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Research article

## Plant–plant interactions, environmental gradients and plant diversity: A global synthesis of community-level studies



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### ABSTRACT

Previous syntheses on the effects of environmental conditions on the outcome of plant–plant interactions summarize results from pairwise studies. However, the upscaling to the community-level of such studies is problematic because of the existence of multiple species assemblages and species-specific responses to both the environmental conditions and the presence of neighbors. We conducted the first global synthesis of community-level studies from harsh environments, which included data from 71 alpine and 137 dryland communities to: (i) test how important are facilitative interactions as a driver of community structure, (ii) evaluate whether we can predict the frequency of positive plant–plant interactions across differing environmental conditions and habitats, and (iii) assess whether thresholds in the response of plant–plant interactions to environmental gradients exists between “moderate” and “extreme” environments. We also used those community-level studies performed across gradients of at least three points to evaluate how the average environmental conditions, the length of the gradient studied, and the number of points sampled across such gradient affect the form and strength of the facilitation–environmental conditions relationship. Over 25% of the species present were more spatially associated to nurse plants than expected by chance in both alpine and dryland areas, illustrating the high importance of positive plant–plant interactions for the maintenance of plant diversity in these environments. Facilitative interactions were more frequent, and more related to environmental conditions, in alpine than in dryland areas, perhaps because drylands are generally stress factorized by a larger variety of environmental stress factors and plant functional traits. The frequency of facilitative interactions in alpine communities peaked at 1000 mm of annual rainfall, and globally decreased with elevation. The frequency of positive interactions in dryland communities decreased globally with water scarcity or temperature annual range. Positive facilitation–drought stress relationships are more likely in shorter regional gradients, but these relationships are obscured in regions with a greater species turnover or with complex environmental gradients. By showing the different climatic drivers and behaviors of plant–plant interactions in dryland and alpine areas, our results will improve predictions regarding the effect of facilitation on the assembly of plant communities and their response to changes in environmental conditions.

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### Introduction

Positive interactions among plants (facilitation) are widely acknowledged as an important driver of ecosystem structure and functioning, particularly in areas characterized by harsh

environmental conditions (e.g., drylands, alpine environments and salt marshes; Callaway, 2007; Brooker et al., 2008). Compared with other ecological processes, however, the relative importance of facilitation as a driver of ecosystem structure and function is poorly understood (Maestre et al., 2010; Cavieres et al., 2014). For example, it is known that the presence of nurse plants is beneficial for many species present in some plant communities under stressful conditions (e.g., Hacker and Gaines, 1997; Cavieres and Badano, 2009; Soliveres et al., 2011), but not in others (e.g., Mitchell et al., 2009; Dvorský et al., 2013). Moreover, while facilitation plays a crucial role as a driver of the productivity and stability in some communities (Mulder et al., 2001; Cardinale et al., 2002), this effect

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is not consistent among different ecosystems (Mitchell et al., 2009) or ecological functions (Maestre et al., 2010).

Differences in the relative importance of facilitation as a driver of ecosystem structure and functioning found in the literature might be explained by the different environmental conditions under which different studies were performed. It has been hypothesized that the frequency of positive plant–plant interactions, and therefore its importance for the maintenance of plant diversity regarding other factors, should increase monotonically with increasing environmental harshness (the Stress Gradient Hypothesis; Bertness and Callaway, 1994). Indeed, facilitative interactions also seem more important for productivity under drought than under more mesic conditions (Mulder et al., 2001). However, other studies suggest that a collapse in facilitative interactions may occur under extremely stressful environments (Tielbörger and Kadmon, 2000; Maestre and Cortina, 2004; Michalet et al., 2006). This has led to development of theories predicting that facilitation is most prevalent under mild environmental conditions (Holmgren and Scheffer, 2010). Interestingly, the environmental conditions representing “extremely stressful conditions” have rarely, if ever, been defined, and are likely to vary from one study to another. Understanding the relationship between positive plant–plant interactions and the environment is crucial if we are to be able to predict how plant communities will respond to a changing climate (Brooker, 2006). The large number of contrasting results and hypotheses has fueled the debate that has raged over the past 15 years attempting to explain the response of plant–plant interactions across widely different environmental gradients. Despite this debate, however, consensus is far to be reached (see Holmgren and Scheffer, 2010; He et al., 2013 for recent reviews).

Most quantitative syntheses of the relationship between plant–plant interactions and environmental severity performed to date are based on studies that have evaluated the outcome of particular pairwise interactions (e.g., Gómez-Aparicio et al., 2004; Maestre et al., 2005; He et al., 2013, but see Cavieres and Badano, 2009; Cavieres et al., 2014). The upscaling of the conclusions gathered from such syntheses to entire communities is controversial, and should be conducted with caution (Maestre et al., 2009; Soliveres et al., 2011). The strength of some positive pairwise interactions undoubtedly increases with drought or other environmental stress factors, or with a lower performance of the beneficiary species growing without a nurse (Gómez-Aparicio et al., 2004; He et al., 2013). However, when multiple species are considered, researchers often find species-specific responses to environmental conditions and, therefore, to the presence of neighbors (Greiner La Peyre et al., 2001; Liancourt et al., 2005; Soliveres et al., 2012). Moreover, in whole communities species do not interact in pairs or in isolation, but rather form multiple species assemblages, and this has important implications for determining the net outcome of the interactions among them (Brooker et al., 2008; Soliveres et al., 2011; Schöb et al., 2013a; Schöb et al., 2014). Therefore, we do not know the extent to which species-specific responses and multiple species interactions translate to a general and predictable response of the frequency of positive plant–plant interactions across different environments. Indeed, the studies conducted to date at the community level report linear, unimodal or non-specific relationships between the frequency of positive plant–plant interactions and environmental harshness (e.g., Hacker and Gaines, 1997; Choler et al., 2001; López et al., 2013, see Table 1).

