

Climatic drivers of plant–plant interactions and diversity in alpine communities

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Abstract Alpine plant communities are particularly amenable to experimentally test the stress-gradient hypothesis (SGH), which predicts that competitive interactions will be more frequent in relatively productive environments, whereas facilitation will be more common in severe systems. Experimental testing of the SGH along latitudinal and elevation gradients within and across continents indicated that particular climatic variables act as drivers of plant–plant interactions and community structure. However, the SGH in its current form remains a

general framework that does not link explicitly climate variables such as temperature and precipitation to plant interactions or diversity. Here, we re-analyse our published data in order to explore whether climate can regulate biotic interactions and species diversity in alpine communities. We applied PCA to meteorological data, introduced latitude as a variable, and also used specially developed composite variables that combine temperature and precipitation during the growing season. The intensity of competitive interactions at low elevations decreased with increasing latitude, whereas the intensity of facilitative interactions at higher elevations did not vary with latitude. Micro-scale spatial patterns followed the same trend indicating that plant–plant interactions could generate these patterns. These findings specify the role of temperature in shifting the balance of plant interactions and can be readily incorporated in the SGH. We also found that species richness correlated positively with a composite climate variable, which is the product of maximum temperature and precipitation. Inclusion of this finding into the SGH will, however, need further studies focusing on the importance of water–energy relations for the dynamic balance of facilitation and competition.

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Introduction

Studies of plants in alpine systems have made many contributions to general ecological theory (see Bowman and Seastedt 2001; Körner 2003 for extensive reviews). Alpine

systems have easily discernable ecological gradients and similar gradients occur across global biogeographic scales, providing opportunities for coordinated macroecological approaches (e.g. Swihart et al. 2002). One of the highly cited global plant ecological experiments supports existing theoretical models of a dynamic balance between positive (facilitative) and negative (competitive) interactions in plant communities (collectively known as the stress-gradient hypothesis or SGH), demonstrating that the impact of facilitation increases relative to competition with increasing abiotic stress (e.g. Callaway et al. 2002). Some studies have documented facilitation as an important and widespread type of plant–plant interaction at higher elevations in alpine systems (Callaway 2007; Brooker et al. 2008) including the Caucasus (Kikvidze 1993, 1996; Kikvidze and Nakhutsrishvili 1998; Kikvidze et al. 2006), the Alps (Choler et al. 2001), and the Chilean Andes (Cavieres et al. 2002, 2006). Others have analysed larger scale regional patterns in Europe (e.g. Dullinger et al. 2007) and mountain systems of Eurasia and North America (Callaway et al. 2002; Kikvidze et al. 2005). These studies have not only provided experimental tests of the SGH, but have also suggested specific climate drivers behind the nature of plant–plant interactions, ecosystem productivity, local spatial patterns, and species richness in communities. For example, the best predictor of plant–plant interactions and productivity in this global-scale data set was temperature during the growing season, while species richness increased dramatically with precipitation (Callaway et al. 2002; Kikvidze et al. 2005). Although these findings suggest the potential for moving away from vague concepts of “productivity” or “severity”, and instead including specific climate variables into the SGH, recent attempts to develop the SGH have not made strong explicit links to particular climate parameters. For example, studies integrating the SGH with the humped-back diversity model of Grime (1973) by suggesting that facilitation increases species richness at moderate stress (Hacker and Gaines 1997; Michalet et al. 2006) have again focused on the concepts of “productivity” and “severity”. Furthermore, although a recent attempt to refine the SGH suggested that different types of environmental stress may have different effects on plant interactions (Maestre et al. 2009), the SGH in its current form remains a general framework that does not link explicitly climate variables such as temperature and precipitation to plant interactions or diversity. Establishing such links is important for better understanding the specific mechanisms behind the SGH, which ultimately have to be driven by climate at some level. It is also important for linking the SGH with other gradient-based concepts such as the abovementioned humped-back relationship between productivity and diversity, or the latitudinal gradient of biodiversity (see e.g. Moya-Laraño 2010 for a recent review).

Therefore, our general goal was to re-analyse the data collected across ten mountain systems representing two continents (Callaway et al. 2002; Kikvidze et al. 2005). As mentioned above, these data showed certain effects of simple climate variables such as temperature and precipitation on plant–plant interactions and species richness. We hypothesized that there were, however, other important links between climate and both plant interactions and species richness. To detect these factors, we used Principal Component Analysis (PCA) to reduce statistical noise and combine climate variables into a reduced number of principal components that can then be used for assessment of correlations with plant interactions or species richness. We also introduced latitude, which can be considered a complex climatic variable, as a factor into our analyses. Finally, we tried combining temperature and precipitation in various ways to quantify “water–energy” balance, since an extensive analysis of literature on the latitudinal gradient of biological diversity undertaken by a large group of ecologists (Hawkins et al. 2003) and a recent meta-analysis (Field et al. 2009) suggest that measures of energy, water, or water–energy balance explain spatial variation in richness better than other climatic and non-climatic variables. Here, we present two such composite variables: Utilizable Energy (hereafter UE), an index constructed herein, and for comparison, the classic Effective Precipitation (EP) measure (de Martonne 1927).

