The stress-gradient hypothesis does not fit all relationships between plant–plant interactions and abiotic stress: further insights from arid environments

FERNANDO T. MAESTRE†, FERNANDO VALLADARES‡ and
JAMES F. REYNOLDS†§

†*Department of Biology, Duke University, Phytotron Building, Science Drive, Box 90340, Durham, NC 27708-0339,
USA, ‡Instituto de Recursos Naturales, Centro de Ciencias Medioambientales, CSIC, Serrano 115, E-28006 Madrid,
Spain, and §Division of Environmental Science and Policy, Nicholas School of the Environment, Duke University,
Durham, NC 27708-0339, USA*

Summary

1 Our earlier meta-analysis of the effects of abiotic stress on the outcome of plant–plant interactions, suggested that the magnitude of the net effect provided by neighbours, whether positive or negative, was not higher under high abiotic stress conditions. This result, which does not support predictions of the stress-gradient hypothesis, has been questioned on the basis of limitations in our analytical approach, on the inappropriateness of some of the studies included in our data bases, and on the criteria used to select the levels of abiotic stress within each study. Here we provide additional arguments in defence of our approach and selection of studies, and perform further analyses of our data base that show that these criticisms are not well founded.

2 The inclusion of studies with contrasting abiotic stress conditions does not invalidate *per se* tests of predictions derived from the stress-gradient hypothesis because the hypothesis does not specify that predictions should hold for a given difference, or range of differences, in abiotic stress.

3 Our re-analyses show that differences in the length of stress gradient between the low and high stress levels across studies do not reduce the ability of meta-analysis to test predictions of the stress-gradient hypothesis, and that our approach does not suffer from 'hypothesis bias'.

4 Species interactions across abiotic stress gradients do not follow a simple pattern, and there are specific circumstances under which the predictions arising from the stress-gradient hypothesis do not hold. This hypothesis requires profound revision if all situations that emerge when evaluating the relationship between plant interactions and abiotic stress are to be 'fit' by a single conceptual paradigm.

Key-words: facilitation, competition, abiotic stress, arid, semiarid, plant–plant interactions, environmental gradients, meta-analysis

Introduction

Lortie & Callaway (2006; L & C hereafter) criticise our recent meta-analyses on the effect of abiotic stress on the outcome of plant–plant interactions in arid and semi-arid environments (Maestre *et al*. 2005). Two key results from our meta-analyses were that: (i) the experimental approach and the estimator of plant performance used had a crucial effect on the net outcome of plant–plant interactions and on the effect of abiotic stress on such outcome, and (ii) the magnitude of the net effect provided by neighbours, whether positive or negative, was not higher under high abiotic stress conditions. L & C question the validity of the latter result

Correspondence and present address: Fernando T. Maestre, Unidad de Biodiversidad y Conservación, Escuela Superior de Ciencias Experimentales y Tecnológicas, Universidad Rey Juan Carlos, c/Tulipán s/n, 28933 Móstoles, Spain (tel. +34–914888511; fax +34 916647490; e-mail: fernando.maestre@urjc.es).

on the basis of limitations in our analytical approach, on the inappropriateness of some of the studies included in our meta-analyses, and on the criteria used to select the levels of abiotic stress within each study. They conduct additional analyses of some of our data bases that led them to support the predictions of the stress-gradient hypothesis (Bertness & Callaway 1994). In this reply we assess the suitability of our approach, discuss the appropriateness of the studies included in our data bases, and evaluate the re-analyses conducted by L & C. We also present further re-analyses of our data bases that show that most of L & C's concerns are not well founded.

Suitability of our approach

L & C implicitly suggest that our meta-analytic approach is inherently flawed because meta-analyses in general are ill-suited to determine the generic predictability of conceptual models such as the stress-gradient hypothesis. We disagree with this assertion. Our aim was to evaluate, using the empirical evidence accumulated to date, a single, testable prediction derived from the stress-gradient hypothesis: that the magnitude of the positive effects of neighbours on a target species/group of species increases with abiotic stress in arid and semi-arid areas. However, we acknowledge that some points of our article require clarification and that there are intrinsic limits in the meta-analyses carried out.

