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LETTER

Facilitative plant interactions and climate simultaneously drive alpine plant diversity

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Abstract

Interactions among species determine local-scale diversity, but local interactions are thought to have minor effects at larger scales. However, quantitative comparisons of the importance of biotic interactions relative to other drivers are rarely made at larger scales. Using a data set spanning 78 sites and five continents, we assessed the relative importance of biotic interactions and climate in determining plant diversity in alpine ecosystems dominated by nurse-plant cushion species. Climate variables related with water balance showed the highest correlation with richness at the global scale. Strikingly, although the effect of cushion species on diversity was lower than that of climate, its contribution was still substantial. In particular, cushion species enhanced species richness more in systems with inherently impoverished local diversity. Nurse species appear to act as a 'safety net' sustaining diversity under harsh conditions, demonstrating that climate and species interactions should be integrated when predicting future biodiversity effects of climate change.

Keywords

Alpine, cushion species, foundation species, nurse plants, positive interactions, species richness.

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INTRODUCTION

Understanding the primary drivers of biological diversity at different spatial scales is a fundamental goal of ecology and evolutionary biology, not least because biological diversity has substantial effects on the functioning of ecosystems and the services they provide (Allan *et al.* 2011; Isbell *et al.* 2011). Ecologists have demonstrated that species diversity is governed not only by local interactions among coexisting species but also by large-scale biogeographic, historical and evolutionary processes (Ricklefs 2004, 2008; Harrison & Cornell 2008). However, our understanding of the interplay and relative importance of factors that control species diversity at different spatial scales is limited by the logistical and conceptual difficulties of scaling up local-scale processes to explain large-scale patterns of biodiversity (Harrison & Cornell 2008; Ricklefs 2008; Brooker *et al.* 2009). The inherent complexity of local-scale processes, such as biotic interactions among coexisting species, makes it difficult to extrapolate from small-scale studies to landscape, regional and global scales (Ricklefs 2004). Such difficulties may contribute to the perspective that biotic interactions play a minor role, relative to the effects of factors such as climate and historical processes, as drivers of large-scale species diversity patterns (Ricklefs 2008).

However, we know that interactions among species generate diversity through evolutionary processes (e.g. Benton 2009), are key to local-scale diversity (e.g. Tilman 1997; Allesina & Levine 2011), and at least in some cases appear to sustain regional-scale diversity (Valiente-Banuet *et al.* 2006; Harrison & Cornell 2008). Thus, the assumption that local-scale interactions do not influence species diversity at large spatial scales may be inaccurate, as there is substantial potential for local interactions to determine species diversity in certain biomes both regionally and globally (Brooker *et al.* 2009; Moya-Laraño 2010). But to accurately assess the relative importance of biotic interactions and other drivers in determining species diversity, we need studies that utilise consistent reductionist approaches over large spatial scales (Fraser *et al.* 2013). These would allow elimination of between-site differences in experimental methods (He *et al.* 2013), enabling more reliable contrasts of the effects of biotic interactions with those of abiotic factors (Moya-Laraño 2010; Freestone & Osman 2011). We address this issue by focusing on the influence of nurse plant species on local species diversity (i.e. species richness at the entire community level) relative to abiotic factors, using a standardised approach applied at a global scale within a particular biome.

Nurse plant species generate favourable conditions for the establishment and growth of other species, controlling much of the structure and composition of a given community (Callaway 2007). Their micro-scale roles are often clear (i.e. patches of nurse plant species contain more species than bare ground), but the extent to which such effects are propagated up to larger scale (i.e. entire community, regional or global) diversity patterns has not been explored. For instance, Butterfield *et al.* (2013) found that nurse plant species are important in maintaining phylogenetic diversity in more severe environments, but did not differentiate the relative importance of abiotic and biotic processes.

Alpine systems are ideal for pursuing this issue; here, we use them to assess how plant species diversity in alpine habitats worldwide is influenced by biotic interactions with nurse species and compare this to the effects of climatic drivers. Alpine ecosystems are found above the upper altitudinal limit of tree growth, and cover 5% of the Earth's land-area, harbouring approximately 10 000 plant species (Körner 2003; Nagy & Grabherr 2009). It is assumed that alpine plant diversity is regulated mainly by large-scale abiotic filters such as climate, geomorphology and historical processes such as glaciation (Körner 2003). However, species interactions, particularly facilitation – the benefits to an organism from the minimisation by neighbouring organisms of physical or biotic stresses (Bertness & Callaway 1994) – can strongly influence local diversity in these harsh environments (Kikvidze *et al.* 2005; Cavieres & Badano 2009; Butterfield *et al.* 2013). Despite many common environmental features (Körner 2003), globally alpine ecosystems display major climatic dissimilarities owing to latitudinal position (seasonality vs. aseasonality, high vs. low altitude, tropical or Mediterranean systems) or degree of continentality (Nagy & Grabherr 2009*)*. Alpine systems also show substantial variation in diversity across local and regional-scale environmental gradients (Nagy & Grabherr 2009). Alpine ecosystems thus provide excellent opportunities to explore the relative effects of local (biotic interactions) and regional (climate) processes in affecting species diversity at a global scale.