We conducted the first global synthesis of community-level studies that have evaluated the frequency of positive plant–plant interactions in alpine and dryland areas. By intrinsically considering the wide variety of species-specific responses and interactions among multiple species assemblages, our synthesis provide a unique opportunity to answer three fundamental questions posed

by community ecologists: (1) how important are facilitative interactions as a driver of community structure?, (2) how predictable is the frequency of positive plant–plant interactions across differing environmental conditions and habitats?, and (3) do general thresholds in the response of plant–plant interactions to environmental gradients exist between “moderate” and “extreme” environments exist? We also evaluated how the degree of abiotic harshness (represented by the average value of the major environmental process driving the gradient), the length of the environmental gradient studied (i.e., difference between the more mesic and drier ends of a given gradient), and the number of points sampled across such gradient affect the form (linear or unimodal) and strength of the facilitation–environment relationship. We expected these factors to act as drivers of this relationship (Lortie, 2010), and therefore to explain, to a large degree, the contrasting results found so far in the literature when evaluating the relationship between environmental severity and the outcome of plant–plant interactions.

## Materials and methods

### Building the database

We limited our survey to those studies that evaluated the effects of facilitation on the diversity of terrestrial plant communities and were conducted in alpine or dryland environments (*sensu lato*). These two environments capture most of studies cited in the facilitation literature (Callaway, 2007), and therefore provide sufficient studies to allow us to perform a global synthesis at the community level. Within these environments, we compiled every study published until May 2013 that reported empirical data on the co-occurrence among all the plant species in the community or between the dominant(s) nurse species and all their neighbors. The search was performed using both Google Scholar and in the ISI Web of Knowledge using all possible combinations of the following terms: “competition”, “facilitation” or “nurse” + “alpine”, “dryland”, “semi-arid”, “gradient”, “elevation” or “rainfall” + “plant diversity”, “diversity”, or “community”. From this search we retained those studies considering all the species in the community and from which we could obtain the following data: (1) site coordinates, (2) total species richness within the sampled community, and (3) the number of individuals of each species found in each of two microsites (beneath the sampled nurse(s) vs open areas). Some community-level studies were based either on species co-occurrences within sampling relatively large quadrats instead of comparing nurse/open microsites (e.g., López et al., 2013), reported results of performance measurements different to the number of occurrences (e.g., Totland and Esæte, 2002), or under environments different to the ones considered here (e.g., salt marshes: Hacker and Gaines, 1997 or rainforests: Wyse et al., 2013). Despite their interest, we decided not to include them in our database because of methodological differences. Overall, we found 48 studies that suited our criteria, which provided community-level data from 71 and 137 sites located in alpine and dryland areas, respectively. These sites varied widely in their vegetation and environmental conditions, with elevations ranging from 0 to 6000 m.a.s.l., average annual rainfall from 67 to 2000 mm, and with latitudes and longitudes ranging between 46.4° N–50.8° S and 147.7° E–106.9° W, respectively.

For every site, we obtained its elevation and 19 climatic variables using Worldclim (<http://www.worldclim.org>; Hijmans et al., 2005). Climatic variables included mean annual temperature and rainfall, rainfall seasonality, temperature annual range, rainfall and precipitation during the driest, wettest, coldest and warmest periods (see Appendix S1 for the full list of these variables). We

**Table 1**  
 Characteristics of the community-level studies performed across gradients with more of three points. AI = aridity index; rAI or rBest = Spearman's rank correlation between the percentage of facilitative interactions and AI or the best climatic predictor, respectively. ISO = Isotermality; PS = precipitation seasonality; PDQ and PWaQ = precipitation during the driest and warmer quarter, respectively; MDR = mean diurnal range in temperature; ELE = elevation; AMT = annual mean temperature; MTCM and MTCQ = mean temperature during the coldest month and quarter, respectively. H superscript in the "Best predictor" column indicates hump-shaped relationships between facilitation and environmental severity. Average data for each group (alpine/dryland) are shown in bold. Studies without references are unpublished data from the authors in Peru (1), Ecuador (2), Chile (3), USA (4), Mediterranean Basin (5), Spain (6), Australia (1), and Venezuela (7; see Appendix S4 for methodological details).

Study	Average AI	#Points sampled	Gradient length	Richness	rAI	rBest	Best predictor
<b>ALPINE</b>							
Dvorský et al. (2013)	21.7	8	33.4	17	−0.44	−0.89	ISO
1	25.9	10	18.4	6	0.72	−0.93	PS
2	29.1	16	16.5	14	0.51	0.53	PDQ
Schöb et al. (2013b)	73.3	5	53.6	16	0.7	0.7	AI
Cavieres and Badano (2009) <sup>a</sup>	73.7	4	73.5	30	0.74	−0.95	ELE
Anthelme et al. (2012)	103.8	3	8.3	36	0.87	0.87	AI
Choler et al., 2001 (exposed slopes)	154.9	3	17.1	17	0.87	0.87	AI
Choler et al., 2001 (sheltered slopes)	154.9	3	17.1	18	1.00	1.00	AI
	74.3	9	30.4	19	0.55	0.09	
<b>DRYLAND</b>							
3	4.6	4	4.6	15	−0.80	1.00	AMT
4	12.4	8	15.2	11	0.07	−0.38	MDR
5	13.4	34	15.7	18	0.24	−0.31	MTCM <sup>H</sup>
Soliveres et al. (2011)	14.4	10	6.6	49	0.06	0.36	MTCQ <sup>H</sup>
Holzappel et al. (2006)	14.6	4	19.5	53	−0.80	−0.80	AI
6	17.3	25	10.7	15	−0.16	−0.42	PWaQ <sup>H</sup>
1	25.9	10	18.4	6	0.72	−0.93	PS
Armas et al. (2011)	26.1	3	25.7	16	−1.00	−1.00	AI
2	29.1	16	16.5	14	0.51	0.53	PDQ
7	31.8	6	0.9	16	−0.96	−0.96	AI
	23.5	13	16.6	21	−0.17	−0.31	

<sup>a</sup> We could retrieve raw data of just four of the 11 sites from this study.

