

## CLIMATE CHANGE AND SPECIES RANGE SHIFTS

# Partitioning net interactions among plants along altitudinal gradients to study community responses to climate change

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### Summary

1. Altitudinal gradients provide a useful space-for-time substitution to examine the capacity for plant competition and facilitation to mediate responses to climate change. Decomposing net interactions into their facilitative and competitive components, and quantifying the performance of plants with and without neighbours along altitudinal gradients, may prove particularly informative in understanding the mechanisms behind plant responses to environmental change.

2. To decouple the inherent responses of species to climate from the responses of plant–plant interactions to climate, we conducted a meta-analysis. Using data from 16 alpine experiments, we tested if changes in net interactions along altitudinal gradients were due to a change in the performance of target species without neighbours (i.e. environmental severity effects only) or with neighbours (neighbour trait mediated effects).

3. There was a global shift from competition to facilitation with increasing altitude driven by both environmental severity and neighbour trait effects. However, this global pattern was strongly influenced by the high number of studies in mesic climates and driven by competition at low altitude in temperate climates (neighbour trait effect), and facilitation at high altitude in arctic and temperate climates (environmental severity effect).

4. In Mediterranean systems, there was no significant effect of competition, and facilitation increased with *decreasing* altitude. Changes in facilitation with altitude could not unambiguously be attributed to either neighbour trait effects or environmental severity effects, probably because of the opposing stress gradients of cold and aridity in dry environments.

5. Partitioning net interactions along altitudinal gradients led to the prediction that climate change should decrease the importance of facilitation in mesic alpine communities, which might in turn exacerbate the negative effects of climate change in these regions. In xeric climates, the importance of facilitation by drought-tolerant species should increase at low altitudes which should mitigate the negative effect of climate change. However, the importance of facilitation by cold-tolerant species at high altitudes may decrease and exacerbate the effects of climate change.

**Key-words:** alpine communities, competitive effects, competitive responses, environmental severity effects, facilitation, meta-analysis, neighbour trait effects, species range shifts

### Introduction

Competition and facilitation are likely to modify the biological impacts of climate change on the distribution and abundance of plant species (Davis *et al.* 1998; Brooker

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2006; Saccone *et al.* 2009). It is therefore important, when attempting to incorporate such biological interactions into climate change response modelling, to have a clear understanding of how such processes operate, and how their effects are linked to variation in climate at both a local and regional scale. Developing a global-level understanding of variation in the role of plant–plant interactions would therefore be of substantial benefit, in particular for predicting how species interactions may promote or diminish range shifts across contrasting climate systems.

Alpine and arctic systems are particularly suited to assess the role of species interactions in altering species range shifts. Climate change is predicted to have large effects on alpine and arctic ecosystems because the rate of warming in these ecosystems is projected to be two to three times higher than that recorded during the 20th century (Guisan & Theurillat 2000; Cavieres & Sierra-Almeida 2012). Additionally, both observational and experimental studies of climate change impacts, and plant interactions have been conducted in alpine and arctic systems, aided by the fast changes in temperature and precipitation – parameters that are changing due to climate change – with altitude (Grabherr, Gottfried & Pauli 1994; Körner 2003). This allows researchers to use altitudinal gradients as surrogates for climate change (Körner 2007).

The stress gradient hypothesis (SGH) provides a relevant conceptual framework for assessing the role of species interactions in range shifts with climate change. The SGH proposes that competitive interactions should be relatively more intense or frequent in low-stress conditions and facilitative interactions more frequent in high-stress conditions (Bertness & Callaway 1994; Brooker & Callaghan 1998). Callaway *et al.* (2002) found support for the SGH in a global set of experiments in alpine and arctic communities, and a recent meta-analysis by He, Bertness & Altieri (2013) found patterns supporting the SGH across many systems and regions. In the context of the SGH, the negative impacts of climate change in alpine systems may be either ameliorated or exacerbated by plant–plant interactions depending on whether climate change increases or decreases environmental stress (Brooker 2006; Brooker *et al.* 2008; Cavieres & Sierra-Almeida 2012). From the Arctic to the boreal (i.e. mesic climates) most warming studies have supported the general predictions of the SGH, finding either an increase in competition (Klanderud 2005; Klanderud & Totland 2005), or a shift from facilitative to negative interactions with warming (Shetsova, Haukioja & Ojala 1997; Rixen & Mulder 2009), although some studies, for example Hobbie, Shevtsova & Chapin (1999), have reported no change in interactions with warming in an Alaskan tussock tundra. Interestingly, warming treatments may not always lead to reduced stress, but their results still concur with predictions of the SGH. For example, Wipf, Rixen & Mulder (2006) found an increase in facilitation in a subarctic system with increasing stress due to simulated advanced snow melt. Early snow melt is known to increase physical stress in arctic and alpine systems because plants are more exposed to cold

temperature in the spring (Choler, Michalet & Callaway 2001; Michalet *et al.* 2002; Wipf, Rixen & Mulder 2006).

However, most of our knowledge comes from warming experiments conducted in the Arctic, with few experiments conducted in temperate regions or in dry climates. In terms of understanding the responses of arctic and alpine systems, the only alpine system warming experiment that we know of in a dry Mediterranean climate was undertaken in the central Andes (Cavieres & Sierra-Almeida 2012), and net facilitative interactions did not change with warming at high altitude where growth was mainly limited by low temperatures. Similarly, in the Mongolian steppe Liancourt *et al.* (2013) did not observe changes in interactions with warming for a highly stress-tolerant fescue. However, watering increased competition in this highly continental and dry climate. Thus, in the context of our attempt to generalize at a global scale about the role of plant–plant interactions in affecting species range shifts in alpine environments with climate change, our knowledge is limited by the lack of experiments manipulating both climate and neighbours, and in particular in dry climates.

