Research

Oikos 118: 1015–1022, 2009
doi: 10.1111/j.1600-0706.2009.17362.x,

Subject Editor: Diego Vázquez. Accepted 27 January 2009

On the relationship between abiotic stress and co-occurrence patterns: an assessment at the community level using soil lichen communities and multiple stress gradients

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The stress-gradient hypothesis (SGH) predicts a shift from predominant competition to facilitation as abiotic stress increases. Most empirical tests of the SGH have evaluated the interactions between a single or a few pairs of species, have not considered the effects of multiple stress factors, and have not explored these interactions at nested spatial scales. We sampled 63 0.25-m^2 plots, each subdivided into 100 5 × 5 cm and 25 10 × 10 cm sampling squares, in a semi-arid Mediterranean environment to evaluate how co-occurrence patterns among biological soil crusts (BSC)-forming lichens changed along natural stress gradients driven by water and nutrient (N, P, K) availability. According to the SGH, we tested the hypothesis that the fine-scale spatial arrangement of BSC-forming lichens should shift from prevailing interspecific segregation to aggregation as abiotic stress increases. Co-occurrence patterns ranged from significant species segregation to aggregation at the two spatial scales studied. When using the 5 × 5 cm grid, more plots showed significant species segregation than aggregation. At this sampling scale, co-occurrence increased as water and nutrient availability decreased and increased, respectively. Small increases in soil pH promoted species co-occurrence. Interspecific segregation was promoted as the cover of highly competitive species, such as *Diploschistes diacapsis*, increased. No significant relationships between co-occurrence and the surrogates of abiotic stress were observed when data was arranged in a 10 × 10 cm grid. Our co-occurrence analyses partially supported predictions from the SGH, albeit the results obtained were dependent on the type of abiotic stress and the spatial scale considered. They show the difficulties of predicting how co-occurrence patterns change along complex stress gradients, and highlight the need of incorporating the effects of abiotic stress promoted by different resources, such as water and nutrients, into the conceptual framework of the SGH.

The study of biotic interactions and their implications for ecosystem structure, functioning and dynamics has been a core ecological research theme for decades (Grime 1979, Keddy 1989, Callaway 2007). Among the ample range of topics covered by this research, the analysis of the spatio-temporal variation of facilitative and competitive interactions along environmental gradients has occupied a prevalent place, especially during the last fifteen years (Brooker et al. 2008). This interest is not surprising, given the importance of this issue to accurately predict global change impacts on plant communities and ecosystems (Brooker 2006), and to understand the conditions under which biotic interactions restrict or enhance biodiversity (Michalet et al. 2006).

The relationship between the outcome of plant–plant interactions and the degree of abiotic stress has been formalized in a conceptual model known as the stress gradient hypothesis (SGH hereafter; Bertness and Callaway 1994, Callaway and Walker 1997). It predicts that the relative importance of facilitation and competition will vary inversely across gradients of abiotic stress, with facilitation being dominant under stressful conditions. Despite many studies have been conducted to test this prediction (reviewed by Callaway 2007), its generality and applicability are the subject of a vigorous and ongoing debate (Maestre et al. 2005a, 2006, Lortie and Callaway 2006). The simplicity of most of these experiments is likely responsible for a substantial part of current uncertainties and discrepancies on the SGH. Many of them have been conducted over two stress levels (but see Callaway et al. 2002), have not controlled for the occurrence of multiple stress factors (but see Kawai and Tokeshi 2007), have not distinguished appropriately between stress induced by resource and non-resource factors such as nutrients and temperature (Brooker et al. 2008), and have not appropriately considered ontogenetic effects (but see Miriti 2006). In addition, testing of predictions from the SGH is often hampered by the experimental design of the vast majority of past studies, which have simplified the complexity of natural communities by evaluating the interaction between a single or a few pairs of species (Maestre et al. 2005a, Brooker et al. 2008; but see Callaway et al. 2002, Valiente-Vanuet and

Verdú 2008). Because co-occurring species differ in their tolerance to abiotic stress, and this tolerance affects the outcome of biotic interactions (Liancourt et al. 2005), moving beyond the study of particular species pairs is crucial to increase our ability for predicting how these interactions change along abiotic stress gradients, and to accurately determine their relevance as a driver of community composition and structure (Brooker et al. 2008, Valiente-Vanuet and Verdú 2008).