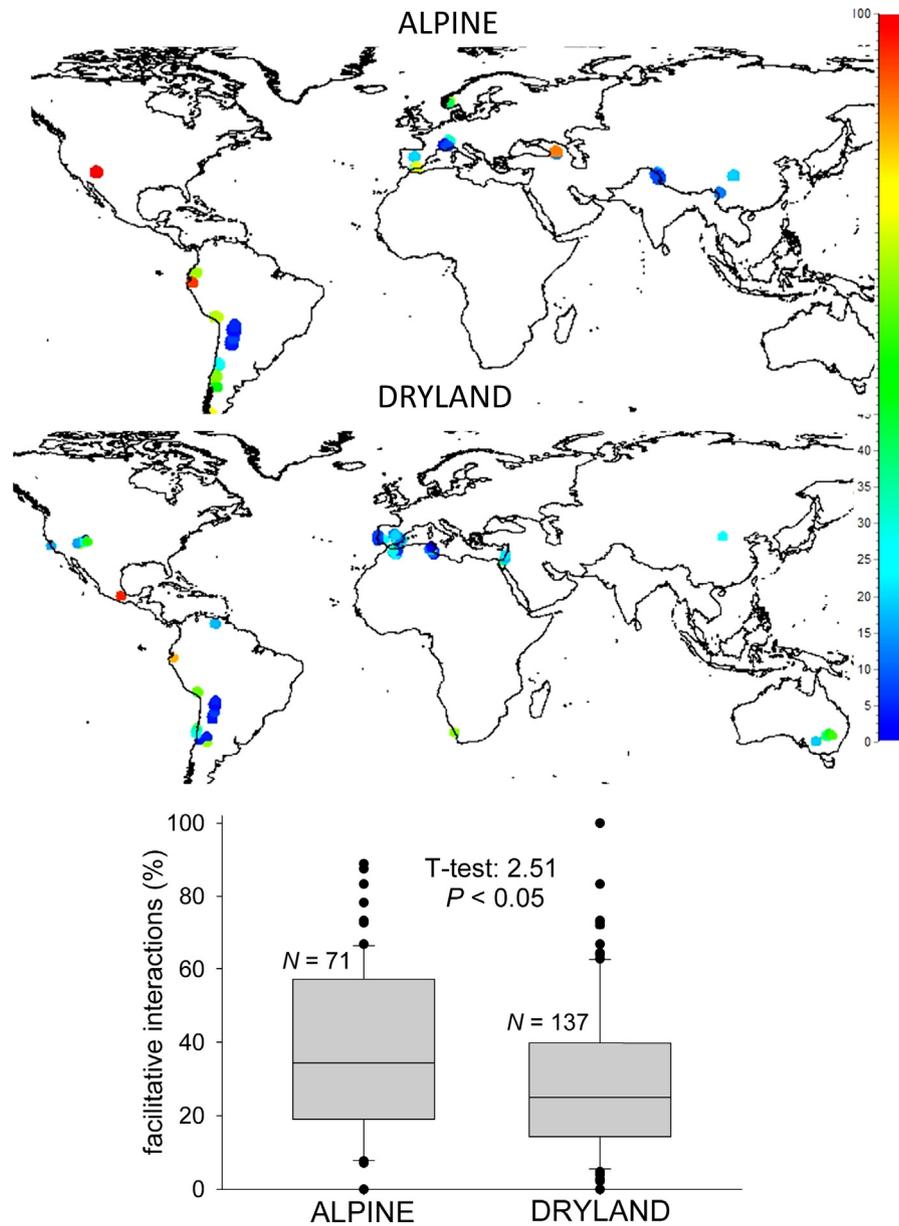
used Worldclim interpolations instead of the original climatic data provided by the authors to homogenize data sources among sites, and to increase the number of climatic variables available for our analyses. Nevertheless, data from Worldclim and those reported by the original authors were highly correlated ( $r_{\text{temperature}} = 0.89$  and  $0.93$ ;  $r_{\text{rainfall}} = 0.84$  and  $0.94$ ;  $r_{\text{elevation}} = 0.94$  and  $0.99$  for alpine and dryland environments, respectively;  $P < 0.0001$ ,  $N > 40$  in all cases). From the Worldclim data, we calculated the Martonne's aridity index (AI) as annual rainfall [in mm]/(mean annual temperature [in °C] + 10), which has been extensively used by previous facilitation research in both alpine and dryland areas (Cavieres et al., 2006; López et al., 2013). It must be noted that higher values of this index mean more available water. We acknowledge that other abiotic and biotic stress factors, such as wind, soil fertility or herbivory, also determine the outcome of plant–plant interactions. However, we could not find data for these variables for all the sites, and thus we did not include them in our analyses.

For each site, we calculated the percentage of facilitative interactions (proportion of species more associated with a given nurse than expected by chance) as our measure of the frequency of plant–plant interactions. The degree of co-occurrence between a given target species and a nurse was measured using the  $\chi^2$  statistic. To do this, we used the number of individuals found in the open and beneath the nurse as the observed values. Since the same sampling effort was devoted to each microsite (nurse/open) within each study, we calculated the expected values as the total number of individuals of a given target species multiplied by 0.5. A given target species was considered as facilitated if: (1) for those target species with more than 15 individuals (minimum sample size to calculate reliable  $\chi^2$  statistics), a significant  $\chi^2$  statistic was associated with a higher number of individuals beneath the nurse, or (2) for those target species with less than 15 individuals, all the sampled individuals were found beneath the nurse(s) (see Tewksbury and Lloyd, 2001; Cavieres et al., 2006; Valiente-Banuet and Verdú, 2007 for related approaches). We acknowledge

that observational studies such as those used to build our database cannot differentiate between plant–plant interactions *per se* and other mechanisms affecting plant co-occurrences, such as dispersal or habitat sharing. However, observational approaches are the only available studies at the community level, and are generally used when studying the role of facilitation as a driver of community assembly and when assessing its behavior across environmental gradients (e.g., Cavieres et al., 2006, 2014; Holzappel et al., 2006; Valiente-Banuet and Verdú, 2007). Moreover, previous studies have repeatedly demonstrated that co-occurrence and positive interactions are tightly linked in harsh environments such as those studied here (e.g., Kikvidze et al., 2005; Tirado and Pugnaire, 2005).