A major objection of L & C is our delimitation of abiotic stress levels (low vs. high) in the primary studies included in our data bases. Whereas abiotic stress is a key concept in the ecological literature, its definition and application continues to be debated (e.g. Körner 2003; Lortie *et al*. 2004). We defined abiotic stress as any external condition, apart from the activities of other organisms, that reduces plant growth, survival and/or fecundity (p. 749 in Maestre *et al*. 2005). We agree with L & C that assigning abiotic stress levels based on the use of environmental surrogates is difficult, and that stress is best defined via patterns of productivity (Grime 1979). However, using productivity as a surrogate of abiotic stress when summarizing primary literature presents many practical problems. Productivity is rarely measured across sites and/or years, and the assumption that plant performance is reduced as abiotic stress increases is not problem-free. Requirements for survival often differ from those for fecundity or growth (Biere 1995; Escos *et al*. 2000), and thus the effects of neighbours on different performance variables for a given level of abiotic stress may differ (Maestre *et al*. 2005), making the assignment of stress levels difficult. For instance, if plant survival does not differ between two sites/years that differ in total rainfall, should we interpret that both sites/years do not differ in abiotic stress? Similarly, if two simultaneously measured indices of plant performance show opposite responses, e.g. a decrease in fecundity but an increase in height, which should be selected as the surrogate of abiotic

stress? Productivity in arid and semi-arid areas often increases with increasing rainfall, nutrient availability and water availability due to topography (e.g. Noy-Meir 1973; Gutiérrez & Whitford 1987; Pickup 1996; Sternberg & Shoshany 2001). Thus, we believe that the criteria we used to define the levels of abiotic stress within each study were reasonable for the purpose of our meta-analyses. In fact, a comparison of our abiotic stress classification scheme with plant performance data (see Appendix S1 in Supplementary Material) showed that, in the majority of cases, plant performance was higher in our 'low' stress category (survival: 60%, growth: 68%, density: 82% and fecundity: 90%).

The approach we followed (the comparison of relative effect sizes across studies at two levels of abiotic stress) is similar to that of a recent meta-analysis evaluating the effect of abiotic stress on the facilitative effect of shrubs in Mediterranean mountains (Gómez-Aparicio *et al*. 2004). L & C argue that this approach cannot be used to test predictions from the stress-gradient hypothesis, posing the question 'were the differences in stress in specific studies sufficient to test the stress-gradient hypothesis?' This question is germane, and raises a related one: how much stress is needed to test the hypothesis? Neither the original study (Bertness & Callaway 1994) nor further refinements to the stress-gradient hypothesis (e.g. Callaway & Walker 1997; Dormann & Brooker 2002) state that all predictions must hold for a given difference, or range of differences, in the degree of abiotic stress considered. This is a critical point that is often overlooked. It is implicit that there must be a 'minimum gradient length' in the degree of abiotic stress to shift the net outcome of a given plant–plant interaction but, as formulated, the stress-gradient hypothesis does not explicitly consider gradient length. In fact, empirical studies have attempted to 'fit' the predictions of this hypothesis over abiotic stress gradients of different lengths and, to our knowledge, none of these have explicitly considered this factor. Thus, we do not believe that the inclusion of studies with contrasting abiotic stress situations *per se* invalidates the test of the predictions of the stress-gradient hypothesis.