To date, few studies have evaluated how interactions at the community level vary along ample and non-manipulated abiotic stress gradients (i.e. involving more than two levels; Kikvizde et al. 2005, Dullinger et al. 2007). Furthermore, and to our knowledge, none of them have been conducted with organisms other than vascular plants. With the aim to fill this gap, we evaluated the interplay between biotic interactions at the community level and abiotic stress using soil lichen communities forming biological soil crusts (BSC). These communities, which are widespread in arid and semi-arid ecosystems throughout the globe, influence ecosystem functioning by affecting soil nutrient cycling, stability, and infiltration, by modulating the establishment and performance of vascular plants, and by serving as habitats for a large number of arthropods and microorganisms (reviewed by Belnap and Lange 2003). BSC-forming lichens are also a good model system to test predictions from the SGH because biotic interactions are though to be important drivers of their structure (Maestre et al. 2008), and because their size and growth form facilitate the study of whole communities. The objectives of this study were twofold: (1) to test the prediction of the SGH that the magnitude of facilitation increases with abiotic stress (Bertness and Callaway 1994), and (2) to evaluate the effects of different stress factors on the outcome of co-occurrence patterns at the community level. To achieve these objectives, we conducted a null model analysis of co-occurrence patterns among BSC-forming lichens (Gotelli 2000), and related them to a complex abiotic stress gradient defined by water and nutrient availability. Recent studies have suggested that increasing competition and facilitation may lead to spatial segregation and aggregation between species, respectively (Purves and Law 2002, Tirado and Pugnaire 2005), and that shifts in net interactions along abiotic stress gradients are linked to shifts in the fine-scale spatial arrangement of species (Kikvidze et al. 2005, Dullinger et al. 2007). Similarly, and albeit the attribution of patterns to processes cannot be made without uncertainty, when potential confounding factors (e.g. differences in habitat suitability or disturbance) are not present, increasing spatial segregation and aggregation between BSC-forming lichens are likely to indicate increasing competition and facilitation, respectively (Maestre et al. 2008).

Methods

Study area and sampling

The study was conducted in gypsum outcrops located next to Belmonte del Tajo, Madrid province, in central Spain (40°7′3″N, 3°18′30″W, 686 m a.s.l.; 8° slope; 220° southwest aspect). The climate is Mediterranean semi-arid, with a mean annual temperature and rainfall of 14°C and 452 mm, respectively. The studied outcrops are surrounded by a well-preserved forest of *Quercus rotundifolia* and *Pinus halepensis*, but perennial plant cover within them remains below 20% (details in Maestre et al. 2008).

We focused only on lichens because they are the dominant component of BSC in gypsum outcrops of central Spain (Martínez et al. 2006). A total of 68 plots (50 × 50 cm), spreading over a homogeneous area of 1.3 ha, were placed non-randomly on bare ground areas with well developed soil lichen communities. This non-random placement of plots is commonly followed with these organisms because of their small size and their high within-site spatial variability (Maestre et al. 2005b, Bowker et al. 2006, Martínez et al. 2006). With this survey we aimed to capture the greatest possible contrast in lichen community composition and structure, avoiding changes in the proportion of suitable habitat among the plots that could confound the interpretation of the co-occurrence patterns observed (Dullinger et al. 2007). However, we established a minimum separation distance between plots of 0.7 m to minimize the risk of sampling non-independent areas because of the small-scale spatial structure of the communities studied (Maestre et al. 2005b). Each plot was divided into 100 5 × 5 cm sampling quadrats, and the cover of every lichen species in was registered in all the quadrats (6800 quadrats were sampled in total). This survey took place during the winter of 2005 and the spring of 2006.

Assessment of biotic interactions in soil lichen communities through co-occurrence patterns

For each plot, the data were organized as a presence–absence matrix, where each row and column represents a different species and sampling quadrat, respectively. With these data we conducted a null model analysis of co-occurrence patterns (Gotelli 2000). Co-occurrence analyses were run for two different spatial grain sizes: 5 × 5 cm (the original sampling scale; 5G hereafter) and 10 × 10 cm (10G hereafter). Data for the latter resolution were derived by aggregating every four neighboring 5 × 5 cm cells, i.e. producing 25 10 × 10 cm non-overlapping sampling squares per 50 × 50 cm plot.