#### Global trends

We looked for global trends in the behavior of the frequency of positive plant–plant interactions (FPI hereafter; *i.e.*, the percentage of species from the total pool that were more associated with a given nurse than expected by chance) in response to the environment. To do this, we used all the sites in our dataset (Fig. 1), separating them into two groups: alpine and dryland environments. We did so because the behavior of FPI in response to the environment differed substantially between these two environments (see Results below). Indeed, the interaction between group (alpine/dryland) and several climatic factors was highly significant when analyzing the data altogether (results not shown). For each group, we reduced the 21 environmental variables used (climatic variables and elevation) using Principal Component Analysis (PCA). We included elevation as an additional environmental variable in our PCA because it varied substantially within our dataset and because it may encapsulate microclimatic features of the sites that might not be captured by the global interpolations used. The first four PCA components of each environment (dryland and alpine) had eigenvectors higher than 1.0, and recovered over 88% of the variance in these variables (see Appendix S2 for details on the



**Fig. 1.** Spatial distribution of all the community-level studies gathered in the database for alpine (71) and dryland (137) environments (upper panel). For this analysis we used all the community-level studies we could gather, not only those performed across environmental gradients. The color of each dot defines the percentage of facilitative interactions (see legend at the left). The lower panel shows a box plot and results for the test comparing the frequency of facilitative interactions (*i.e.*, percentage of the total species pool more associated to the nurse than expected by chance) between alpine and dryland environments. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

PCA conducted); therefore, we selected these four components as predictors of plant–plant interactions in subsequent analyses. This allowed us to simplify the multi-model inference approach (explained below) by drastically reducing the number of variables to be introduced in the models.

We first tested for differences in FPI between alpine and dryland environments using a Student's *t*-test. Second, we evaluated the importance of climatic (the four PCA components), geographic (latitude and longitude), and their interaction, as drivers of FPI by using multi-model inference based on information theory (Burnham and Anderson, 2002). Longitude and the four longitude  $\times$  climate interaction terms were removed due to multicollinearity problems in both drylands and alpine areas. In the alpine models, the latitude  $\times$  PCA4 (four component of the PCA, which was related to mean temperature of the wettest quarter, and temperature and

precipitation during the warmest quarter; Appendix S2) interaction term was removed for the same reason. The relative importance of each predictor was calculated by summing the Akaike weights for each of them across all the possible models (511 in drylands, 255 in alpine environments) in which each predictor occurred. A larger value of this metric (which ranks between 1 and 0) indicates a higher importance of this predictor regarding the rest of predictors introduced in the model (Burnham and Anderson, 2002).

To aid in the interpretation of the multi-modeling results, we also performed separate regressions between FPI (our response variable) and the climatic variables most related to the PCA components identified as important by the multi-model inference, and with other variables widely acknowledged as important for plant–plant interactions (Callaway et al., 2002; Holzapfel et al.,

2006; Soliveres et al., 2011; López et al., 2013). The predictors studied were annual rainfall, Martonne's AI, elevation, and mean temperature of the warmest month for alpine environments, and temperature annual range, Martonne's AI, mean temperature during the wettest quarter, and precipitation during the driest quarter for drylands. These variables were selected because they explained most of the variance found in FPI. Nevertheless, we performed the same analyses with the rest of climatic variables to avoid missing any important predictor; none of these variables rendered better results (higher proportion of variance explained) than those listed above, and thus these results are not presented here. Both linear and quadratic regressions were performed with each predictor, and we selected the most parsimonious models based on the Akaike's Information Criterion (AIC). The response of the environmental variables studied may likely vary with latitude; for example, the same elevation may suppose more stressful conditions as the distance from the Equator increases (Körner, 2007), and a similar behavior is likely to occur with the effect of climatic variables such as temperature or rainfall on FPI (Anthelme et al., 2012; Kikvidze et al., 2011). To control for this, and in a similar fashion as in the multi-model inference, we performed also multiple regression analyses introducing, in addition to the environmental predictors mentioned above, latitude and latitude  $\times$  environmental predictor interaction terms. Similar to the results found for the latitude  $\times$  PCA interaction terms in the multi-model inference, only one of the eight interaction terms tested between latitude and each separate environmental variable was a significant predictor of FPI (*t* values between  $-2$  and  $2$ ; detailed results in Appendix S3). We also checked the relationship between the residuals of the linear and quadratic regressions explained above, and both latitude and longitude to assess for spatial autocorrelation in our analyses. We failed to detect any clear trend in the residuals, and Spearman's rank correlation coefficients were always below 0.6. Lastly, we conducted a series of mixed GLMs (additive, multiplicative and nested) with each one of the climatic predictors and adding each independent study gathered for our database as a random factor. Both the analyses of the residuals and the mixed GLMs results (not presented here) supported the main results found here. Overall, these latter analyses suggest lack of spatial autocorrelation in our data. Therefore, we do not further discuss these results for simplicity.

#### *Relationship between the frequency of facilitative interactions and aridity*

We studied what determined the differences in the direction and shape of the facilitation-aridity relationships found across studies. To do this, we selected from our database those studies performed within the same habitat and along an environmental gradient consisting of more than two points. We selected these studies because it is not possible to determine the shape of the facilitation-environment relationship with fewer than three points. Overall, eight and 10 studies fulfilled these requirements in alpine and dryland environments, respectively (Table 1). For each of these studies, we established the Spearman's rank correlation between the percentage of facilitative interactions and aridity (hereafter rAI). As our surrogate for aridity we choose Martonne's AI since it is widely accepted as a surrogate of water availability (the most limiting factor in both dryland and alpine environments), and it was the only climatic variable selected among the best climatic predictors of the frequency of facilitative interactions in all the gradients studied. Therefore, AI was the most suitable candidate to unify the climatic predictor used across studies. It is important to note that AI is directly related to water availability and, therefore, positive correlations between FPI and AI indicate a decrease in FPI with drought stress.

To explore potential drivers of the variation in rAI values, we first obtained, for each study, three variables that have been suggested as crucial drivers of the facilitation-environmental severity relationship (Lortie, 2010): (1) the average level of aridity (average AI across all the sites within a study), (2) the length of the gradient (difference in AI between the driest and wettest ends of the gradient), and (3) the number of points (sites) sampled across the gradient. We then conducted separate linear and quadratic regressions for each group (alpine/dryland) and predictor (average aridity level, length of the gradient and number of points sampled) using rAI as the response variable. We choose the most parsimonious linear/quadratic fit for each relationship using AIC. We also performed Spearman's rank correlations between the percentage of facilitation and the 21 environmental variables for each gradient, choosing among them the variable with the best fit (hereafter rBest). For the alpine gradients, we also calculated the correlation between the frequency of facilitative interactions and elevation (rEle). Results using rAI, rBest and rEle were qualitatively similar, and thus we only present here those relating to rAI (see Figs. S1 and S2 for results using rBest and rEle, respectively).