As recommended by L & C, we tested the 'internal validity' of the experiments used in the survival and growth data bases by evaluating the relationship between the absolute difference in effect size and the length of the abiotic stress gradient within each study. As proposed by L & C, we used the standardized difference in survival (survival data base) or growth (growth data base) of the controls (plants growing in the absence of neighbours) between the low and high-stress sites to measure this length. L & C's Fig. 2 predicts that the absolute difference in effect size should increase with the length of abiotic stress gradient within each study until an asymptote is reached. The results of our re-analyses do not follow this prediction. There was no effect of within-study gradient length on effect size when evaluating survival data (Fig. 1a) and a linear relationship for growth data (Fig. 1b). It is worth
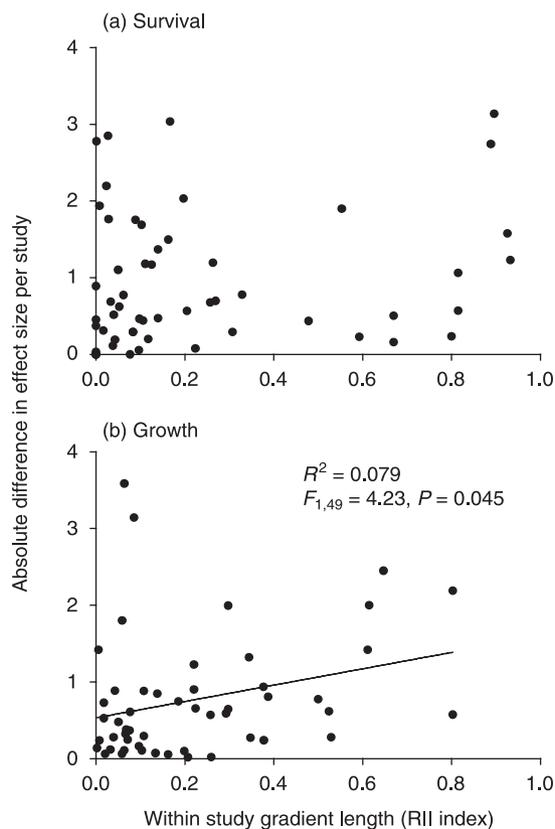
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the stress-gradient
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Fig. 1 Relationships between the absolute difference in mean effect size per study (*y* axis) and the length of the abiotic stress gradient within each study (*x* axis) for the (a) survival and (b) growth data bases. Data in the *y* axis represent the absolute difference in the mean effect sizes of survival or growth between the low and high abiotic stress levels. Data in the *x* axis represent the absolute standardized difference (measured with the RII index) in either survival or growth of the controls (plants growing in the absence of neighbours) between the low and high-stress sites. RII was calculated as $(P_1 - P_h)/(P_1 + P_h)$, where P_1 and P_h are plant performance data (survival or growth) in the control treatment (i.e. in absence of neighbours) in the low and high abiotic stress levels, respectively (Armas *et al.* 2004). The data were fitted to polynomial (linear, quadratic and cubic) and non-linear (exponential of the form $y = y_0 + a[1 - e^{-bx}]$) models. Only significant relationships ($P < 0.05$) are shown.

emphasizing, however, that this relationship explained less than 8% of the variation found in the data, and that some of the largest differences in effect size between low- and high-stress levels were found in studies that had short abiotic stress gradients. A thorough discussion of these results is beyond the scope of this reply, but any extrapolation should bear in mind the low number of studies available. Nevertheless, this re-analysis suggests that the concerns of L & C regarding the delineation of abiotic stress levels within each study were not entirely justified. However, we do agree with L & C that the effect of the length of abiotic stress gradient on the outcome of plant–plant interactions is an important topic that deserves further attention and discussion.

Appropriateness of the studies included in our data bases

L & C criticise the inclusion of many of the studies we entered into our analyses because they 'were not conducted along stress gradients, did not identify a stress gradient within the study, focused on invasive species, or were not peer reviewed'. As stated (p. 750 in Maestre *et al.* 2005), we selected studies that evaluated the net outcome of a given plant interaction under contrasting abiotic stress conditions, without specifying *a priori* the magnitude of such differences. As discussed in the preceding section, we do not believe that this fact *per se* invalidates our analyses. In addition, we do not agree that inclusion of studies focusing on invasive species and of non peer-reviewed studies is necessarily a drawback. The gradient-stress hypothesis does not restrict its predictions to plants of a given geographical origin, and using multiple search strategies (e.g. journals, theses, conference proceedings) when selecting studies has been recommended for ecologically based meta-analyses (Gates 2002).