We studied treeless alpine plant communities at 78 sites in 16 countries across five continents. For consistency, we focused on communities dominated by plants exhibiting a 'cushion' growth form (see Appendix S1 for examples of the communities and cushion species sampled), one of the most conspicuous morphologies found in alpine habitats, and which appears to have evolved convergently across a very wide range of plant families (Rauh 1939). The low stature and compact architecture of cushion plants has repeatedly been shown to attenuate the effects of severe alpine conditions (see Appendix S2 for a compilation of environmental modifications by alpine cushion plants), allowing them to act as nurse plants for other alpine species (Appendix S2). The presence of different cushion species in different regions across the globe provides a model system for systematically assessing and generalising the effects of facilitative interactions on species diversity while introducing minimal bias from local or regional biogeography and phylogenies (Butterfield *et al.* 2013). The global distribution of cushion-dominated plant communities also provides an excellent opportunity to scale up from local community effects to a global scale such that the relative importance of local processes can be directly evaluated. Furthermore, facilitative interactions have been found in every biome on Earth (Callaway 2007). Thus, although focusing on alpine environments, our study is a test of widely applicable and general ecological principles.

Using our global data set of alpine plant communities we asked the following questions: (1) Is the relationship between nurse species and total species richness at the community-level comparable in scale to the relationship of broad-scale variation in climate with total species richness? (2) Do associations between nurse plants and species richness vary with local productivity, suggesting that the outcome of biotic interactions depends on environmental context? We also used structural equation modelling (SEM) to ask (3) whether total species richness is related to climate or productivity due to (i) direct effects beyond those of nurse species or (ii) indirect effects related with the magnitude of facilitation by nurses, or both?

MATERIALS AND METHODS

Study sites

Data were collected from 78 predominantly alpine plant communities in North and South America, Europe, Asia and New Zealand.

Sites were selected to include sufficiently large populations of nurse cushion plants, located in generally low productivity habitats within alpine belts (i.e. above natural tree line). Forty-one cushion plant species were sampled across the 78 sites (Appendix S3).

Sampling

Data collection occurred between January 2004 and July 2010, and all researchers used a standardised sampling protocol (see below). At each site, within an area of *c.* 0.5 × 0.5 km, we haphazardly selected a large enough number of plants of each individual nurse cushion species (see Appendix S3 for details of sample size at each site) for robust statistical analyses, and all established plants (i.e. no seedlings) growing within these selected cushions were identified to species and their abundance recorded. Cushions are usually roughly elliptical, and so at the majority of sites we measured the maximum and minimum axes of each cushion to estimate its area (see Appendix S3 for details of cushions' size at each site, where available). To obtain comparable samples for assessing species richness in surrounding 'open' areas (areas not covered by the cushions), areas matching the size of each sampled cushion were surveyed at haphazardly selected paired points away from each sampled cushion. In those cases where cushion size was not measured, a wire hoop was shaped to match the size of the sampled cushion and used to regulate the size of patch sampled in the 'open' areas. Again, all established plant individuals within these selected open areas were identified to species and recorded. The percentage cover of cushions and open area was determined at each site along 50 m linear transects. Across all sites cover was relatively low, with an across-site mean of 16%, ranging from 2 to 50% (see Appendix S3 for details). We sampled a mean (± 1 SE) of 81 (± 3) sets of paired cushion and open plots per site. At all sites, the non-cushion species were mostly herbaceous perennials with the small size and prostrate growth typical of alpine species (Körner 2003). In a very few sites (e.g. central Chile Andes, Sierra Nevada Spain), the vegetation also contained small prostrate shrubs and annuals that usually grow in open areas. The mean density of individuals was 13 (± 23 SD) individuals per m^2, ranging from 1 to 143 individuals per m^2 (see Appendix S3 for details).