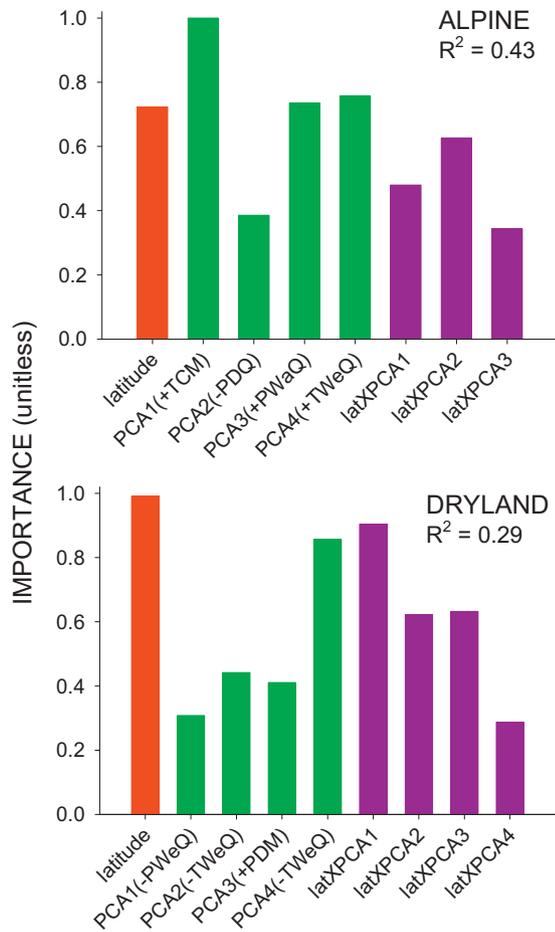
All of our data either met the assumptions of the analyses conducted or were transformed to achieve them. Multi-model selection was performed with the SAM 4.0 software (Rangel et al., 2010); other analyses were conducted with SPSS 13.0 for Windows (Chicago, IL, USA). The data used in our analyses are available from figshare (Soliveres & Maestre, 2014).

## Results

### *Global trends*

Plant–plant interactions in alpine and dryland environments varied across the whole possible range (0–100% of the species present in a given site were spatially associated with a given nurse more frequently than expected by chance) in the studies contained in our database. There were substantial differences in the way that these interactions responded to the environmental factors studied. Positive interactions among plants were more frequent in alpine environments (37% of the species were associated to nurse plants) than in drylands (29%, Fig. 1). They were also generally more associated with climatic factors in alpine than in dryland areas. Geographical and climatic predictors explained  $\sim 43\%$  of the global variability in the frequency of positive plant–plant interactions (FPI) in alpine environments, but substantially less ( $\sim 29\%$ ) in drylands (Fig. 2).

In alpine environments, the most important predictor of FPI was the first PCA climatic component (related to lower elevations [eigenvalue =  $-0.26$ ] and higher temperatures [eigenvalue =  $0.29$ ]; Appendix S2), with FPI increasing linearly with higher values of this component ( $R^2 = 0.28$ ,  $P < 0.001$ ; data not shown). Indeed, FPI significantly diminished with elevation in alpine areas, and increased with higher mean temperatures during the warmest month (Fig. 3). The relationship between FPI and average annual rainfall was unimodal, with the highest frequencies found at rainfall levels  $\sim 1000$  mm year $^{-1}$  (Fig. 3). It must be noted that this unimodal relationship was consistent even after removing two apparent outliers, the two points with the highest rainfall values in Fig. 3 ( $R^2 = 0.37$  vs  $0.38$  with and without these points, respectively;  $P < 0.001$ ; quadratic regression had lower AIC values than linear regression in both cases). In drylands, the best predictor of FPI was latitude and its interaction with the first climatic PCA component (related to lower rainfall and higher temperature annual range; Fig. 2). Higher FPI values were found at higher latitudes ( $R^2 = 0.12$ ;  $P < 0.001$ ). Climatic variables *per se* were generally poor predictors of changes



**Fig. 2.** Relative importance of the geographical (red), climatic (green) and geographical  $\times$  climate interaction terms (purple) predictors for the percentage of positive plant–plant interactions in the database. For this analysis we used all the community-level studies we could gather, not only those performed across environmental gradients. The amount of variance explained by the multi-model approach ( $R^2$ ) is shown for alpine (upper panel) and dryland (lower panel) environments. The climatic variables most related to each PCA component and the sign of each eigenvalue are shown between parentheses (see further details in Appendix S1). Abbreviations are: TCM = average temperature of the coldest month; PDQ = precipitation during the driest quarter; PWaQ = precipitation during the warmest quarter; TWeQ = temperature most related to the wettest quarter; PDM = precipitation during the driest month. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in FPI in drylands; temperature annual range and the AI were the best predictors, but in any case explained more than 11% of the variance found in FPI (Fig. 3). For both climatic predictors, FPI increased toward more benign conditions (*i.e.*, lower temperature annual ranges or higher AI values).