L & C question whether the original studies are appropriate tests of the stress-gradient hypothesis. We acknowledge that many of the studies included in our data bases did not originally aim to test this hypothesis (in fact, many were conducted prior to its formulation). However, this does not invalidate our study selection because, as stated above, this hypothesis does not state that predictions apply to a given abiotic stress gradient 'length'. Without clearer indications on the 'minimum length' of the abiotic stress gradient needed to shift interactions from competition to facilitation, how can one decide if a given study constitutes an appropriate test of the stress-gradient hypothesis? The answer to this question is difficult from a practical point of view, because the 'real' within-study gradient length is dependent on many aspects not considered by the stress-gradient hypothesis; namely, the source of stress, the species being tested, the experimental approach used and the estimator of plant performance employed. Thus, further elaboration of the stress-gradient hypothesis is required so its predictions can be tested in a meaningful way.

L & C identify specific studies they deem inappropriate or that violate one of our inclusion criteria (see column 1 of their Table 2). However, they do not indicate the criteria violated or the reasons why such studies are inappropriate. Furthermore, they conduct an alternative search that led to additional studies not considered in our analyses (columns 2–3, their Table 2). A careful examination of these additional studies reveals that most of them do not meet all of our inclusion criteria (Appendix S2). Surprisingly, some of the studies listed by L & C as 'papers that adequately identified an abiotic gradient and showed a significant shift from negative to positive plant–plant interactions with abiotic stress' do not show such a shift (e.g. Maestre *et al.* 2002), do not evaluate the effect of abiotic stress

on plant–plant interactions (e.g. Gutiérrez *et al.* 1993) or do not assess plant–plant interactions (e.g. Hastwell & Facelli 2003). L & C highlight the absence of the Gómez-Aparicio *et al.* (2004) paper in our data base in spite of the fact that we specifically noted that it was conducted in dry subhumid Mediterranean mountains, and thus was excluded (see p. 749 in Maestre *et al.* 2005).

We acknowledge that it is difficult, if not impossible, to include all relevant primary studies in a meta-analysis, and certainly our search may have missed some pertinent studies. However, it was thorough and comprehensive, and we believe that the studies included in our meta-analyses are both representative and appropriate. We agree with L & C that conclusions derived from meta-analyses are necessarily conditioned to the studies included in it. In fact, we noted some of the limitations of our meta-analyses and clearly indicated that our results should be interpreted with caution (p. 754 in Maestre *et al.* 2005).

Interpretation of additional analyses conducted by L & C

L & C conduct thorough re-analyses of our survival data base, which provide important results for further discussion (see L & C's Table 1 for summary). They repeat the meta-analysis of survival data excluding multiple species from single studies and conducting separate meta-analyses separately for each functional group. The results of these analyses do not modify the outcome of our original analyses, and thus will not be further discussed here. L & C also evaluate the coefficients of variation for survival effects, and the results of these analyses led them to question again the delineation of our abiotic stress levels ('… was not sufficient [ecologically different enough] to allow meaningful shifts between competition and facilitation'). Our analysis of the relationship between the absolute difference in mean effect size per study and the length of the abiotic stress gradient within each study (Fig. 1a) does not support their view. Thus, we believe that this criticism is not fully justified, and that alternative explanations should be explored when discussing the lack of differences in the relative variation between survival effects.