We estimated co-occurrence in each of the 68 sampled plots (matrices) with the C-score index. It is calculated for each pair of species as $(R_i – S)(R_j – S)$, where R_i and R_j are the matrix row totals 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). If a community is structured by competitive or facilitative interactions, the C-score should be significantly larger or smaller than expected by chance, respectively. We selected the C-score among different available indices because it is robust to the presence of noise in the data and has good statistical properties (reviewed by Gotelli 2000).

The indices obtained from each matrix were compared with those derived from 10 000 randomly assembled matrices (null matrices). Their statistical significance was calculated as the frequency of simulated matrices that had indices that were equal to or more extreme to them. The null matrices were generated using a fixed rows–equiprobable columns null model (Gotelli 2000). It retains species frequencies in the random matrices (i.e. rare species remain rare, and 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). It has also good statistical properties (low type I error and good power to detect nonrandomness; Gotelli and Entsminger 2003), and two features that make it suitable for the objective of this study (Gotelli 2000): (1) it maintains the observed species occurrence frequencies, a conceptually satisfying assumption corresponding to a colonization model in which species colonize a given plot randomly with respect to one another, and (2) the species occurrences are random with respect to one another, which gives an appropriate null model for detecting patterns caused by species interactions. Null matrices were created with a sequential swap algorithm by repeatedly swapping randomly selected submatrices of the form 01/10 (see Gotelli and Entsminger 2006 for details). Extensive simulation analyses have shown that this algorithm is statistically well behaved (Gotelli and Entsminger 2003).

Because the values of the C-score are dependent on the number of species and the number of co-occurrences within each plot, and to make the results of different plots comparable, we obtained a standardized effect size (SES) for each plot. It was calculated 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 10 000 null communities (Gotelli and Entsminger 2006). Values of SES higher and lower than 0 indicate prevailing spatial segregation and aggregation among the species within a community, respectively.

Assessment of abiotic stress

Despite stress is a key concept in the ecological literature, its definition, application and measurement are still under debate (Körner 2003, Lortie et al. 2004). We define abiotic stress as any external condition that reduces the growth, survival and/or fecundity of the target individual/s (Grime 1979). According to this view, it has been suggested that abiotic stress is best measured using either the productivity of the community (Lortie and Callaway 2006) or the performance (e.g. survival, growth) of individuals of particular species without neighbors (Kawai and Tokeshi 2007). However, estimating abiotic stress in this way is difficult, if not impossible, when studying soil lichens because of their physiology and inherently low growth rate (Belnap and Lange 2003). Therefore, we used the total cover of each plot as an integrative indicator of abiotic stress at the community level (Dullinger et al. 2007). As BSC-forming lichens grow mostly in two dimensions, and none of the sampled plots had a cover higher than 70% (Table 1), total cover is likely to be well correlated with total biomass and productivity in the communities studied (Bowker et al. 2008). In addition to this integrative estimator, which includes the effects of both resource and non-resource stress factors, we evaluated stress promoted by both soil water and nutrient availability, as they are the main resources limiting performance of BSC-forming lichens in semi-arid areas (Bowker et al. 2006, Lange et al. 2006).

Table 1. Summary statistics of the lichen communities and of the surrogates of abiotic stress evaluated. n = 63 in all cases.

Variable	Mean ± SE	Range
Species density (number of species 2500 cm^{-2})	10.36 ± 0.44	3–17
Standardized effect size, 5 × 5 cm grid (unitless)	0.33 ± 0.22	−5.38–3.01
Standardized effect size, 10 × 10 cm grid (unitless)	−0.65 ± 0.21	−5.06–2.67
Total lichen cover (%)	26.61 ± 2.01	5.3–66.7
Soil surface roughness (unitless)	0.26 ± 0.09	0.14–0.44
Total soil N (mg g^{-1} soil)	0.71 ± 0.03	0.33–1.47
Total soil P (mg g^{-1} soil)	0.10 ± 0.004	0.04–0.19
Soil K (mg g^{-1} soil)	0.02 ± 0.001	0.01–0.04
Soil pH (unitless)	7.16 ± 0.02	6.58–7.49