#### Drivers of the relationship between the frequency of facilitative interactions and aridity

The relationship between FPI and the AI within each environmental gradient included in our database ( $rAI$ ) varied widely, from 1.0 to  $-0.44$  in alpine environments (mean  $\pm$  SE =  $0.62 \pm 0.16$ ) and from 0.72 to  $-1.0$  in drylands (mean  $\pm$  SE =  $-0.21 \pm 0.16$ ; Table 1). In alpine environments, all relationships between FPI and the environmental gradients studied were linear, and the best predictor of half of the studies included in the database was AI. In drylands, AI was the best predictor in three of the ten studies included, but not all the relationships were linear (Table 1). When AI was considered, only one of the alpine studies followed predictions from the

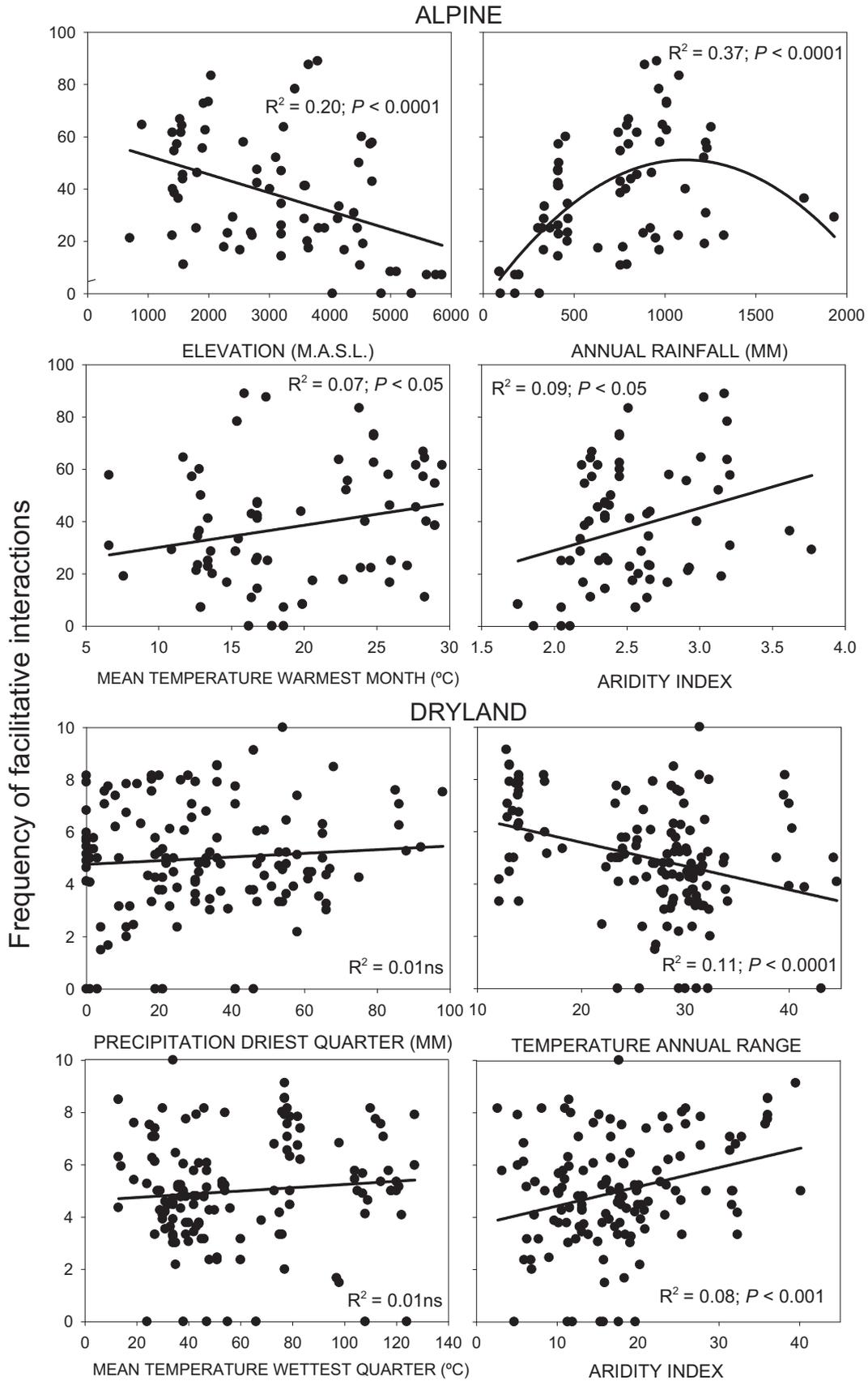
stress gradient hypothesis (SGH), *i.e.*, increasing the frequency of positive plant–plant interactions toward drier environments. These SGH predictions, however, were supported by 75% of the alpine studies when elevation, the most common environmental gradient studied in alpine environments, was used as a predictor instead of AI (Fig. S2). In drylands, 50% of the studies supported predictions from the SGH.

We found substantial differences between alpine and dryland environments in the relationship between  $rAI$  and the level of aridity, the length of the gradient, and the number of points/sites sampled at each study (Fig. 4). In alpine environments,  $rAI$  was only negative (more FPI toward drier conditions) in the most arid gradient (*i.e.*, that with the lowest Martonne's aridity index). Conversely, in drylands, the most important drivers of  $rAI$  were the number of points sampled and the length of the gradient. Predictions of the SGH were supported in those gradients with the largest or smallest – but not average – lengths, and for those studies with five points or fewer sampled across the gradient (Fig. 4). Irrespective of the significance of these relationships, virtually all the relationships between  $rAI$  and the predictors studied differed substantially between alpine and dryland environments.

