional traits of BSC species may allow a test of this hypothesis (Bowker, Maestre & Escolar 2010).

WHY DOES THE RELATIONSHIP BETWEEN RICHNESS AND COMPETITION–FACILITATION SWITCH?

The most unexpected result in our study was that competition is positively related to richness at low abiotic stress and negatively related to richness at high abiotic stress. We cannot fully explain these patterns here, but we can offer a hypothesis that can at least partially reconcile our results with prevailing theory (Fig. 4). The first step is to identify which mechanisms might result in positive or negative relationships between the C-score and richness. Intransitivity arises when there is no strict competitive hierarchy in a community [e.g. no one 'best competitor', only relative ones (e.g. a may outcompete b, b may outcompete c, c may outcompete a); Laird & Schamp (2008)]. In these circumstances, and countless other variations, the simultaneous negative interactions could result in a stalemate which precludes the complete exclusion of a, b, or c via indirect facilitation. In this way, competition may enhance local richness (Laird & Schamp 2008). This is easy to envision in the BSC system where chemical diversity, parasitism probability and variance in hydrological properties are so great; it is difficult to imagine that a single competitive hierarchy exists in this system. The mechanisms that could lead to a negative effect of competition (or positive effect of its converse, facilitation) are twofold, both related to the niche
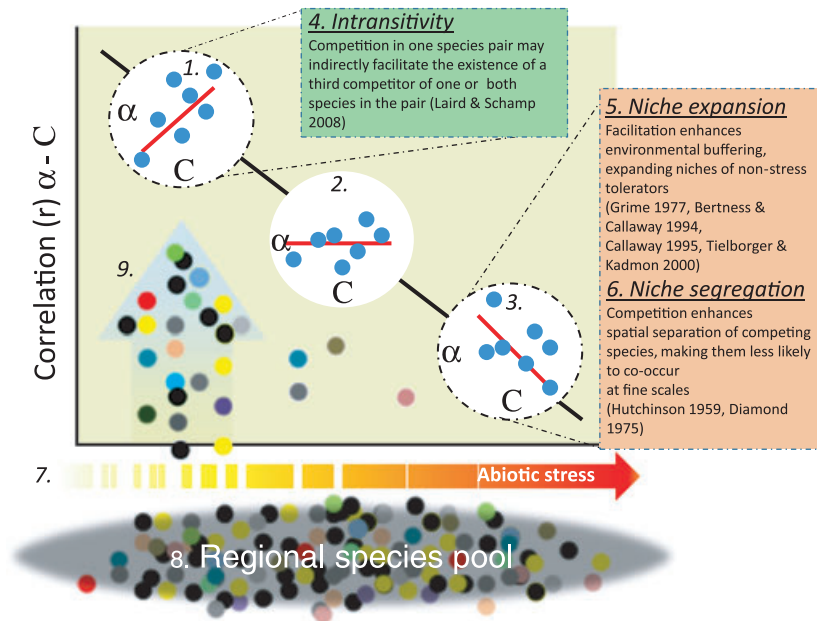
Fig. 4. Conceptual diagram of the shifting relationship between competition–facilitation (C) and richness (α) along a stress gradient (as stress increases, the slope of the relationship switches from positive to negative; illustrated in 1–3). The prevailing hypothetical mechanism by which competition could enhance richness is through transitivity (4). The prevailing hypothetical mechanism by which facilitation could enhance richness is niche expansion (5). The prevailing hypothetical mechanism by which competition could reduce richness is through niche segregation (6). Either (4) or (5) or their combined effects could result in a negative relationship between α and C. Abiotic stress (7) is pictured as increasingly permeable at the low end of the stress gradient. This reflects its efficacy in filtering suitable species from the regional species pool (8). We hypothesize that at low abiotic stress, the larger number of species combinations and ecological traits (multi-coloured dots) due to a less-filtered species pool, increases the dominance of intransitivity in controlling the effects of competition–facilitation upon richness (9).

concept (Hutchinson 1959): when facilitation prevails (often under high stress as predicted by the SGH), facilitative bene-factors can lessen abiotic stress for neighbours, expanding the niche of non-stress tolerators (Bruno, Stachowicz & Bertness 2003; Michalet *et al.* 2006); competition, on the other hand, has long been offered as an explanation for why local species richness is lower than the available species pool and why different samples contain different species compositions (Diamond 1975; Gotelli & Graves 1996). Competition may force a spatial segregation of competing species that may push some out of some samples, thereby lowering the species richness per sample. Indeed, co-occurrence analysis was designed to detect this (Gotelli 2000). Regardless of whether facilitation-driven niche expansion or competition-driven niche segregation is prevalent, either one would result in a negative dependency of richness upon the C-score.

What might account for a shift in the prevalence in these mechanisms from intransitivity to niche segregation or expansion as abiotic stress increases? We propose that, consistent with species pool theory, abiotic stress acts as an environmental filter (Keddy 1992) that is decreasingly porous as stress increases. The functional consequences are that more species from the species pool are available for community entry when abiotic stress is low. This leads us to the hypothesis that a greater variety of available species – and thus a greater number of combinations of allelochemicals, host-parasite relationships or resource acquisition strategies – leads to an enhanced prevalence of intransitivity, outweighing effects of niche segregation

or expansion. The conceptual model proposed in Fig. 4 is also consistent with recent conceptual developments in plant community ecology suggesting that both environmental conditions and biotic interactions are key determinants of community structure by filtering the species that can be found at any given site (Lortie *et al.* 2004).

CONCLUDING REMARKS

Our BSC study system displayed an overall enhancement of competition as abiotic stress increased, a result that does not match predictions of the SGH. We attribute this to the net balance of competition and facilitation mechanisms which prevail in BSCs. If our hypothesis is correct, this suggests that along with the type of stressor (resource versus non-resource) and life-history strategies of interacting species (stress-tolerator versus competitor; Maestre *et al.* 2009a), prevalent mechanisms of competition and facilitation should be considered as determinants of the response of species interactions to stress. This result might not have been observed using a vascular plant study system and highlights the utility of novel study systems for revising and broadening future iterations of the SGH. Furthermore, we observed that the expected negative relationship between spatial segregation of species and diversity also depends upon abiotic stressors. At low abiotic stress, we propose that more species are available for community entry, leading to an intransitivity-driven positive relationship between spatial segregation and diversity. Our conceptual model brings

together multiple lines of ecological theory including species pool theory (Keddy 1992), the competitive exclusion principle (Grime 1973) and the SGH (Bertness & Callaway 1994). We do not know the generality of these observations, but present this model as a testable hypothesis.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Main characteristics of the study sites along the abiotic stress gradient evaluated.

Appendix S2. Biological soil crust functional traits.

Appendix S3. Effect of soil type upon species co-occurrence.

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