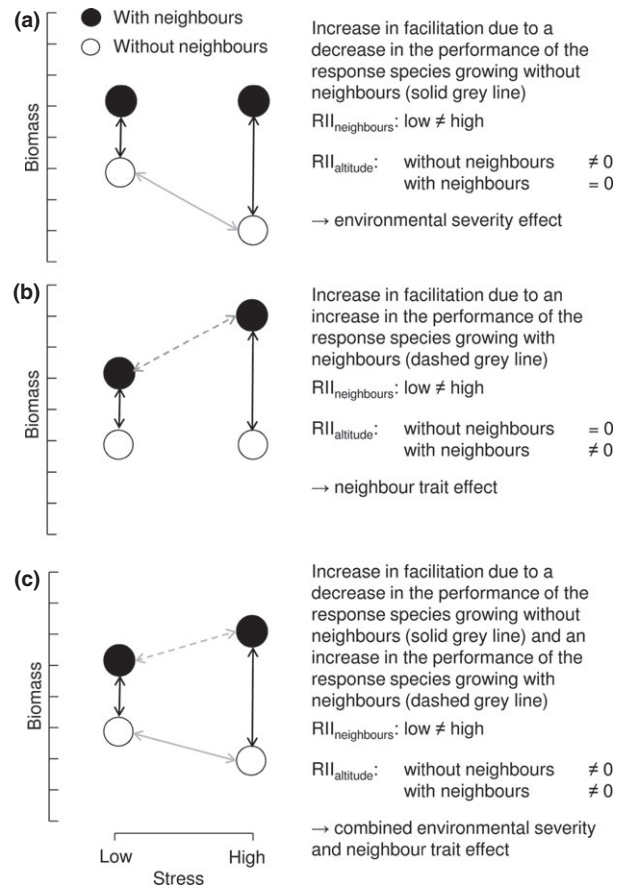
But we might be able to overcome this limitation. Rather than focusing on climate change experiments, we suggest turning instead to the processes underlying changes in competition and facilitation using the results of studies of altitudinal contrasts. The relative importance of competition and facilitation often shifts along altitudinal gradients, but in ways that vary within the broader climatic context. For example, most studies conducted in mesic climates have found that competition is more common or more important at low altitudes, whereas facilitation becomes more important at high altitude where productivity is lower and abiotic stress is presumed to be greater (e.g. Choler, Michalet & Callaway 2001; Callaway *et al.* 2002; Kikvidze *et al.* 2005; McIntire & Fajardo 2011; Cranston *et al.* 2012). In xeric climates, the opposite altitudinal pattern has been reported (Callaway *et al.* 2002; Cavieres *et al.* 2006; Michalet 2006; Stultz, Gehring & Whitham 2007), most likely because of the abiotic stress imposed by lower water availability at lower altitude. In general, these patterns are consistent with the SGH and show that results from altitudinal contrasts and warming experiments can concur. The use of altitudinal contrasts for developing understanding of the potential impacts of climate change is not novel in mesic climates, (e.g. see Grabherr, Gottfried & Pauli 1994). Indeed, in mesic northern latitude climates, climate change will mostly decrease cold (and nutrient) stress for plant species in a similar manner to the changes associated with decreasing elevation and the switch from high to low alpine vegetation. At lower latitudes, such as in Mediterranean areas, predicted increases in temperature and decreases in summer precipitation with climate change will primarily increase drought stress rather than reduce cold stress (IPCC 2007; Maalouf *et al.* 2012). However, we still can use altitudinal contrasts to mimic climate change in Mediterranean areas because decreasing elevation in these mountain ranges is also

known to primarily increase drought stress (Gomez-Aparicio *et al.* 2004; Cavieres *et al.* 2006; Schöb *et al.* 2013).

In addition to making use of data from these altitudinal comparisons, we suggest that our predictive ability would benefit substantially from decomposing the *net* effects of competition and facilitation (e.g. Callaway, Nadkarni & Mahall 1991; Callaway & Walker 1997). For example, an overall net facilitative effect of a species is likely to incorporate some component of competition in the balance of interaction mechanisms, and a net competitive effect will also probably include at least some underlying facilitative components in the mix (Hunter & Aarssen 1988; Kikvidze *et al.* 2001; Callaway 2007). Thinking in this way starts to help us understand likely changes in the processes underlying observed climate response patterns, and how these may differ between climates. For example, increasing temperature in mesic climates may increase the occurrence or intensity of the competitive component of net interactions at low altitude and decrease the facilitative component of net interactions at high altitude. In contrast in arid conditions, such as in Mediterranean and highly continental climates, the facilitative component of net interactions should increase with increasing temperatures and decreasing precipitation, and in particular at low altitude (Maalouf *et al.* 2012; Wang *et al.* 2013). To understand more fully, the response of interactions and hence, community structure to climate change, we need to better understand which components of these net interactions are influenced by changes in climate – competition or facilitation.

Another important limitation to predicting the effects of plant–plant interactions on community scale responses to climate change is that most studies of shifts in interactions along environmental gradients use indices that quantify the relative difference in performance between targets grown with and without neighbours. But an increase in net facilitation along an altitudinal gradient may be due to (i) a decrease in the performance of the beneficiary (i.e. the ‘response species’) growing in the absence of neighbours as a result of increasing environmental severity, hereafter called the ‘environmental severity effect’; (ii) an increase in performance of the beneficiary species growing with neighbours as a result of changes in those benefactor (i.e. ‘effect species’) traits that are important for facilitation; hereafter called the ‘neighbour trait effect’; or (iii) a combination of both effects (Fig. 1). Different underlying changes may result in an observed decrease in competition or a switch from competition to facilitation with increasing stress.

Theoretical and empirical studies of competition have emphasized that separating competitive ‘effects’ from competitive ‘responses’ is necessary to fully understand how competition regulates community organization (Gaudet & Keddy 1988; Goldberg 1990; Liancourt, Viard-Crétat & Michalet 2009; Violle *et al.* 2009). For example, an increase in competition with decreasing stress is primarily due to a decrease in the performance of the target species growing with neighbours, that is, to an increase in competitive effects, or neighbour trait effects, which is linked to



**Fig. 1.** Increase in facilitation intensity ( $R_{II_{neighbours}}$  at low stress is smaller than  $R_{II_{neighbours}}$  at high stress) with increasing stress either due to a reduced performance without neighbours (a: environmental severity effect, where  $R_{II_{altitude}}$  without neighbours is negative), an increased performance with neighbours (b: neighbour trait effect, where  $R_{II_{altitude}}$  with neighbours is positive) or their combination (c).  $R_{II_{neighbours}}$  and  $R_{II_{altitude}}$  quantify the effects of neighbours and the effects of altitude (environmental stress), respectively, following Armas, Ordiales & Pugnaire (2004), see Materials and methods for the formulae.

the plasticity of competitors (Grime 1974). But such attempts to separate effects from responses are rare in studies that include facilitation (but see Gross *et al.* 2008; Le Bagousse-Pinguet *et al.* 2013; Schöb *et al.* 2013), and it might be assumed that an increase in facilitation is due generally to an increase in the facilitative effect, in the same way that an increase in competition is due to an increase in the competitive effect. But such a shift in this component of the net effect may be less common for facilitation than for competition, unless there is turnover in nurse species with altitude. This is because stress-tolerant species are generally not very plastic (Grime 1974). Plants with cushion morphologies tend to be strong nurses in many alpine systems, and also appear to be very stress-tolerant (Körner 2003), and hence are unlikely to show a plastic morphological response with increasing altitude that would result in their having an increased facilitative impact on beneficiaries (but see Schöb *et al.* 2013). Additionally, since nurse fitness is expected to decrease with

increasing cold stress (and hence altitude), it is unlikely that the role of the 'effect species' will increase with increasing altitude.