L & C show a positive relationship between the magnitude and variance in the effect size of growth and survival responses (L & C's Fig. 4). Based on this relationship, L & C claim that the stress-gradient hypothesis 'clearly fit some studies less well than others', that our analyses suffer from 'hypothesis bias', and that the variability of studies reduces the ability of meta-analysis to test predictions of the stress-gradient hypothesis. We repeated the analyses made by L & C by using all the studies that reported survival and growth responses for the same plant/plant or plant/group of plants interaction, and found only 6 studies for these analyses (not 16 as reported in L & C's reply), which

provide 14 cases for each abiotic stress level. Our re-analyses show no significant relationship between the magnitude of effect sizes or variance in survival and those in growth at either stress level (Appendix S3). Thus, we are not able to reproduce the results reported by L & C. Without knowing which studies were used by L & C in their re-analysis of our data we cannot fully explore this discrepancy. However, the results of our re-analysis rebut L & C's claims.

L & C evaluate the potential of meta-analysis to test predictions from the stress-gradient hypothesis under the most favourable conditions by conducting a meta-analysis with a subset of studies showing a switch from competition to facilitation with increasing levels of stress (L & C's Fig. 5). Surprisingly, this re-analysis does not support the stress-gradient hypothesis. In L & C's Fig. 5, the mean effect of neighbours in the low stress category is higher than that obtained in the high stress category, a result that is not possible if each included study shows a significant switch in net interactions from competition to facilitation (i.e. if the effect of neighbours in each study case is more positive at the high stress level). Given this unexpected result, we attempted to repeat this analysis by using all the studies used by L & C to run this analysis (studies that overlapped between our survival data base and those presented in column 2 of L & C's Table 2). We were not able to derive a data base with 52 suitable cases, as reported by L & C. Without knowing the studies used by L & C we were not fully able to evaluate how they get the results presented in their Fig. 5. However, we repeated the meta-analyses using our survival, growth and density data bases but restricted to only those case studies that have a switch in net interactions from competition to facilitation or that have an increase in the positive effect of neighbours with increasing levels of stress. The number of case studies in the reduced data bases is 32, 28 and 18 for survival, growth and density, respectively; a 71%, 73% and 82% reduction from the size of our original meta-analyses, respectively. These data bases were analysed using the same software (Metawin 2.1.4, Rosenberg *et al.* 2000) and procedure as in Maestre *et al.* (2005) (random-effects model with confidence intervals estimated using bootstrapping procedures). These analyses revealed significant differences in the effect of neighbours on the performance of the target species between stress levels in all cases (survival: $Q_B = 8.17$, d.f. = 1, $P = 0.004$; density: $Q_B = 4.93$, d.f. = 1, $P = 0.026$; growth: $Q_B = 4.91$, d.f. = 1, $P = 0.026$), as predicted by the stress-gradient hypothesis (Appendix S4). There is no evidence of bias in reporting results within this reduced set of studies (as suggested by the funnel plots, weighted histograms and the Spearman's rank correlation test). The overall heterogeneity of the model is not significant ($Q_H = 34.35$, d.f. = 31, $P = 0.310$), marginally significant ($Q_H = 26.03$, d.f. = 17, $P = 0.074$) and significant ($Q_H = 47.82$, d.f. = 27, $P = 0.008$) in the survival, growth, and density meta-analyses, respectively. Based on their re-analysis of our survival data

base, L & C claim that the variation in the length of abiotic stress between studies 'introduces variation into the meta-analysis that renders it incapable of detecting significant differences between low and high sites across studies'. Our results clearly rebut this criticism. Whereas a thorough discussion on the power and robustness of meta-analysis is beyond the scope of this reply (for reviews see Arnqvist & Wooster 1995; Osenberg *et al*. 1999; Gurevitch *et al*. 2001), our re-analyses have shown that it is fully capable of detecting differences between the low and high stress levels across studies, even when sample sizes are very low.

Concluding remarks: does one model fit all?