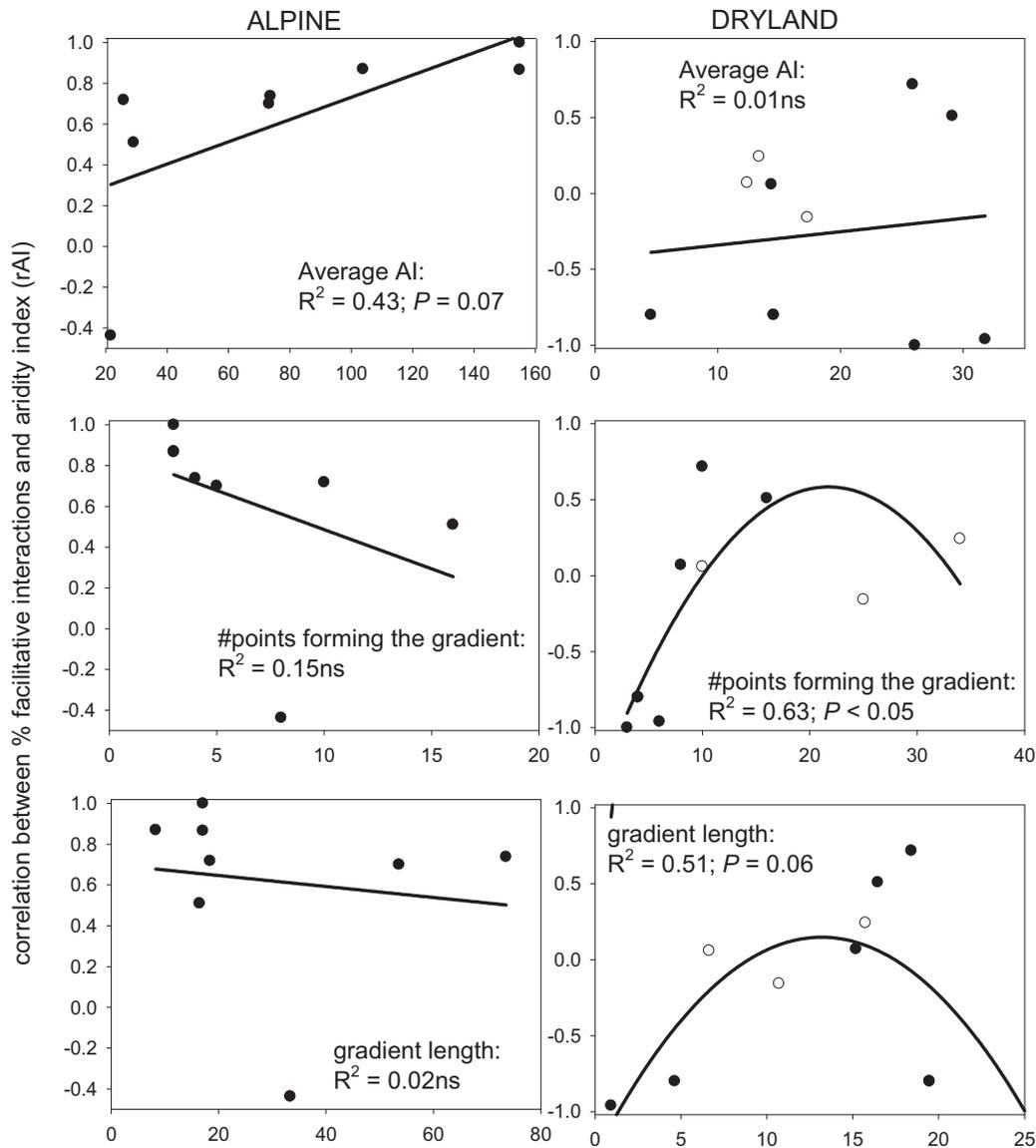
## Discussion

### Global trends

Contrary to the results found in a previous global survey in alpine environments (Callaway et al., 2002), we found decreases, rather than increases, in FPI with increasing elevation and declining temperatures during the warmest month at a global scale. These contrasting results might be explained by substantial differences in the methodology used among studies. First of all, in this first part of the study we assessed the shape of the FPI across a global elevation gradient, while every previous study evaluated regional elevation gradients. It must be noted that when addressing the generality of FPI–elevation relationships within each regional gradient (Fig. S2), we found that 75% of the studies supported results from Callaway et al. (2002), in line with the predictions from the SGH (see also Cavieres et al., 2014). Surprisingly, this overall general pattern commonly found within each region did not translate to the global scale, likely because this scale involved a variety of habitat-types, soil conditions and plant compositions. Our results when including solely those studies performed across environmental gradients of more than three points indicate that positive FPI–elevation relationships shift to negative in longer elevation gradients (Fig. S2), and the large extent in elevation found within our database (from ca. 0 to ca. 6000 m.a.s.l.) might be the explanation of these striking results. Interestingly, global trends in the relationship between FPI and the climatic predictors remained consistent even after constraining our database to cushion-dominated communities, the most widely studied habitat-type in alpine areas (Fig. S3). Secondly, we focused on the level of co-occurrence between the dominant nurse(s) and all the species forming the community, while Callaway et al. (2002) performed a manipulative experiment to assess the effect of the dominant nurse(s) on the biomass production of a subset of species forming the community. It is known that different performance measures (number of individuals vs biomass) or experimental approaches (observational vs manipulative) render different results regarding the net outcome of plant–plant interactions (Maestre et al., 2005; Michalet, 2007). Lastly, the high species-specificity in the outcome of pairwise interactions, and the existence of interactions among multiple species, likely caused differences in the conclusions we reached compared with those of Callaway et al. (2002). Our results, however, support those of



**Fig. 3.** Relationships between the frequency of facilitative interactions and the four most important climatic predictors for alpine and dryland environments. For this analysis we used all the community-level studies we could gather, not only those performed across environmental gradients. Regression results and the variable used as predictor in each relationship are shown within each panel. The frequency of facilitative interactions in drylands and the Aridity index in alpine environments were sqrt-transformed to fulfill normality assumptions.



**Fig. 4.** Behavior of the facilitation vs stress relationship (rAI) across the differing average aridity levels (upper panels), number of points sampled across the environmental gradient (mid panels) and length of the gradient (lower panels) found in the different gradient studies in alpine (left) and dryland (right) environments. For this analysis we only used those community-level studies performed across environmental gradients of  $\geq 3$  points. Negative and positive rAI indicates increase and decrease of the frequency of positive plant–plant interactions with water scarcity, respectively. White dots show those regional gradients showing a unimodal relationship. Regression results are shown within each panel.

previous community-level studies reporting a decrease of facilitation with elevation, or the lack of relationship between both variables (Cavieres et al., 2006; Dvorský et al., 2013). It must be noted that a recent global-scale study using a similar methodology found the proportion of plant species facilitated by cushion nurses to be inversely related to productivity (Cavieres et al., 2014) and therefore in partial contrast to our findings. However, these authors did not consider, as far as we know, neither spatial autocorrelation in their data nor different environmental effects across different latitudes, which could partially account for the different their results (Körner, 2007; Anthelme et al., 2012; Kikvidze et al., 2011).