Despite the probability that low plasticity will prevent strong changes in the roles of 'effect species' with increasing stress, increased facilitative neighbour trait effects might occur if the benefactor is limited by a different form of stress than the target; for example, if in a dry climate, the target (beneficiary) is limited by nutrient supply or low temperatures at high altitude, while the benefactor is limited by water scarcity at low altitude. In this case, the benefactor's facilitative traits may be improved under conditions that are more stressful for the beneficiary (Schöb *et al.* 2013). Thus, we propose that, depending on the climate of a system and the limiting stress factor for the nurse species involved in the interaction, an increase in facilitation with increasing altitude may either be due to an environmental severity effect (Case 1, Fig. 1) or due to a neighbour trait effect (Case 2, Fig. 1).

Overall, climate change might affect the direction and intensity of plant–plant interactions differently depending on whether changes in interactions with changing temperature or precipitation are due to environmental severity effects or neighbour trait effects, and if climate change has different effects on the level of stress experienced by the neighbour and target species (Gross *et al.* 2010). Disentangling the role of environmental severity effects and neighbour trait effects would substantially improve our ability to predict how biotic interactions might mediate species and community responses to climate change.

In order to explore the processes involved in changes in net interactions with altitude, we conducted a meta-analysis of experiments on variation in plant–plant interactions along altitudinal gradients in alpine and arctic environments. The fundamental objective of this quantitative review was to examine the role of plant–plant interactions as regulators of species and community responses to climate change and identify research gaps. More specifically, our goal was to determine whether changes in plant–plant interactions with altitude in alpine communities are mainly due to changes in the performance of the effect species (neighbour trait effects) or changes in the performance of the response species, growing without neighbours (environmental severity effects). We also assessed if the bioclimatic classification of the system (e.g. arctic, temperate, tropical, Mediterranean) and the performance metric used (e.g. survival, biomass, abundance, richness) influenced our detection of either environmental severity or neighbour trait effects.

## Materials and methods

### SYSTEMATIC REVIEW AND DATA COLLECTION

An extensive literature search was conducted on 10 December 2012 to compile a list of eligible studies associated with the study of alpine gradients in the primary, peer-reviewed literature. The following

sets of terms were used to populate the initial list: alpine\*altitude\*gradient, alpine\*altitude\*interaction, alpine\*altitude\*plant, alpine\*altitude\*plant\*competition, alpine\*altitude\*plant\*facilitation, alpine\*elevation\*gradient, alpine\*elevation\*interaction, alpine\*elevation\*plant, alpine\*elevation\*plant\*competition and alpine\*elevation\*plant\*facilitation. The primary search engine used was Web of Knowledge; however, this list was also cross-checked with Scopus and Google Scholar to ensure that this process was representative of the relevant literature. After removal of redundant studies that emerged from more than a single set of search terms, there were a total of 533 unique studies.

Each study was individually reviewed, and the following exclusion criteria were applied: no plant interactions were reported in the study, other interactions were reported such as animal interactions or plant–animal interactions including grazing, species richness was reported at the mesoscale however no plant interactions were reported, plant interactions were reported but only at a single altitude, the study was a review or simulation model or conceptual model, a correlative relationship with altitude was reported within the vegetation, species distribution patterns were reported but interactions between species were not provided, and a gradient with plant interactions was reported at various altitudes but the gradient was neither described nor altitudes provided (limited number of cases). This selection process generated a short list of 16 studies (Appendix S1, Supporting information). Both nurse plant interactions and neighbourhood level studies were used if the appropriate response data were reported, including biomass, relative abundance, species richness or survival. In addition, the climatic region was also recorded, and the relative frequency of extracted effect sizes is summarized in Appendix S3 (Supporting information). From this set of studies, a total of 930 effect size estimates were calculated from the reported means, variances and sample sizes (standardized across all studies for calculation purposes). If a mean was not reported but a graph was provided, data extraction software was used to generate mean and variance estimates for that study. Each data instance was treated as independent in this meta-analysis because we were interested in contrasting altitude and trait-level effects on species (Appendix S2, Supporting information shows relative frequency of measures). For the measurement of effect size, we used the relative interaction index (RII), since it is both a symmetrical effect size estimate and common in the plant ecology literature (Armas, Ordiales & Pugnaire 2004). We calculated RII to quantify both the effect of neighbours and the effect of altitude. For the effect of neighbours, we calculated the following metric:

$$RII_{\text{neighbours}} = (r_N - r_C) / (r_N + r_C) \quad \text{eqn 1}$$

where  $r_N$  is the target response with neighbour and  $r_C$  is the target response without neighbour (= control). In a similar fashion, we calculated the effect of altitude as follows:

$$RII_{\text{altitude}} = (r_H - r_L) / (r_H + r_L) \quad \text{eqn 2}$$

where  $r_H$  is the target response at high altitude and  $r_L$  is the target response at low altitude (= control).

$RII_{\text{neighbours}}$  was calculated separately for high and low altitudes, whereas  $RII_{\text{altitude}}$  was calculated separately for target species growing with and without neighbours.  $RII_{\text{neighbours}}$  indicates the effect size of neighbours at high and low altitudes where values below 0 point towards competition and values above 0 indicate facilitation.  $RII_{\text{neighbours}}$  can therefore be used to reveal changes in competition and facilitation with altitude. On the other hand,  $RII_{\text{altitude}}$  indicates the effect size of altitude on target plant performance either when growing with neighbours or growing without neighbours, where values below 0 indicate better performance of the target species at low altitude, and values above 0 show a better performance of target species at high altitude.  $RII_{\text{altitude}}$  can



therefore be used to reveal changes in the effect of altitude on target performance with or without neighbour. If there is a significant change in  $R_{II\_neighbours}$  between low and high altitude, then  $R_{II\_altitude}$  can be used to attribute changes to a significant environmental severity effect (if  $R_{II\_altitude}$  without neighbours is significantly different from 0), to a neighbour trait effect (if  $R_{II\_altitude}$  with neighbours is significantly different from 0) or to a combined environmental severity and neighbour trait effect (if  $R_{II\_altitude}$  with and without neighbours are significantly different from 0), as explained in Fig. 1.