Based on a re-analysis of the data in Maestre *et al*. (2005), L & C conclude that the stress-gradient hypothesis is supported. We do not believe that they have presented convincing evidence to support this conclusion, and argue that their main criticisms are not well founded. We applaud their insightful methodological and conceptual review of meta-analysis, which will certainly be useful in guiding further ecological syntheses using this statistical tool. We also agree with L & C that very few studies, if any, have adequately and simultaneously controlled for species effects, local conditions, gradient length and interannual variability, when evaluating the effects of abiotic stress on the net outcome of plant–plant interactions, and on the need to conduct field experiments considering these issues.

The stress-gradient hypothesis as presented in Bertness & Callaway (1994) has been highly influential, as illustrated by the fact that it has been cited more than 300 times to date (ISI Web of Science), and has fostered much needed research on an important topic in community ecology. Our meta-analyses by no means undermine the importance of facilitation in arid and semi-arid environments, nor do they suggest a need to discard the stress-gradient hypothesis. However, they clearly raise important questions regarding the generality (*sensu* L & C) of some of the predictions of the stress-gradient hypothesis, and emphasize the roles of both the estimator of plant performance and the experimental approach followed when interpreting the net outcome of plant–plant interactions. The latter aspects are, surprisingly, not mentioned by L & C despite being important conclusions of our article (Maestre *et al*. 2005). L & C also raise relevant questions regarding the importance of the amplitude of the abiotic stress gradients, the scale at which these gradients occur, and the potential influence of the responsiveness of the target species when testing (and summarizing) the predictions of the stress-gradient hypothesis. Surprisingly, to our knowledge no previous study has thoroughly evaluated the circumstances under which these predictions should be tested, or the estimators of plant performance and experimental approaches which are the most suited to test them. Rather, the predictions of the stress-gradient hypothesis have been 'fitted' to empirical data obtained

from all sorts of abiotic stress gradients, estimators of plant performance and experimental approaches.

L & C claim that we used the results of our meta-analyses to 'reject the applicability of an idea (the stress-gradient hypothesis) entirely'. What we stated in our article, and maintain here, is that there are specific circumstances under which the predictions arising from the stress-gradient hypothesis do not hold. The hypothesis suggests that the presence of a neighbour *always* ameliorates abiotic stress in stressful environments, and that the positive effects derived from such amelioration increase in importance concomitantly with increases in abiotic stress. However, this is not always the case (see Tielbörger & Kadmon 2000; Maestre & Cortina 2004; Armas & Pugnaire 2005; and Barchuk *et al*. 2005 for examples and discussions). Whereas this does not invalidate the stress-gradient hypothesis, it suggests that further conceptual developments are needed for it to encompass or fit all situations that occur in nature. One unambiguous conclusion is suggested by our meta–analyses: species interactions across abiotic stress gradients do not follow a simple pattern. In fact, this conclusion emerges from L & C's re-appraisal of our data bases, and is reinforced with the results presented here. In our view, it is useful to critically re-examine current models that purport to describe the relationship between plant interactions and abiotic stress in order to elucidate and further refine those circumstances under which their predictions will hold, and which estimators of plant performance and experimental approaches are best-suited to test them. We believe that only by active debate and questioning of paradigms such as the stress-gradient hypothesis, can a full understanding of the influence of abiotic stress on plant–plant interactions in arid and semi-arid areas be achieved. We hope that our original meta-analyses and these reactions stimulate much-needed theoretical and empirical research on the ecology of interacting plants across stress gradients.

Acknowledgements

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Supplementary material

Appendix S1 Comparison of our original classification of abiotic stress with that resulting from using plant performance data.

Appendix S2 List of studies suggested by Lortie & Callaway (2006) as appropriate for testing the stress-gradient hypothesis, and reasons why they were not included in our data bases.

Appendix S3 Regression analyses of magnitude (or variance) in effect size of growth vs. the magnitude (or variance) of survival.

Appendix S4 Results of the random-effects model for the reduced (a) survival, (b) density and (c) growth data bases.

Appendix S5 References included in Appendices S1–S4 and not cited in the main text.