Climatic data

There is a scarcity of weather stations for high elevation habitats in general, and for some highly remote alpine areas such as the tropical Andes or the Himalayas in particular. To obtain comparable long-term climate data we used Worldclim (http://www.worldclim.org; Hijmans *et al.* 2005). Worldclim is a set of global climate grids with a spatial resolution of about 1 km^2, and is widely used in species distribution modelling. Based on the coordinates of our sampling sites, for every site we extracted from the Worldclim database monthly values of temperature and precipitation that were later used to calculate temperature and precipitation during the summer (see below). It is important to note that for all sites the pixels in the Wordlclim database were above the treeline, and that spatial resolution of WorldClim is not substantially different from the area that we explored at each site when obtaining the field data. Further, for each site estimates of the monthly near-surface relative humidity, actual evapo-transpiration and soil wetness were extracted from the archive of the Global Land Data Assimilation System (GLDAS). GLDAS is a global, high-resolution, terrestrial modelling system that merges satellite and ground-based observations to produce optimal estimates of land surface states and fluxes (Rodell *et al.* 2004). For this study, data were drawn from the GLDAS 0.25° for the period 2001–2010. Although GLDAS fields of 0.25° (i.e. *c.* 25 km^2) resolution reflect a broader spatial average than WorldClim data, they provide climate variables (i.e. actual evapo-transpiration) not available in climate databases. At this spatial resolution, the GLDAS data do not fully capture microclimate effects related to local topography, but are useful in capturing larger scale climatic differences between the ranges of alpine regions included in the study (see Appendix S4 for climate variables for each site).

Data analyses

Nurse cushion species can have effects on the presence of non-cushion species in the local community (with some non-cushion species being restricted to cushion habitats) and on the abundance of species that are already present (with some non-cushion species occurring at higher abundance within cushions than in open areas, suggesting that the presence of many non-cushion species in the community depends on the presence of cushions). Thus, to properly explore the effects of cushions on local species richness both effects should be taken into account.

To assess the impact of nurse cushions on the abundance of non-cushion species, for each non-cushion species in each community we calculated the Relative Interaction Index (RII) (Armas *et al.* 2004) based on the species' abundance (number of individuals) as follows:

$$\mathrm{RII} = (\#\text{within cushion species} - \#\text{in open})/(\#\text{within cushion species} + \#\text{in open})$$

Thus, RII = 1 when all individuals of a species occur within cushions, 0 when equally distributed in cushions and open areas, and −1 when all occur in the open. Mean RII across all species within a community was then used as an estimate of the average effect of the nurse cushion species on other species at that site (Community RII). For several alpine sites, it has been demonstrated that spatial associations of non-cushion species with cushion species are largely determined by facilitation of survival, growth and/or reproduction of the non-cushion species (e.g. Cavieres *et al.* 2006; Schöb *et al.* 2013). Thus, community RII provides a good indication of the frequency and intensity of positive interactions of nurse cushion plants on non-cushion species at the community level.

To examine the impact of cushion species on the presence of non-cushion species, we used rarefactions to quantify the effects of nurse cushion species on community-level species richness (S_{Total}) at each site. This allowed us to account for differences in the total area sampled across study sites (Badano *et al.* 2006). To estimate S_{Total} per site, we generated synthetic data sets combining data taken within the cushion species and from the open areas into a single species x samples matrix for each study site, and a rarefaction analysis was run for each site. For each rarefaction, 500 resamples were randomly drawn without replacement for each sample size (from one sample to the maximum number of samples). The Mau-Tao estimator of species richness at the asymptote was calculated as recommended for interpolations on sample based rarefactions

(Colwell *et al.* 2004). The species richness of the community without cushions (S_{Open}) was estimated from the asymptotes of rarefaction curves constructed using only open area samples (Badano *et al.* 2006). To assess the magnitude of the increase in species richness at the community level due to the presence of cushion species, we calculated the proportion of increase in non-cushion species richness (ISR) as follows:

$$ISR = (S_{Total} - S_{Open})/S_{Total}$$

This index gives a qualitative idea of the magnitude of the effect of cushion species on species richness at the scale of the entire local community. All rarefaction analyses were performed with the software EstimateS v. 8 (Colwell 2006).

The importance of different climatic drivers of global diversity patterns, such as temperature, precipitation, water balance and energy-related variables during the growing period (Currie *et al.* 2004; Kreft & Jetz 2007) was assessed by estimating their effect sizes on total species richness. For this, linear regressions with S_{Total} (log transformed) were tested for summer precipitation (June to August in northern hemisphere, January to March in southern hemisphere), precipitation of the warmest quarter of the year as provided by Worldlcim, precipitation to temperature ratio for summer, actual evapotranspiration, summer means temperature of air and minimum temperature of the coldest month (January or June) as a measure of continentality and maximum and minimum temperatures at the onset of the growing season (June or January). For those climatic variables that correlated significantly ($P < 0.05$) with S_{Total}, mean effect size and parametric 95% confidence interval were calculated as $[\mathrm{range}(x) \times b]/[\min(x) \times b + a]$, where x is the environmental variable, b the estimated slope of the regression of species richness on x and a the estimated species richness intercept of the regression. Confidence intervals were estimated through bootstrapping each regression 1000 times, using the 'boot' and 'boot.ci' functions in R (R Development Core Team, 2011).