## STATISTICAL ANALYSIS

The meta-analysis was carried out using the program MetaWin 2 (Rosenberg, Adams & Gurevitch 2000). Confidence intervals (CI) of effect sizes were calculated using bootstrap resampling procedures (Adams, Gurevitch & Rosenberg 1997) with 9999 iterations. Alpha was set at 0.05 using the 95% biased-corrected bootstrap CI that did not overlap 0 (Rosenberg, Adams & Gurevitch 2000). Random-effect models were used because there is likely a valid random component of variation in effect sizes between studies in this context (Gurevitch, Curtis & Jones 2001). Heterogeneity was examined using  $Q$ -statistics (Hedges & Olkin 1985), whereas publication bias was explored statistically with fail-safe numbers (Rosenberg 2005).

Because our meta-analysis revealed inherent biases in the available data, due in particular to differences in methods used to measure plant interactions between temperate and arctic climates vs. Mediterranean and tropical climates (see Results), we reanalysed temperate and arctic sites separately using raw biomass data. We used linear mixed models with log-transformed biomass data of target species as response variable, and altitude (low vs. high) and neighbour (yes vs. no) as categorical predictor variables. Species was included as a random effect to account for differences in biomass among species. Additionally, based on data from a single study in a temperate climate (Choler, Michalet & Callaway 2001), we studied changes in target species biomass in response to altitude and neighbour presence for competition and facilitation cases separately. This study was selected because it included three altitudinal positions (high subalpine, low alpine and high alpine) with dominant competitive interactions at the lowest altitude switching to dominant facilitative interactions at the highest altitude and thus, the possibility to clearly separate competitive from facilitative cases from low to medium and medium to high altitude, respectively. Competition cases included all cases from low and medium altitudes that did not show significant facilitation (i.e. that showed either significant competition or no significant net interaction), whereas facilitation cases included all cases from medium and high altitude that did not show significant competition (i.e. that showed either significant facilitation or no significant net interaction). Statistical significance of altitude and neighbour presence was assessed as described above with linear mixed models with log-transformed biomass data and species included as the random factor. All statistics on raw data and figures were carried out in R version 2.15.2 (R Core Team 2012) using the packages nlme (Pinheiro *et al.* 2012), car (Fox & Weisberg 2011) and effects (Fox 2003).

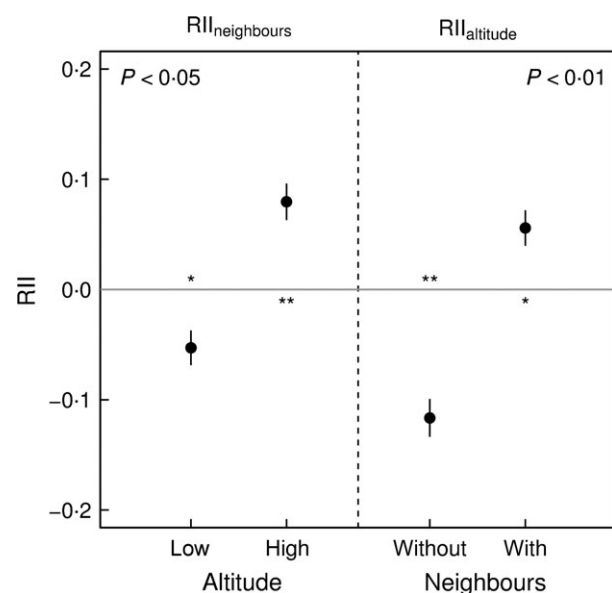
## Results

The overall analysis including all climatic regions and performance variables showed that the effects of neighbours in alpine communities shifted from significantly negative at low altitude (subalpine and low alpine sites) to significantly positive at high altitude (high alpine sites) ( $R_{II\_neighbours}$  in Fig. 2). This overall shift from competition to facilitation