We used soil surface roughness as a surrogate of soil water availability, rather than direct measurements of this variable, because of logistic difficulties associated to measuring relevant sources of water for soil lichens (mostly dew and soil moisture at the first cm of the soil profile; Belnap and Lange 2003, Kidron et al. 2002). It has been shown that soil surface roughness is directly related to infiltration, surface runoff and soil water availability in arid and semi-arid environments (Solé-Benet et al. 1997, Kidron 2007), and that this variable is a key driver of the performance and growth soil lichens in these areas (Davidson et al. 2002, Bowker et al. 2006). We estimated soil surface roughness using a dimensionless profile index (PI) obtained with the roller chain method (Jester and Klik 2005). PI was obtained as [(measured profile length/projected length)–1]. The PI value of each plot was obtained as the average of the PI obtained from five transects, separated 10 cm each and parallel to the maximum slope. A small chain (size of each link: 5 mm) was used to account for small-scale differences in surface roughness. An independent calibration proved that soil surface roughness measured with this index was negatively related to soil moisture at the 0–2 cm depth after spring rainfalls at the study site (Supplementary material Appendix 1). Therefore, we assumed that high values of surface roughness were associated to high abiotic stress promoted by low water availability.

We measured soil K, N and P as surrogates of nutrient availability. Soil K has previously been related to the abundance of BSC-forming lichens in gypsum soils (Martínez et al. 2006), and both N and P are limiting elements for these organisms in semi-arid environments (Belnap and Lange 2003, Bowker et al. 2006). In addition, we also measured soil pH, which controls the availability of macro- and micronutrients and has been related to the abundance of BSC-forming lichens in semi-arid environments (Bowker et al. 2006). Soil sampling was conducted in all plots in late September 2006, when the soil was dry after a pronounced summer drought. Five plots were excavated by rabbits between the vegetation and soil surveys, and thus were discarded for subsequent analyses. Twelve randomly-placed 19.63 cm^2 circular soil cores (5 cm ø × 1 cm depth) were sampled in each plot, bulked and homogenized in the field. Prior to sampling, the lichens were carefully removed with a knife to avoid measuring those nutrients incorporated in or adherent to them. Samples were air-dried for a month in the laboratory. Total soil N and P were obtained using a SKALAR San^{++} Analyzer after digestion in sulphuric acid; soil K was obtained using the same analyzer, but using water as the extracting agent. Nitrogen, P and K values were highly correlated among them ($r > 0.630$, $p < 0.001$ in all cases, $n = 63$). Therefore, we used in subsequent analyses the first axis of a principal component analysis conducted with these variables. This axis had an eigenvalue of 2.49, and explained 83% of the variance of N, P and K, which were strongly and positively correlated with it ($r > 0.840$, $p < 0.001$ in all cases, $n = 63$).

Statistical analyses

If co-occurrence patterns vary along abiotic stress gradients as predicted by the SGH, the fine-scale spatial arrangement of BSC-forming lichens should shift from prevailing interspecific segregation to aggregation as abiotic stress increases (Kikvidze et al. 2005, Dullinger et al. 2007). Therefore, we should find a positive relationship between the SES obtained at each plot (dependent variable) and the soil variables (independent variables), and a negative relationship between the SES values and microtopography (because its negative relationship to soil moisture, Supplementary material Appendix 1). We evaluated these relationships by using structural equation modelling (SEM). Details of this statistical approach can be found elsewhere (Shipley 2002, Iriondo et al. 2003), and only a concise description will be given here. In brief, a SEM analysis comprises three main steps: (1) model specification; (2) parameter estimation; and (3) model testing. Step (1) involves postulating a working model, which represents a hypothesis about essential causal mechanisms among a set of variables, as a path diagram. In this diagram, arrows indicate putative causal relationships among the variables. The model used in this study predicts that the different surrogates of abiotic stress measured determine co-occurrence patterns in BSC-forming lichen communities (Fig. 1). The relative effect of a variable upon another, indicated by an arrow (or path) in the path diagram, is evaluated through standardized path coefficients, which are equivalent to standardized partial regression coefficients. Step (2) estimates these coefficients by optimally adjusting the observed variance-covariance matrix to the path diagram. As recommended for our sample size ($n = 63$), the maximum likelihood method was used to estimate the standardized path coefficients in our model (see Shipley 2002 for details on this estimation). The significance of these coefficients was assessed using multivariate Wald-tests. Step (3) tests statistically whether the initial hypothesis fits the data. This is accomplished with a goodness-of-fit test that compares the covariance in the observed data with that expected if the working model is true. The test statistic is asymptotically distributed as a χ^2. Since the working null hypothesis is the exact opposite of that normally used in standard tests, a non-significant value indicates that the pattern of covariance predicted by the hypothesis is not distinguishable from that observed (Iriondo et al. 2003). In addition, the Bentler and Bonett's normed-fit index (NFI) and the goodness of fit index (GFI) were also used here as measures of the goodness of fit of the working model (Iriondo et al. 2003). These indexes range between 0 and 1, with values above 0.9 suggesting a good fit of the model to the data. Variance inflation factors were in all cases well below 10, suggesting the absence of collinearity (Iriondo et al. 2003). SEM analyses were performed with the CALIS procedure of SAS (SAS Inst.). Prior to these analyses, total cover was arcsine-transformed to achieve the normality in its distribution.