We wished to compare the magnitude of climatic vs. facilitative effects on species richness. To qualitatively accomplish this, we first compared the magnitude of the standardised effect sizes (SES) of the climatic variables that were significantly correlated with S_{Total} with the magnitude of the mean effect of cushions on S_{Total} assessed as the average of ISR (and parametric 95% confidence interval) considering all sites together. Although SES values and mean ISR come from different analyses, both indicate the mean size of the effect of a climate variable or the presence of cushion species on S_{Total} considering all sites together (i.e. global scale).

Some environmental factors may affect community diversity directly, while others may act indirectly. Both direct and indirect drivers can have positive and negative effects on local diversity, and indeed in some cases the same driver might have, for example, a positive direct effect and a negative indirect effect that may be obscured by looking at simple bivariate correlations. Thus, we used SEM to further assess and quantitative compare the simultaneous direct and indirect relationships between climate and nurse cushion species on S_{Total} considering all site together (Grace 2006; Harrison & Cornell 2008). SEM is one of the most powerful tools available for revealing the structure linking variables that are correlated in a multivariate way (Shipley 2002; Grace 2006). Hypothetical relationships between the variables need to be explicitly defined, and the congruence between observed and expected covariances under the causal relationships proposed is used to estimate the efficiency of the model.

Our *a priori* model of the interactive relationships of climate, productivity and the presence of nurse cushion species on S_{Total} at local scales was based on the following premises: (1) There is a direct relationship between climate and S_{Total}. (2) Species diversity accumulated in open areas (S_{Open}) is related to two main abiotic constraints – climate and local productivity. The latter is also related with climate, but is modulated by other small-scale factors driving environmental heterogeneity such as microtopography. (3) Whole community diversity (S_{Total}) is related to the diversity contributed from the open areas (S_{Open}), but depends also on a complex set of direct and indirect relationships involving climate, productivity and the modulatory effect of the nurse cushion species, which is also affected by local productivity. (4) The nurse cushion species effect, primary productivity and climate are unobserved variables with no unit of measurement, and so are included as latent variables along with suitable indicators for each. We considered evapotranspiration and precipitation during summer months to be the best indicators of local climate (see results); total cover and density of individuals in open areas as indicators of productivity; and mean RII and ISR as indicators of the cushion species effect. The relationship between climate and productivity was set as a covariance between both variables. Thus, we determined how whole community diversity (S_{Total}) depended on the direct effects of species already present in open areas (S_{Open}) and the contribution of biotic interactions with cushion species, as well as how these factors are modulated by the indirect effects of productivity and climate. To solve the scale indeterminacy problem, we standardised the unit of measurement of the indicator variable that best represented the latent construct (that with the largest standardised coefficient in a preliminary exploratory analysis) by fixing its path coefficient to 1. Path coefficients were estimated using the maximum likelihood algorithm, and congruence between observed and expected covariances was assessed by a χ^2 goodness-of-fit test. A significant goodness-of-fit test would indicate that our aprioristic model does not fit the data. Since this test may be affected by large data sizes, model fit was also evaluated by means of the goodness-of-fit index (GFI) and the Bentler and Bonett's normed-fit index (NFI), which are often used in SEM (Grace 2006). Values of these two indices range between 0 and 1, and values above 0.9 would indicate an acceptable fit of the model to the data, or in other words an adequate congruence between observed and expected covariances. Our SEM model was tested with AMOS 19 (Amos Development Corporation, 2009).

RESULTS

Rarefaction curves reached an asymptote at most study sites (Appendix S5), indicating that the sampling effort was large enough to fully capture the composition of species assemblages in both cushion and open area habitats. At 92% of sites we found positive values of ISR, indicating that at the majority of sites nurse cushion species enhance species richness at the whole community level (S_{Total}) (Fig. 1a). Likewise, at 81% of the sites we found a positive value for community RII, indicating that at most sites most species were associated with, and likely facilitated by, the nurse cushion species (Fig. 1b).

The effects of cushion species on both interaction outcomes (RII) and increase in species richness (ISR) were not constant at the global scale when all sites are considered, and showed interactions with other environmental drivers or indicators of richness (Fig. 2). Vegetation cover – a good surrogate for local productivity in