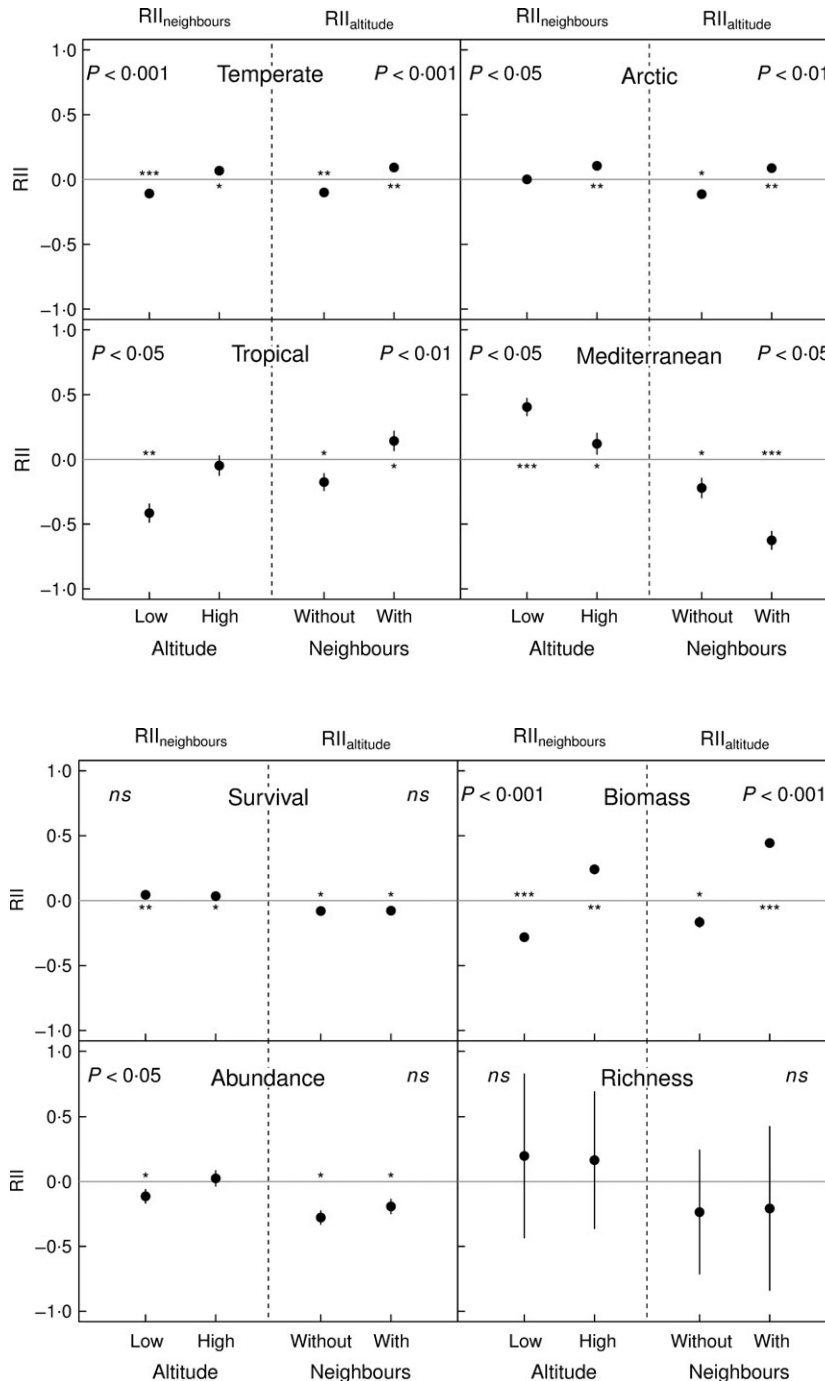
with altitude was due to both an environmental severity effect and a neighbour trait effect (Scenario 3, Fig. 1).  $R_{II\_altitude}$  was negative without neighbours (i.e. the performance of the target without neighbours decreased with increasing altitude) and positive with neighbours (i.e. the impact of neighbours became increasingly beneficial with increasing altitude), respectively (Fig. 2).

In temperate climates, the patterns of change in  $R_{II\_neighbours}$  (low vs. high altitude) and  $R_{II\_altitude}$  (+/- neighbours) were the same as in the global pattern, but with statistically stronger effects (Fig. 3). Results for arctic and tropical studies were similar to those from temperate climates, except that there was no significant competition at low altitude in the arctic climate and no significant facilitation at high altitude in the tropical climate (Fig. 3). In studies from Mediterranean climates, the direction of the changes in  $R_{II\_neighbours}$  with altitude was opposite to the global pattern, that is, there was an increase in facilitation with decreasing altitude. Additionally,  $R_{II\_altitude}$  was more negative with neighbours than without neighbours (Fig. 3). The higher negative effect size of altitude for the target with neighbours indicates that the increase in facilitation at lower altitude is mostly due to a neighbour trait effect.

Patterns of RII response to altitude and the presence of neighbours differed between different performance variables (Fig. 4). Survival metrics showed weak effects, and no significant change with either altitude or the presence or absence of neighbours. For biomass, the switch from competition to facilitation with increasing altitude was



**Fig. 2.** Overall mean with 95% confidence limits of  $R_{II\_neighbours}$  at low and high altitudes (left) and of  $R_{II\_altitudes}$  without and with neighbours (right). Stars below or above dots indicate significant RII values obtained from sample  $t$ -tests (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , ns: not significant).  $P$ -values on each graph indicate the result of the one-way ANOVAS for the altitude (left) and neighbour (right) effects.



**Fig. 3.** Mean with 95% confidence limits of  $RII_{neighbours}$  at low and high altitudes (left) and of  $RII_{altitude}$  without and with neighbours (right) in four climatic regions (temperate, arctic, tropical and Mediterranean). Stars below or above dots indicate significant RII values obtained from sample *t*-tests (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , ns: not significant). *P*-values on each graph indicate the result of the one-way ANOVAs for the altitude (left) and neighbour (right) effects.

**Fig. 4.** Mean with 95% confidence limits of  $RII_{neighbours}$  at low and high altitudes (left) and of  $RII_{altitude}$  without and with neighbours (right) for four performance variables (survival, biomass, abundance and richness). Stars below or above dots indicate significant RII values obtained from sample *t*-tests (\* $P < 0.05$ , \*\* $P < 0.01$ , \*\*\* $P < 0.001$ , ns: not significant). *P*-values on each graph indicate the result of the one-way ANOVAs for the altitude (left) and neighbour (right) effects.

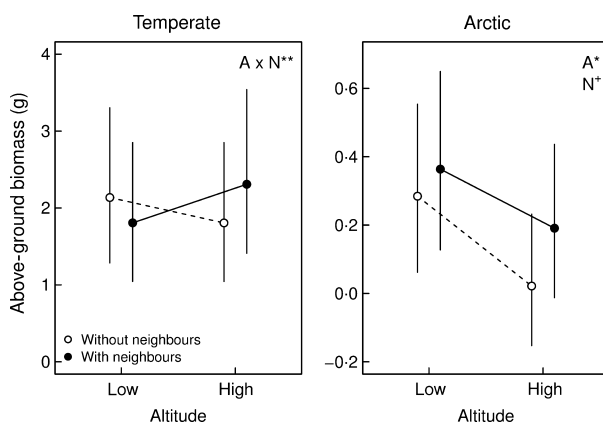
highly significant, and driven by both an environmental severity and a neighbour trait effect. For abundance, there was a shift from competition to no significant interactions with increasing altitude due to an environmental severity effect (negative  $RII_{altitude}$  with and without neighbours). Finally, there were no detectable significant responses of richness metrics due to very high variability in RII values.