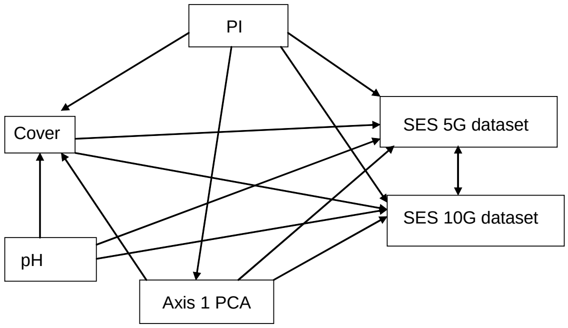

Figure 1. Hypothetical structural model showing the postulated relationships between the standardized effect sizes (SES) and the different surrogates of abiotic stress evaluated. PI = soil surface roughness, 5G = data obtained from the 5 × 5 cm grain size, 10G = data obtained from the 10 × 10 cm grain size.

Results

Our survey captured a wide range in the abiotic conditions in the study area, and in the species density and co-occurrence patterns of the lichen communities studied (Table 1). These patterns did not differ from randomness in most of the plots, regardless of the spatial scale considered (Fig. 2). More plots showed species segregation (i.e. observed C-scores significantly larger than the average of simulated C-scores) than aggregation (i.e. observed C-scores significantly smaller than

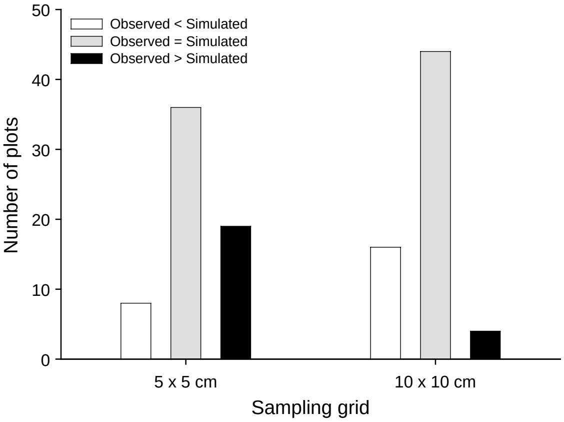

Figure 2. Number of plots where observed C-scores were significantly larger, smaller, or not significantly different from the average C-score of the randomized data. Differences were considered significant if observed values fell within the upper or lower 2.5% tails of the distribution of the 10 000 simulated C-scores.

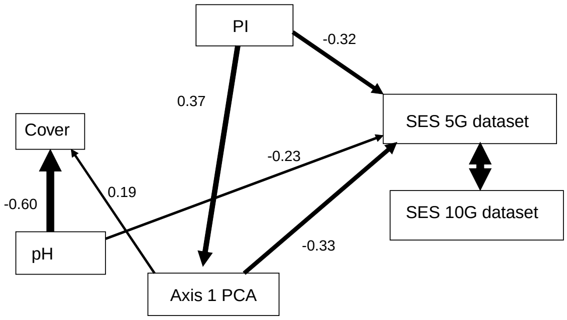

Figure 3. Results of structural equation modelling. Only significant paths are shown. The breadth of the arrow is proportional to the standardized path coefficient, which is indicated by the corresponding number. Rest of legend as in Fig. 1.

the average of simulated C-scores) when using the 5G dataset. The opposite pattern was found for the 10G dataset.