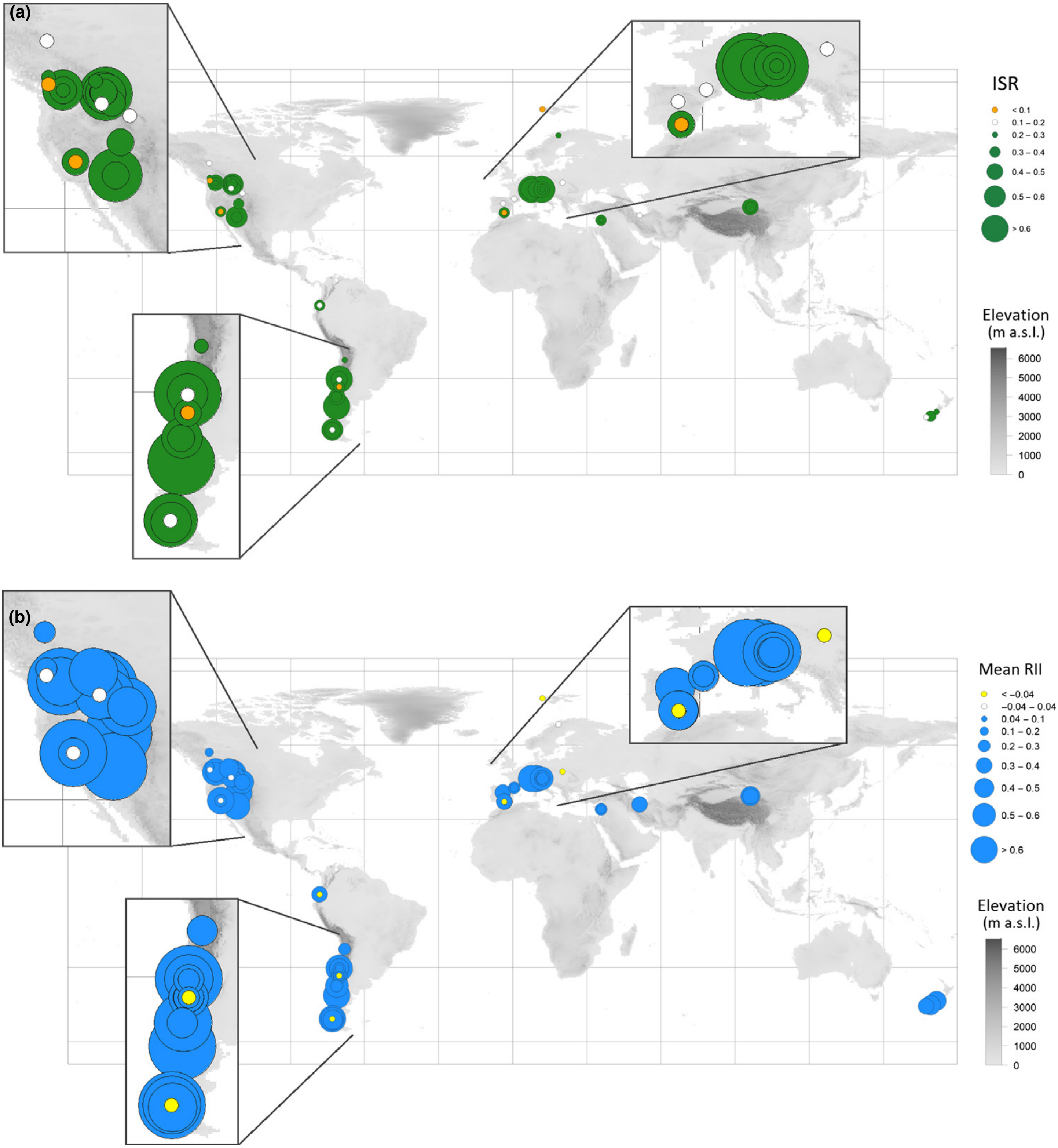

Figure 1 World map showing the sign (colour scale) and magnitude (size scale) of (a) the proportional increase in species richness due to the presence of nurse cushion species (ISR) and (b) the mean interaction (calculated using the mean Relative Interaction Index, RII) between cushion species and the rest of the plant community at our studied alpine sites.

vegetation of relatively constant height (Kikvidze *et al.* 2005) – was negatively correlated with community RII. As vegetation cover increased, community RII became less positive, moving towards net neutral interactions (Fig. 2a). Further, the facilitative effects of cushion species on whole community diversity (ISR) decreased roughly four to fivefold with an increase in plant cover from 10 to 50%