Notably, the experimental approach and metrics used to measure biotic interactions were not equally well represented in the literature or between climatic regions (Appendix S3, Supporting information). Broadly speaking,

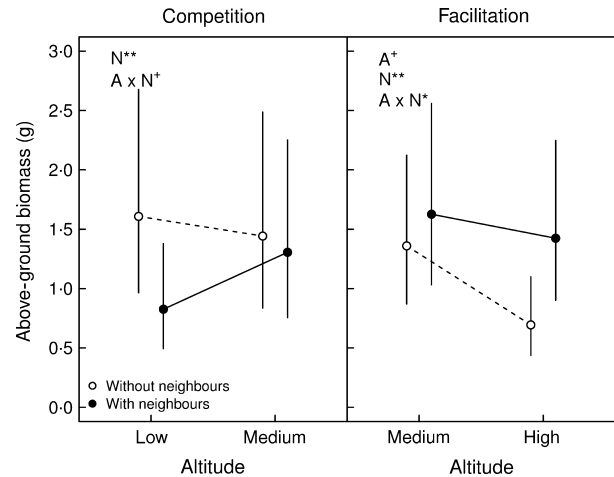
there was no publication bias in any instance as the Rosenthal's Fail-safe numbers were very large (i.e.  $5k + 10$  rule, Rothstein, Sutton & Borenstein 2005) in each meta-analysis conducted herein. However, cross-latitudeally, most contrasts in the arctic ( $\chi^2 = 80.0$ , d.f. = 1,  $P < 0.001$ ) and temperate climates ( $\chi^2 = 284.8$ , d.f. = 1,  $P < 0.001$ ) used a removal procedure within a diffuse neighbourhood (i.e. with multiple neighbour species removed), whereas most case studies conducted in the Mediterranean ( $\chi^2 = 129.1$ , d.f. = 1,  $P < 0.001$ ) and tropical climates ( $\chi^2 = 72.0$ , d.f. = 1,  $P < 0.001$ ) used an observational

procedure focusing on a specific nurse species, and generally on a cushion species (Appendix S3, Supporting information). Differences in overall experimental approach were also associated with differences in the types of performance variables used: removal studies (mostly from temperate and arctic climates) measured survival and above-ground biomass of target species, whereas observational studies (mostly from Mediterranean and tropical climates) measured the abundance and richness of all naturally occurring beneficiary species. Both within and between group heterogeneity tests within each meta-analysis were significant ( $P < 0.05$ ). Not surprisingly, this indicates that other factors also introduce significant variation into the groupings we used. In this systematic review, the most likely candidates are specific species-level differences that cannot be tested without replications of sets of species.

To account for these inherent biases in the available data, we focused our analyses of interactions between environmental severity and neighbour trait effects on unbiased data, that is, comparing biomass performances of target species in removal studies between studies from temperate and arctic climates (Fig. 5), and within studies from temperate climates (Fig. 6). With target plant biomass as the response variable, we found contrasting responses to removal experiments between temperate and arctic climates (Fig. 5). In temperate climates biomass varied significantly with altitude and neighbour presence due to a switch from competition to facilitation with altitude driven by both an environmental severity and a neighbour trait effect (Fig. 5 and scenario 3 in Fig. 1). In contrast, in the Arctic, there was only a weakly significant altitude effect, and a marginally significant neighbour effect, due to weak facilitation at both low and high altitudes and a dominant environmental severity effect on decreasing biomass with altitude (Fig. 5).



**Fig. 5.** Mean with 95% confidence limits of above-ground biomass of the target species grown without and with neighbours and at low and high altitudes for temperate (left) and arctic (right) sites. Significant altitude (A), neighbour (N) effects and their interaction ( $A \times N$ ) are displayed on each graph ( $*P < 0.05$ ,  $**P < 0.01$ , +: marginally significant,  $P < 0.1$ ). For temperate  $n = 164$ , for arctic  $n = 82$ .



**Fig. 6.** Mean with 95% confidence limits of above-ground biomass of the target species grown without and with neighbours and at low (subalpine) and medium (low alpine) altitudes for cases where net interactions were competitive (left) and at medium (low alpine) and high (high alpine) altitudes for cases where net interactions were facilitative (right). Significant altitude (A), neighbour (N) effects and their interaction ( $A \times N$ ) are displayed on each graph ( $*P < 0.05$ ,  $**P < 0.01$ , +: marginally significant,  $P < 0.1$ ). Data are from Choler, Michalet & Callaway (2001); temperate climate (French Alps). For competition  $n = 30$ , for facilitation  $n = 40$ .

Using data only from the study by Choler, Michalet & Callaway (2001) – conducted in an environment typical of temperate alpine climates – we found that biomass responses to altitude were dependent on the dominant type of interaction (competition vs. facilitation; Fig. 6). From low to medium altitudes (i.e. from high subalpine to low alpine conditions), and for the cases where competition was the dominant net interaction, there was a marginally significant altitude  $\times$  neighbour interaction effect on biomass due to a decrease in competition with increasing altitude driven by a neighbour trait effect (i.e. decreasing competition suffered by plants with neighbours). In contrast, from medium to high altitude (i.e. from low alpine to high alpine conditions), and for the cases where facilitation was the dominant net interaction, there was a significant altitude  $\times$  neighbour interaction effect on biomass due to increasing facilitation with increasing altitude driven by an environmental severity effect (i.e. a decrease in the success of plants in the absence of neighbours; Fig. 6).

## Discussion

The purpose of our meta-analysis was to assess the relative contribution of environmental severity and neighbour trait effects as drivers of change in plant–plant interactions along altitudinal gradients in alpine systems around the world. Our ultimate goal was to use the insights from the meta-analysis to improve our ability to predict when and how biotic interactions might modulate alpine community responses to climate change and alter species range shifts. Our analysis of 16 studies showed that the shift from net

competition to net facilitation with increasing altitude found in earlier facilitation literature (Callaway *et al.* 2002) was robust, but with the novel contribution of showing that this shift is driven both by environmental severity effects (changes in the performance of species without neighbours) and neighbour trait effects (changes in the impact of neighbours on target species). Neighbour trait effects generally acted to increase net competitive interactions at low altitudes, while environmental severity effects drove increasing net facilitative interactions at high altitudes.

Our overall results were influenced by the predominance of data from temperate climate alpine systems. Comparisons between climate types revealed interesting differences in the altitudinal responses of plant interactions and their underlying processes. But they also revealed limitations in the existing data and thus, in our ability to understand at a global scale how plant–plant interactions respond to variation in climate in alpine systems around the world. We could not conduct within-biome analyses for studies in tropical climates because there were not enough case studies that utilized comparable experimental methods. For those systems where such comparisons were possible, the overall/temperate climate patterns were not repeated in other biomes. In arctic climates, we found responses that matched those found in other mesic (i.e. temperate) environments in terms of environmental severity effects, with increasing negative impacts of the environment at higher altitude. But we found no increase in neighbour effects at lower altitude. In Mediterranean climates, the patterns diverged even further from those of temperate climates, with increasing facilitation at lower altitudes apparently driven by increasing beneficial effects of neighbours (increasing neighbour trait effects). However, the differences in responses between Mediterranean and mesic (arctic/alpine) climates found by our analyses were also potentially influenced by the methodological approaches, and performance variables commonly adopted in these different types of system. Below, we explore these response patterns – and the possible causes of between-climate differences in responses – in more detail.