The frequency of positive plant–plant interactions showed a unimodal relationship with rainfall in alpine ecosystems, as previously found in tropical alpine environments (Anthelme et al., 2012). These results suggest that the unimodal plant interactions–environmental gradient relationship holds for rainfall gradients in alpine environments, with a collapse in facilitative interactions at both extremes of gradients determined by rainfall (Michalet et al.,

2006; Maestre et al., 2009). However, this unimodal relationship was only found in alpine environments, and only when rainfall was used as a predictor. Although further empirical testing is needed, our study suggests that the specific environmental conditions where the forecasted facilitation waning under “extremely harsh conditions” may commence around 1000 mm of annual rainfall in alpine communities. Although this collapse in facilitative interactions may occur within particular regional gradients (Table 1), our results question the widely held belief that a predictable decay in the global frequency of positive plant–plant interactions occurs across any environmental gradient in drylands (see also Maestre et al., 2005).

Plant–plant interactions in drylands were much less predictable than in alpine areas. The variety in the number and temporal distribution of environmental factors found in dryland is higher than that present in alpine environments (but see Hedberg and Hedberg, 1979; Anthelme and Dangles, 2012). This is illustrated several times in our dataset. For example, aridity was the best predictor for

plant–plant interactions in 50% of the alpine regional gradients, but only in 30% of the same gradients in drylands, where some non-linear facilitation–aridity relationships can be found (Table 1). In addition, the first component of our PCA captured more variance in the same climatic variables in alpine environments than in drylands (Appendix S2), suggesting that climatic variables were more weakly correlated among each other in drylands. Furthermore, the coefficient of variation (CV) in precipitation seasonality was higher in drylands than in alpine environments (0.51 vs 0.41; raw data in Appendix S1), supporting the notion that climatic conditions in drylands are highly unpredictable (Whitford, 2002). In addition, the variety of plant functional traits is also typically higher in drylands than in alpine environments. For example, in a study involving the same number of species, Reich et al. (1999) reported a higher CV in specific leaf area, an important functional trait driving plant–plant interactions (Butterfield and Callaway, 2013), in a desert than in an alpine community (0.69 vs 0.51). The higher variety in the climatic factors and plant functional traits often found in drylands, and the complex relationships existing among plant functional traits, environmental conditions and plant–plant interactions (Soliveres et al., 2011, 2012; Gross et al., 2013; Butterfield and Callaway, 2013) can explain the low predictability of plant–plant interactions across environmental gradients found in drylands.

#### *Drivers of the relationship between the frequency of facilitative interactions and the environment*

Our second set of analyses, focused on those community-level studies performed across environmental gradients of at least three points, shows a relatively high influence of average aridity, gradient length and number of points sampled on the relationship between the frequency of plant–plant interactions and aridity (rAI). In alpine environments, rAI was negative (*i.e.*, the frequency of plant–plant interactions increased with water stress) in the driest region, but showed the opposite behavior under wetter environments (Fig. 4). Interestingly, this region had also the lowest number of species (Table 1) and, therefore, the SGH was supported in the most arid and less diverse habitats. We speculate that predictions from the SGH are more likely to hold in those regions where the different potential stress factors are likely aligned (co-vary together) and the responses to the environment of the different species are homogeneous. Under such circumstances, the microclimatic amelioration promoted by nurse plants will be important for a higher proportion of species as more extreme conditions are reached. However, generally richer plant communities were found in wetter areas (Table 1). The increase in the frequency of positive plant–plant interactions with water availability in these wetter areas might be explained by: (1) more productive environments and a higher species richness likely increased the chances of indirect positive interactions to take place (*e.g.*, Cuesta et al., 2010), and (2) the more benign conditions generate a larger species pool, thus it is more likely that more species establishes far from their ecological optimum and therefore may benefit from the presence of nurses (Holmgren and Scheffer, 2010; but see Cavieres et al., 2014). We must note, however, that these results are based on a relatively low number of studies, and thus should be interpreted with caution.

The relationship between plant–plant interactions and elevation (rEle) was not influenced by the average elevation of the sites in a given study, or by the number of points sampled across the gradient. Interestingly, average elevation was not related to changes in species richness, supporting our previous comments that SGH predictions hold in species-poor, but not species-rich, communities. However, rEle linearly decreased with gradient length (*i.e.*, difference in elevation between the highest and lowest sites; Fig. S2). That is, the relationship between the frequency of positive

plant–plant interactions and elevation was positive in the shorter gradients, but it shifted to neutral and then to negative in the longest ones. A similar (although unimodal) trend was found for the rAI in drylands. This suggests that predictions from the SGH may hold true for those (shorter) gradients likely including the same species pool, which homogeneously depart from their ecological optimum. However, SGH predictions do not seem to hold in longer gradients including a larger species turnover, where the species forming the community differ in their ecological optima and therefore in the outcome of their species-specific interactions. These species-specificity in the outcome of plant–plant interactions, together with the high species turnover across longer gradients, might be the cause of the absence of clear trends in the frequency of plant–plant interactions at the community level (*i.e.*, individual strain or individual-stress concept: Liancourt et al., 2005; Gross et al., 2010; Soliveres et al., 2011). In drylands, negative rAI (facilitation increasing with water stress) dominated those gradients with fewer (>5) points, while positive or nil rAI were found in the other gradients. Shorter environmental gradients seem more likely to be homogeneous in terms of their relevant stressors, and are also likely to be characterized by a lower species turnover than larger gradients. These features characterizing shorter gradients could increase the chance of finding increases in the frequency of plant–plant interactions as the level of the main environmental stress factor forming the gradient (*i.e.*, drought) increases.

#### **Conclusion**

In this first synthesis of community-level studies conducted to date, we show that a large fraction (>25%) of the species are significantly more associated to the presence of nurses. Plant–plant interactions are more frequent (37 vs 29%) and predictable in alpine than dryland environments. We also found that strong and positive facilitation–stress relationships are more likely to be found across shorter environmental gradients or in communities formed by fewer species. Our results contribute to our understanding of the importance of plant–plant interactions for community structure, and help to reconcile contrasting results and to solve the ongoing and rehashed debate regarding the behavior of plant–plant interactions across environmental gradients. Our synthesis casts doubt on the widely-held notion that a single model can adequately explain the behavior of plant–plant interactions across markedly different environmental gradients. Hence, future research should further investigate the factors driving the contrasting results found among community-level studies so far, rather than attempting to fit all of them with a single model. Until we do this we will not be able to fully understand the nature of plant–plant interactions in contrasting environments, and therefore the response of plant communities to ongoing climate change.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ppees.2014.04.001>.

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