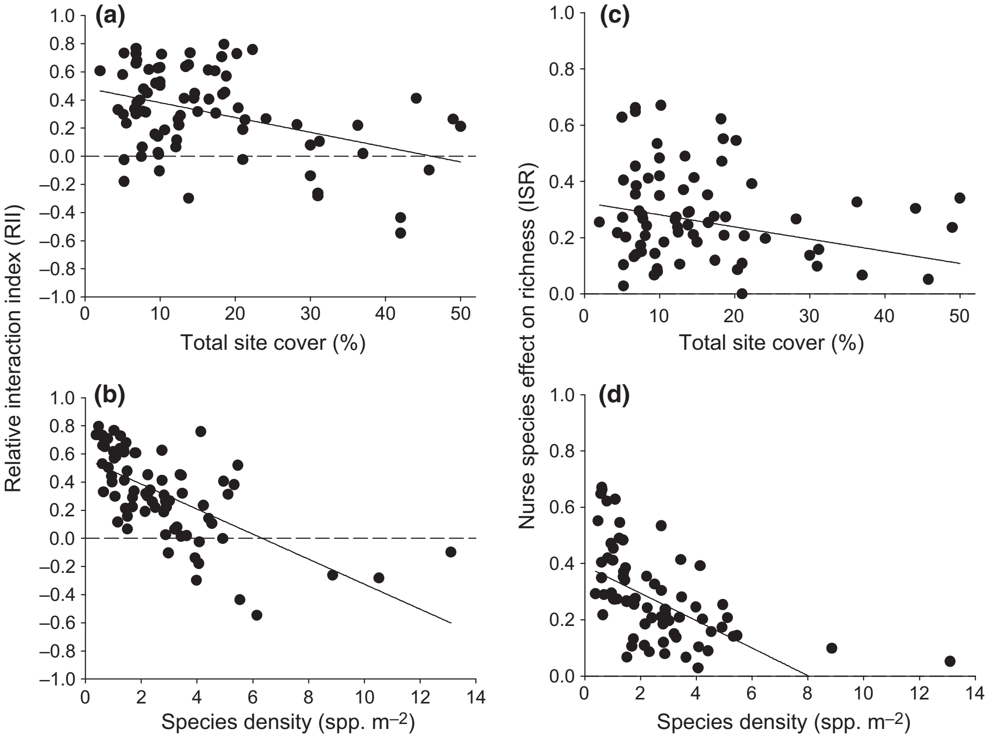

Figure 2 Relationships between nurse cushion species interaction effects [Relative Interaction Index; (a) and (b)] and foundation species effects on richness (c) and (d), and total site cover (a) and (c) and species density in open areas (panels (b) and (d). Major axis linear regression results are as follow: (a): $r = 0.40$, $P < 0.01$; (b): $r = 0.39$, $P < 0.01$; (c): $r = 0.27$, $P < 0.05$; (d): $r = 0.38$, $P < 0.01$.

Table 1 Results of linear regression models tested for the relationship between climate variables and total species richness and effect size (± CI) of those climate variables significantly related with species richness. The effect of cushion species on richness at the global scale (estimated as the mean ISR) is also indicated

Variable	*a* (intercept)	*a* (SE)	*b* (slope)	*b* (SE)	*P*	r^2	Effect size	± CI
Minimum temperature of the coldest month	26.0	3.40	−0.045	0.170	0.792	0.001		
Summer mean temperature	26.5	3.81	0.043	0.415	0.917	<0.001		
Maximum temperature summer	32.3	5.05	−0.256	0.227	0.264	0.016		
Minimum temperature summer	26.9	1.74	−0.039	0.472	0.934	<0.001		
Soil temperature summer	27.9	1.76	−0.293	0.320	0.363	0.011		
Precipitation: temperature summer	26.0	1.67	0.123	0.114	0.284	0.015		
Evapotranspiration summer	18.5	3.08	0.131	0.044	0.004	0.106	0.26	0.02
Precipitation summer	22.0	2.12	0.026	0.009	0.005	0.100	0.63	0.09
Precipitation warmest quarter	22.0	2.12	0.026	0.009	0.005	0.100	0.64	0.12
Nurse cushion species effect on richness (mean ISR)							0.31	0.02

(Fig. 2c). Species density in open areas was negatively correlated with both mean (community) RII and with ISR (Fig. 2b, d).

Only variables related with water balance (summer precipitation, precipitation of the warmest quarter of the year and actual evapo-transpiration) during the growing season showed a significant correlation with S_{Total} (Table 1). No measures of temperature *per se* were correlated with species richness (Table 1). The effect sizes estimation for summer precipitation, precipitation during the warmest quarter of the year and actual evapo-transpiration during the growing season were 0.63 ± 0.09, 0.64 ± 0.12 and 0.26 ± 0.02 respectively (Table 1). While effect sizes based on correlations are statistically limited by the observed range of both variables, our global data set covered the very large breadth of environmental conditions that exist in alpine biomes, therefore providing reasonable estimates of environmental effects on species richness. Importantly, the effect size of cushion species on S_{Total} (as measured by mean ISR) was 0.31 ± 0.02, which is lower than, but of the same order of magnitude as the SES of climatic variables from regressions (Table 1).