#### PROCESSES DRIVING PLANT–PLANT INTERACTIONS IN MESIC CLIMATES

The overall pattern of changes from competition to facilitation with increasing altitude supported the SGH (Bertness & Callaway 1994; Brooker & Callaghan 1998) and was consistent with the recent meta-analysis of He, Bertness & Altieri (2013), the intercontinental pattern in alpine systems reported by Callaway *et al.* (2002) and smaller scale patterns reported in a number of other temperate alpine studies (Choler, Michalet & Callaway 2001; Arroyo *et al.* 2003; McIntire & Fajardo 2011; Cranston *et al.* 2012). However, our analyses give further insight into underlying processes, revealing that this change in the direction of net plant–plant interactions is due to both an

environmental severity and a neighbour trait effect (Fig. 1, third scenario) and is largely driven in our meta-analysis by the studies conducted in temperate climates (Figs 2 and 3). Using data from Choler, Michalet & Callaway (2001), a study conducted in the French Alps and including three altitudinal positions and a high number of target species, we were able to separate net effects resulting in competition from those that resulted in facilitation compared to no interactions (Fig. 6). This analysis showed that the change from net neutral interactions to net competitive interactions that occurred from medium to low altitude was mainly a neighbour trait effect (our second scenario, Fig. 1), whereas the change from neutral to facilitative net interactions that occurred from medium to high altitude was predominantly due to an environmental severity effect (our first scenario, Fig. 1). The former effect is consistent with Grime's (1974) CSR model which proposed that the competitive effect of neighbours increases with increasing resource availability and decreasing stress. In contrast, from medium to high altitude, the increase in net facilitation was due to an environmental severity effect: only the performance of the target plants without neighbours decreased significantly, and the effect of the stress-tolerant benefactors was unchanged with increasing cold stress.

Interestingly, results in the Arctic, obtained from experiments using generally the same methods to measure plant–plant interactions, were different from those in the temperate climate in that there were no significant net competitive interactions. However, the change from net neutral interactions to facilitation was again driven by an environmental severity effect, similar to that in temperate climates. The absence of net competition in low alpine communities in arctic climates was discussed by Kikvidze *et al.* (2011), who proposed that the recently glaciated infertile soils of arctic environments may explain the absence of competition at low altitudes.

In summary, partitioning neighbour trait and environmental severity effects allowed us to show that in mesic climates an increase in net facilitation along low temperature-based stress gradients (i.e. with increasing altitude) is primarily driven by an environmental severity effect, specifically by reduced success of target species in the absence of neighbours, rather than by an increase in the impact of benefactor species. At the same time, increases in net competition at lower altitudes in mesic climates are likely due to a neighbour trait effect, that is, changes in the competitive impact of neighbours rather than changes in the success of targets in the absence of neighbours.

#### WHY DO PATTERNS DIFFER BETWEEN MESIC AND XERIC CLIMATES?

Changes in net interactions with altitude detected by our analyses are very different in Mediterranean climates compared to temperate and arctic climates. There are a number of reasons why this might be the case.



First, these mesic–xeric differences in response pattern may reflect genuine differences in the processes that underlie them. The meta-analysis in xeric climates yielded nonsignificant net competitive interactions at low and high altitudes, and a stronger net facilitation effect size at lower altitudes. This is consistent with Cavieres *et al.* (2006) and other studies in xeric climates. In such a climate, decreasing water availability with decreasing altitude creates an aridity stress gradient which runs in an opposite altitudinal direction to the more common low temperature stress gradient (Gomez-Aparicio *et al.* 2004; Michalet 2006; Stultz, Gehring & Whitham 2007; Schöb *et al.* 2013). Partitioning the net effect showed that the increase in net facilitation with increasing drought stress at lower altitudes appeared to be due to a neighbour trait effect: an increase in performance with neighbours (negative  $\text{RII}_{\text{altitude}}$  with neighbours).

Differences detected in the meta-analyses between Mediterranean and mesic (arctic and temperate) climates might also be due to the use of different study methodologies in mesic and xeric climates. These methodological differences reflect the characteristics of vegetation in these climates. In many mesic alpine communities, vegetation cover is continuous. In contrast, most xeric communities have patchy vegetation cover with a mosaic of vegetated patches and natural open areas (Aguilar & Sala 1999; Cavieres & Badano 2009). This may explain why most plant–plant interaction experiments conducted in xeric climates use an observational approach (comparisons of diversity, density or performance of individuals inside and outside of nurse plants), whereas experiments conducted in mesic climates often remove vegetation to provide a no-neighbour treatment. In turn, these methodological differences may influence study results (Schöb, Kammer & Kikvidze 2012). For example, more positive interactions might be found with the observational method than with the removal method, perhaps because of legacy effects (remaining fertile soils or release of nutrient pulses) during plant removals (Michalet 2006; Callaway 2007) that may lead to an under-estimate of facilitation. Additionally, in the patchy vegetation of xeric climates, nurses tend to be discrete individuals with strong species-specific direct effects, whereas in the closed vegetation of mesic climates, the neighbourhood is generally composed of multiple species that can elicit diffuse effects. Consequently, fairly consistent methodological differences between xeric and mesic climates may have biased the data available for our meta-analysis, such that cross-climate comparisons also represent contrasts of methodologies.

However, these methodological differences cannot be responsible for the pattern of neighbour trait effect that we detected in Mediterranean climates, that is, increasing benefactor impact with decreasing altitude. This is because the effect is due to changes in the responses of those targets that occur with neighbours. But it is possible that the performance variables commonly measured in xeric climates may have in part induced this effect. Beneficiary

species richness and abundance – commonly measured in xeric climates – can readily be influenced by regional species pools. These are known to increase with decreasing altitude in alpine systems (Körner 2003; Michalet *et al.* 2011), and the influence of this effect is demonstrated by the negative  $\text{RII}_{\text{altitude}}$  observed in Mediterranean climate sites even in the absence of neighbours (Fig. 4). At high altitudes, the species pool likely consists almost exclusively of stress-tolerant species, whereas at low altitudes (where the total species pool is larger) the proportion of stress-intolerant species is higher (Choler, Michalet & Callaway 2001; Pellissier *et al.* 2010). The higher proportion of stress-intolerant species in the species pool at lower altitude could drive facilitation at lower altitude sites (Choler, Michalet & Callaway 2001; Liancourt, Callaway & Michalet 2005) and would be responsible for the apparent neighbour trait effect. But because beneficiary abundance and species richness tend to be measured in xeric rather than mesic environments, these patterns are not detected in mesic climates.