The hypothetical structural model created was satisfactorily fitted to our data, as suggested by a non-significant χ^2 value (7.53, DF = 1, p = 0.061) and by NFI and GFI values of 0.93 and 0.96, respectively. Microtopography, the first axis of the PCA conducted with N, P and K (PCA1) and soil pH were all negatively related to the SES values obtained with the 5G dataset (Fig. 3). None of these relationships were observed with the 10G dataset. Soil pH and PCA1 were negatively and positively related to total lichen cover, respectively, which was not related to the SES values at any of the spatial scales studied.

Discussion

Biotic interactions among BSC-forming lichens

More than 12% of the sampled plots (8 and 16 out of 63 when using the 5G and 10G dataset, respectively) showed higher co-occurrence than expected by chance, suggesting the presence of positive inter-specific relationships between BSC-forming lichens. These interactions can occur through mechanisms such as increased nutrient availability close to N-fixing species like *Collema* sp. (Belnap 2002), and increased water availability in the surrounding of those species capturing dew (Kidron et al. 2002) or promoting moisture retention (Verrechia et al. 1995). They can also be found when the mycobiont of particular lichen species can use the photobionts of other species to form a new thallus (Ott et al. 1995). On the other hand, negative interactions can arise through mechanisms such as allelopathy (Souza-Egipsy et al. 2002), genuine competitive displacement (Armstrong and Welch 2007), or physical interferences of some lichens acting as barriers to the propagules of other species (Cantón et al. 2004).

Our observational approach and measurements cannot provide fully mechanistic explanations for the results observed, but some insights can be gained by correlating the abundance of particular species on the results of co-occurrence analyses. The SES values showed a positive correlation with *Diploschistes diacapsis*, the most abundant species in the study area (significant and marginally significant when using the 10G and 5G databases, respectively; Supplementary material Appendix 2), suggesting that interspecific segregation was promoted as the cover of this species increased. *Diploschistes* contains lecanoric and diploschistesic acids (Nimis and Martellos 2004), secondary substances that could have allelopathic effects (Whiton and Lawrey 1984, Souza-Egipsy et al. 2002). In this direction, *Diploschistes* has been found to inhibit the emergence and early performance of annual plants (Escudero et al. 2007). This species can also negatively affect others by reducing soil moisture, as it forms compact mats that seal the soil surface (Cantón et al. 2004), and its wide and thick lobes are characteristic of highly competitive species (Armstrong and Welch 2007). On the other hand, the SES values showed negative correlations with the abundance of species like *Placidium squamulosum* and *Toninia albilabra*, suggesting that increases in the cover of these species promoted species aggregation. Interestingly, none of these species have secondary substances that could act as allelochemicals (Nimis and Martellos 2004). These patterns could also be explained by mycobiont-photobiont interactions; the mycobiont of *Fulgensia* sp. can successfully parasitize that of *T. sedifolia*, *Squamarina cartilaginea* and *Psora decipiens* to take over their photobionts and form a new thallus (Schaper and Ott 2003). If the mycobionts of other species can use those of *Placidicum scuamulosum* or *T. albilabra*, increases in their cover are likely to promote species co-occurrence.

Variations in co-occurrence patterns and the stress-gradient hypothesis

Total cover, which we assumed to be an integrative measure of all the abiotic factors limiting lichen growth, was not related to co-occurrence patterns at any of the two spatial scales studied. These results contrast with those of Dullinger et al. (2007) and Kikvidze et al. (2005), who found a positive relationship between co-occurrence patterns and vascular plant cover and biomass, respectively, in alpine plant communities. The lack of relationships found in this study suggest that, contrarily as hypothesized for vascular plants (Grime 1979, Michalet et al. 2006), productivity/overall biomass may not be a suitable surrogate of abiotic stress for BSC-forming lichens, at least at the spatial scales studied here. Alternatively, it is also possible that changes in net interactions along cover gradients are not important enough to translate in recognizable changes in co-occurrence patterns.

Species co-occurrence augmented as soil pH increased when using the 5G database, as indicated by the negative relationship between this variable and the SES values (Fig. 3). These results agree with those of Bowker et al. (2006), who found a positive relationship between soil pH and the abundance of moss- and lichen-dominated BSC at spatial scales similar to those used in this study. The observed variation in species co-occurrence in response to increases in soil pH was most likely driven by the effects of this variable on the abundance of those species apparently driving the SES values observed (e.g. *Diploschistes diacapsis*; Supplementary material Appendix 3).