The overall SEM fit was good, i.e. the expected covariance matrix under our aprioristic model did not deviate significantly from the observed covariances, and fit indices were far above 0.9 ($\chi^2_{14} = 23.5$, $P > 0.05$; NFI = 0.967; GFI = 0.938). As predicted, the SEM showed a direct relationship between aspects of climate and total species richness (S_{Total}), and that both species richness in open habitats (S_{Open}) and the presence of cushion species had positive effects on S_{Total} (Fig. 3). Interestingly, the standardised coefficients indicated that although the effect of climate and S_{Open}

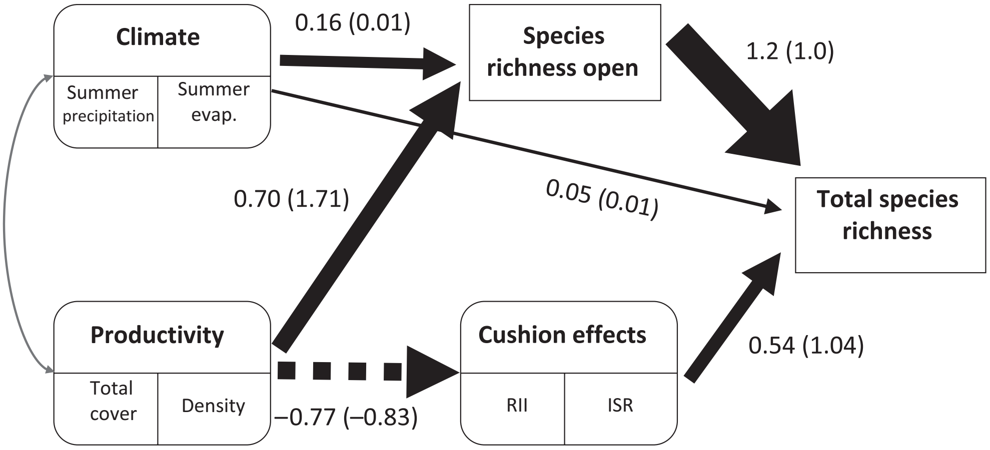

Figure 3 Structural equation model of proximate and distal controls on total species richness. Latent variables are in bold font, with associated indicator variables below. Numbers adjacent to unidirectional arrows are standardised (and unstandardised) partial regression coefficients. Width of arrows is proportional to the magnitude of the standardised coefficient, with solid arrows indicating a positive effect and dashed arrows a negative effect. A double headed arrow indicates a correlation and not a linear-causal relationship between variables. All relationships are significant at the $\alpha = 0.05$ level.

on S_{Total} is higher than that of cushion species, again they are of the same order of magnitude (Fig 3). However, these two proximate controls of total species richness were affected by productivity in different ways. Productivity showed a positive relationship with (S_{Open}), and in turn was positively related with S_{Total}, but productivity had a negative relationship with the effect of cushion species (i.e. facilitative effects declined under greater productivity). As the effect of the cushion species had a positive relationship with S_{Total} (Fig. 3), the negative effect that a decline in productivity might have on S_{Total} via the positive relationship between productivity–S_{Open} and S_{Open}–S_{Total}, may be counteracted by the increasing role of facilitation on S_{Total} in low-productivity environments. Cushion species thereby function – at a global scale – as important modulators of environment–diversity relationships by significantly reducing declines in species richness as environmental severity increases.

DISCUSSION

Positive interactions are widely recognised as playing a major role in the organisation of community structure and diversity, especially in environmentally harsh habitats (Michalet *et al.* 2006; Brooker *et al.* 2008). Experiments in alpine habitats indicate that positive spatial associations are mostly determined by facilitative interactions among species (e.g. Choler *et al.* 2001; Kikvidze *et al.* 2005), where the presence of neighbours can ameliorate environmental factors that would otherwise limit survival in cold habitats, e.g. strong winds and low temperatures (Carlsson & Callaghan 1991; Callaway *et al.* 2002). Thus, neighbours that ameliorate those limiting factors might be important in determining the presence of some species in alpine habitats and hence affect local species richness. The architecture of alpine cushion plants ameliorates some environmental factors, increasing the survival, growth and reproduction of species growing within the cushions (Appendix S2). It is very likely that these factors are involved in the cushion-driven increase in species richness at the community scale (ISR) observed in most of the sites (Fig. 1a). For example the intensity of freezing temperatures and duration of the growing season are known to determine the altitudinal distribution of alpine and subalpine plant species (Guisan *et al.* 1998). Amelioration of these conditions, as observed in some cushion plants, may allow the presence of these other plant species at higher elevations than would be expected in the absence of cushion plants, thereby increasing local plant species richness.

Importantly, although the positive effects of facilitative interactions on diversity are understood, previous assessments of their role in regulating diversity have focused only at a within-community level (e.g. Silliman *et al.* 2011; Soliveres *et al.* 2011). Here, we found that although the effect sizes of climatic variables (i.e. precipitation and actual evapotranspiration during the growing season) on total species richness at a global scale (i.e. considering all sites together) were higher than those of facilitator cushion species (mean ISR), all effects were of a similar order of magnitude (Table 1). In other words, local-scale positive interactions with cushion species were manifest as positive effects on species richness at a global scale, with the size of this effect being substantial even in relation to key climate drivers. In addition, SEM results revealed that although the effect of facilitator species on total species richness was lower than that of climate on the number of species in open areas (S_{Open}) and hence on total species richness (Fig. 3), the magnitude of the cushion effect was again substantial. Our results are the first to show that positive interactions not only enhance local diversity, but do so globally as much as climatic drivers of diversity appear to.