The final explanation for our observed mesic–xeric differences is that the pattern of neighbour trait effects associated with increasing facilitation at lower altitudes in xeric climates results from the two opposing altitudinal stress gradients occurring in these xeric climates. In the Mediterranean climate of the Sierra Nevada Mountains in south-eastern Spain, Schöb *et al.* (2013) showed how the cold-adapted but drought-sensitive nurse species, *Arenaria tetraquetra* ssp. *amabilis*, demonstrated better physiological performance at high altitudes. This improvement in vigour corresponded with a set of morphological traits that were better for ameliorating limiting conditions at high altitudes, for example nutrient availability. In contrast, at low altitudes, the performance of *A. tetraquetra* was poor, suggesting that the nurse itself was stressed and less able to ameliorate harsh conditions for other species. Consequently, if nurse plants become stressed by drought, facilitation may increase with altitude even in xeric climates. Keeping this in mind, our analysis indicated that the most common scenario in xeric climates is an increase in net facilitation with decreasing altitude, likely due to higher performance of cold-intolerant but drought-tolerant nurse species. In fact, this is the case for a number of spiny shrubs dominating low altitude alpine communities from the Mediterranean Basin, that show increased fitness and facilitative effects with decreasing altitude (Callaway *et al.* 2002). In the two examples provided above (Schöb *et al.* 2013 and our analysis), it appears to be the tolerance of the nurse to the prevailing stress factor that contributes the most to changes in plant–plant interactions on opposing stress gradients in xeric climates.

In summary, unlike mesic climates, change from net neutral interactions to net facilitation or net competition in xeric climates cannot be unambiguously attributed to either environmental severity or neighbour trait effects. Furthermore, due to the occurrence of opposing stress (temperature and aridity) gradients in xeric climates almost

any effect is possible, and the observed response then depends very much on the specific life strategies of the interacting species. This makes it difficult to predict how interactions among plant species might affect their responses to climate change.

#### IMPLICATIONS FOR UNDERSTANDING COMMUNITY RESPONSES TO CLIMATE CHANGE

We propose that partitioning net interactions among plants along altitudinal gradients may improve our ability to predict alpine community responses to climate change, in particular in xeric alpine environments where facilitative interactions are of disproportionately high importance (Cavieres & Badano 2012). Climate change in xeric regions might affect the direction and intensity of net plant–plant interactions differently depending on whether changing temperature or precipitation affects the fitness of the response species directly (environmental severity effect) or indirectly, that is, mediated through the impacts of neighbours (neighbour trait effect). Predicted increases in temperature and decreases in summer precipitation in Mediterranean climates will lead to more drought stress and less cold stress (IPCC 2007). In this case, drought-tolerant nurse species such as spiny shrubs will likely increase their facilitative effects for drought-intolerant beneficiary species and buffer the effects of increasing drought stress. At low altitudes, the predicted increase in facilitation will likely be due to an environmental severity effect where the response species will suffer from increasing stress in the absence of the nurse. In contrast, at high altitudes, the increase in facilitation will more likely be through a neighbour trait effect where the nurse plant improves its facilitative traits due to less experienced cold stress. On the other hand, facilitative effects of cold-tolerant nurse species such as the cushion *Arenaria tetraquetra* ssp. *amabilis* in the Sierra Nevada (Schöb *et al.* 2013) will likely wane due to their sensitivity to drought. These opposite changes in interactions depending on the neighbours involved in the interaction will have contrasting effects on species range shifts with climate change. Increased facilitation of spiny drought-tolerant shrubs through environmental severity effects will likely limit the loss of stress-intolerant species at low elevations; whereas increased facilitation at high elevation through neighbour trait effects will extend their upper altitudinal limits. In opposition, a decrease in the facilitative effect of cold-tolerant alpine cushion species will likely accelerate species loss at drier and lower sites.

In contrast, we expect warming in mesic climates to only reduce the importance of facilitative interactions and do not expect facilitation to buffer the effects of warming. In temperate climates, we expect increasing competition at low altitudes through neighbour trait effects and decreasing facilitation at high altitudes through environmental severity effects to exacerbate any temperature increases that might occur. Thus, we predict that in temperate

climates, biotic interactions should accelerate alpine species range shifts towards higher elevation, in particular through increased species loss at low elevations with increasing competition. In the Arctic, competition may not be very significant at low altitudes even with warming, because poor soils might limit increases in competitive effects (but see Cornelissen *et al.* 2001 and Sturm, Racine & Tape 2001). We might expect facilitation to diminish in importance at high altitudes through environmental severity effects, as in temperate climates. In both cases, we might expect interactions among plants either to have minimal effects or to slightly exacerbate any temperature increases. However, and as noted, we do not have the data necessary to test whether these trends – based on extrapolation from a handful of studies, where experimental approach is confounded with climatic zone – are consistent at a global scale. Although they suggest novel general predictions about how species interactions could affect community responses to climate change, our work also highlights an acute need for standardized approaches and experimental manipulations at geographic scales if we are to move beyond predicting future distributions of species using climate parameters fitted to existing distributions (Davis *et al.* 1998; Fraser *et al.* 2013). Without appropriate interaction estimates, we have a very limited ability to predict future rates of community change, the mechanisms that drive such change, and how warming effects will vary biogeographically.

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## Supporting Information

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

**Appendix S1.** A list of studies used in the current meta-analysis to examine the importance of altitudinal gradients on plant-plant interactions including both nurse-plant and neighbourhood level effects.

**Appendix S2.** A summary of the relative frequency of effect sizes estimates calculated from the available literature on plant-plant interactions on altitudinal gradients.

**Appendix S3.** A summary of the relative frequency of effect size estimates calculated from the literature on plant-plant interactions on altitudinal gradients summarized by climatic region and by nurse-plant effects studied or by neighbourhood-level effects.