Along the water availability gradient, higher co-occurrence than expected by chance was found under high stress conditions (with the 5G database). This pattern resembles that observed by Armstrong (1991, 2002), who found the intensity of competition within a saxicolous lichen community to be greater in north-facing than in south-facing rocks, the former characterized by higher water availability. Contrarily, co-occurrence among BSC-forming lichens was increased as nutrient availability augmented. According to these results, studies focusing on how nutrient additions affect the competitive interactions among saxicolous lichens have found that under conditions of high nutrient availability competition becomes more symmetrical, allowing species co-existence (Armstrong 2000, Welch 2002; but see Lawrey 1981, Vagts and Kinder 1999). Experimental studies have also found that the effect of particularly strong competitors is reduced in diverse lichen communities, allowing weaker competitors to coexist (Armstrong 1991, Armstrong and Welch 2007).

It could be argued that the observed co-occurrence patterns were promoted by between-plot changes in non-measured habitat attributes that could influence BSC development, such as micronutrients (Davidson et al. 2002, Bowker et al. 2006). Because the small size of our plots and sampling cells (5 × 5 cm cells), we expect such potential bias to be not relevant. Furthermore, the avoiding of unsuitable sites for BSC-forming lichens through the non-random placement of the plots, the location of nine of the 17 species found in more than 70% of the sampled plots, and the frequency of species like *Diploschistes diacapsis*, observed in all the sampled plots (Supplementary material Appendix 2), indicate that differences between plots in non-sampled habitat attributes alone are unlikely to be driving the results obtained. Albeit our study was conducted in a single year, we expect its results to be representative of what is happening in mature BSC communities. Without disturbances, these communities are very stable, and hardly change at the short to mid term because the slow growth rate of the constituting species, and the low amount of resources characterizing their habitat (Belnap 2003, Eldridge et al. 2006, Lázaro et al. 2008).

In short, our co-occurrence analyses partially supported predictions from the SGH, albeit the results were dependent on the estimator of abiotic stress and the spatial scale employed. As in this study, Dullinger et al. (2007) found that co-occurrence patterns among alpine plants weakly followed predictions of the SGH, with the detectability of the trends observed depending on the surrogate of stress and the spatial scale employed. The SGH predicts that positive interactions should be 'particularly common' or increase in 'frequency' under stressful conditions (Bertness and Callaway 1994), but co-occurring species do not respond equally to stress promoted by a given resource (see Lange and Green 2006 and Lange et al. 1997 for examples with lichens), in the same manner that stress created by resources such as water has different effects on the outcome of biotic interactions than that created by non-resources such as temperature (Maestre et al. 2009). Our results call attention to this limitation of the SGH when predicting how co-occurrence patterns change along complex environmental severity gradients. Current uncertainties and discrepancies on the SGH are driven by issues such as the variety of approaches used when examining biotic interactions, the scale at which processes are examined, and the type of abiotic stress gradient used (Brooker et al. 2008). Indeed, new refinements of the SGH are considering how different types of stress gradients (created by resources vs non-resources) may affect shifts between competition and facilitation between pairs of species (Maestre et al. 2009). Our results suggest that such developments should go further to include the effect of stress promoted by different resources on the outcome of biotic interactions at the community level. They also open the window for incorporating positive interactions into the study of soil lichen ecology, as they are likely more widespread than have been reported in the past.

Acknowledgements – We thank the owners of La Encomienda Mayor de Castilla estate for allowing us to work on their property, Nicholas J. Gotelli for insightful discussions on the use of null model analyses, and Matthew A. Bowker for revising the English of the manuscript. María D. Puche, Mónica García, Marta Carpio, Esther Polaina, Andrea Castillo and Santiago Soliveres helped during the field and laboratory work. FTM was supported by a Ramón y Cajal contract co-funded by the Spanish Ministerio de Ciencia e Innovación (MCINN) and the European Social Fund. CE was supported by a Studentship from the British Ecological Society (231/1975). This research was funded by an Early Career Project Grant from the British Ecological Society (ECPG 231/607). Additional support were provided by the Comunidad de Madrid projects GR/AMB/0932/2004 and REMEDINAL (S-0505/AMB/0335), by the MCINN project CGL2006-09431 and by the Fundación BBVA project INTERCAMBIO (BIOCON06/105).

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Supplementary material (available online as Appendix O17362 at <www.oikos.ekol.lu.se/appendix>). Appendix 1–3