We found no relationship between any measurement of temperature *per se* and species richness, likely because alpine systems around the world, and particularly cushion-dominated alpine communities, have a relatively narrow temperature range (Körner *et al.* 2011). Some regional studies found that climatic variables like temperature or potential evapotranspiration (PET) are the most important predictors of species richness at spatial scales of 30 km^2 (e.g. Moser *et al.* 2005; Marini *et al.* 2008). However, although these studies support climatic variables as primary determinants of vascular plant species richness, they suggest that the presence of favourable habitats (including the presence of facilitator species) may have higher predictive power at lower spatial resolutions, with important consequences in the context of species richness modelling.

Interpolated climate products and land surface models such as WorldClim and GLDAS contain errors/uncertainties derived from the scarcity of reliable long-term climate records in alpine regions. Interpolation of precipitation data in complex terrain is particularly challenging. Thus, inaccuracies relative to the genuine values for the climate parameters at the point where our diversity measurements were made, suggest that some caution is needed with respect to our findings. However, the spatial resolution of the WorldClim database (1 km^2) is not substantially different from the area explored at each site during field recording. In addition, although having a coarser spatial resolution, analyses using data derived from GLDAS (25 km^2) produced similar results to those run using data from WorldClim (i.e. only water related variables correlated with species richness). Thus, we believe that the conclusion that facilitation has comparable effects on diversity relative to climatic gradients is robust to the lack of high-resolution climate data.

Recent theoretical studies indicate that positive interactions among resource competitors can produce species-rich communities (Gross 2008). Indeed, in meta-community models it has been observed that in communities with reduced regional pools of species and/or with low environmental quality, positive interactions among species can rapidly evolve, generating higher species richness than that predicted from competitive or neutral processes (Filotas *et al.* 2010). Thus, our empirical results, where positive interactions with cushions increase local species richness at the entire community level, are in line with results derived from theory.

In our study the average interaction of non-cushion with cushion species was positive (i.e. positive values of RII) at more than 80% of sites. Thus, our results agree with the many previous studies demonstrating a significant role of facilitation in alpine habitats. However, it must be noted that not all previous studies have found strong facilitation effects in alpine systems, even in those dominated by cushion species (Mitchell *et al.* 2009; De Bello *et al.* 2011; Dvorsky *et al.* 2013). Indeed, we found sites where the average effect of cushions on non-cushion species abundance (RII) was negative. In these cases, it may be that environmental conditions in the open areas are not highly stressful, that the cushions and open area microhabitats at those sites are equally beneficial or restrictive for non-cushion species (i.e. De Bello *et al.* 2011), or that the competitive effects of some cushion species are stronger than their facilitative effects.

The relationships between community RII and the effect of cushions on species richness (ISR) with surrogates of environmental severity (Fig. 2) suggest that cushion species effects correlate *inversely* with cover (indicative of productivity) and species density, indicating that the facilitative role of cushion species is much greater in unproductive environments. This corresponds closely with predictions of the relationship between abiotic environmental severity and the outcome of biotic interactions – the Stress Gradient Hypothesis (SGH) of Bertness & Callaway (1994) – wherein increasing productivity is associated with a shift from facilitation to competition (or at least towards more neutral interactions, as in this study). The detected relationships between RII and ISR with surrogates of environmental severity also indicate that cushion plants had more important effects on maintaining local diversity in systems with an inherently low number of species. This concurs with an earlier study indicating that the beneficial impacts of cushion species on phylogenetic diversity were stronger in more extreme and species-poor sites (Butterfield *et al.* 2013).

Our results suggest that local-scale biotic processes might be important determinants of diversity patterns at a global scale. Biotic interactions appear to buffer the effects on diversity that are commonly related to climate change and reduced productivity (Michalet *et al.* 2006). In particular, nurse cushion species in these alpine systems may act as a 'safety net' that sustains diversity under very harsh conditions. Perhaps, most importantly, the facilitative effects of nurse species on species diversity are not negligible when compared to those of widely recognised and powerful climatic drivers. Climate and the biotic effects of facilitator species appear to combine to explain global patterns of alpine plant diversity, and thus both factors should be integrated in attempts to predict the effects of a dynamic global climate.

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AUTHORSHIP

L.A.C and R.M.C conceived the study and designed sampling procedure. All authors contributed data. L.A.C. and R.M.C. organised the collaboration, and oversaw data collection and management with R.W.B. L.A.C., R.M.C., B.J.B., B.F.Z., R.M., A.E. and R.W.B. analysed data. L.A.C., R.M.C., B.J.B. and R.W.B. wrote the manuscript with contributions from all co-authors.

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