Methods

This study represents a re-analysis of data collected in 2001. Field methods are described in several previous publications (Choler et al. 2001; Callaway et al. 2002; Kikvidze et al. 2005). Here, we briefly highlight the most relevant details of these methods. We used data collected at the following ten locations in West Eurasian and North American mountain systems: the Abisko mountains in Sweden, the Absaroka mountains of Montana, USA, the Alps of Eastern France, the Banff mountains in Alberta, Canada, the Brooks Range of Alaska, USA, the Cairngorms of Scotland, UK, the central Caucasus mountains in Georgia, the central Rocky mountains of Colorado, USA, the Kluane mountains in the Western Yukon, Canada, and the Sierra Nevada in Spain. Nine of these sites are located within the continuum of arctic to temperate climates, but one—Sierra Nevada—notably stands out from this continuum, as it represents one of the driest Mediterranean mountain regions. Two study sites were used in each of these ten locations (Table 1). At each location one site was placed in subalpine herbaceous vegetation (below the natural treeline), and the other was placed from 300 m (Cairngorms) to 900 m (the Caucasus) higher in alpine vegetation (above the natural treeline). Therefore, all our sites

Table 1 Study sites: geographical location, topography, some climate variables and vegetation cover values ($T7_{max}$ July maximum temperature, Pr precipitation during growing season)

Site	Plot and elevation (m asl)	Aspect	Slope (°)	$T7_{max}$ (°C)	Pr (mm)	Cover (%)	Height (cm)
Abisko, N68.20, E18.45	ABI-H, 1100	NW	20	12.5	159	90	5
	ABI-L, 580	N	10	15.0	124	60	50
Brooks, N68.1, E211.00	BRO-H, 1400	E	15	12.5	245	60	5
	BRO-L, 800		0	15.5	152	95	5
Kluane, N60.53, E221.88	KLU-H, 1750	S-SE	40	13.5	275	75	20
	KLU-L, 900	SE	25	17.5	152	30	35
Cairngorms, N57.12, E3.50	CAI-H, 740	N	2	12.5	337	95	10
	CAI-L, 400	NW	5	15.5	306	70	30
Banff, N51.3, E244.0	BAN-H, 2300	E	25	16.0	199	70	10
	BAN-L, 1400	S	30	20.5	163	100	50
Absaroka, N45.10, E250.80	ABS-H, 3000	W	5	18.5	262	70	10
	ABS-L, 2350	W	25	22.0	190	90	30
Alps, N44.54, E6.39	ALP-H, 2900	SW	30	16.0	224	40	10
	ALP-L, 2100		0	17.0	483	100	30
Caucasus, N42.48, E44.39	CAU-H, 3000	NW	3	23.0	332	40	20
	CAU-L, 2100	NW	0	26.0	316	100	100
Central Rockies, N40.20, E254.60	CRO-H, 3500	E	10	18.0	155	80	10
	CRO-L, 2930	NE	10	22.0	152	90	60
Sierra Nevada, N37.13, E3.41	SNE-H, 3100	SW	30	18.5	70	10	5
	SNE-L, 2400	SW	15	22.0	68	100	10

represented typical herbaceous communities (Table 1) with shrub species mixed with herbaceous plants at some locations (especially Sierra Nevada). We assessed standing mass by cover (percent cover) and height (in centimetres).

Environmental conditions at these sites were characterized by data collected from nearby meteorological stations. Temperature data were corrected for elevation (Appendix 1, see also details in electronic supplement 2 of Callaway et al. 2002; Kikvidze et al. 2005). For PCA, we used the following meteorological data: January daily minimum temperature ($T1_{min}$, °C), June daily maximum temperature ($T6_{max}$, °C), July daily minimum temperature ($T7_{min}$, °C), July daily maximum temperature ($T7_{max}$, °C), and mean precipitation from May to August (Pr , mm). Due to strong continentality, maximum July temperatures at high and low sites of the Alps were similar.

We calculated two composite variables combining temperature and precipitation. The first is UE which we calculated as a product of July maximum temperature and precipitation during the growing season:

$$UE = T7_{max} Pr$$

(see above for definitions for Pr and $T7_{max}$). This index was compared to the classic EP which we calculated using a formulation modified from de Martonne (1927):

$$EP = Pr(T7_{max} + 10).$$

We re-analysed data on plant–plant interactions derived from the neighbour-removal experiments conducted from 1996 through 1999 at the 20 sites (Callaway et al. 2002; Kikvidze et al. 2005). At each site, three to nine target species were chosen (see Callaway et al. 2002 supplement for species names). Target individuals were selected using the following criteria: small relative to nearby conspecifics, distinct individuals or ramets could be identified, and generally not clonal species. In these experiments, the aboveground mass of all neighbouring species was clipped within 10 cm of the target individuals at the beginning of the growing season. For each species, 8–12 pairs were chosen and one of each was randomly selected for neighbour removal. The performance of target plants with neighbours removed was then compared to that of control target plants with neighbours intact. To confirm that in the few instances when clonal target species were selected the results were robust, a separate analysis of non-clonal species at the experimental sites in the Alps yielded virtually the same results as the analysis for all species combined. However, there were three common species in total for which discrete individuals were difficult to find (*Nardus stricta*, *Carex sempervirens*, *Sesleria coerulea*), and these species were not included in the experiments. Plants were harvested at the end of the following (second) growing season with the exception of the Cairngorms and the Banff locations, where the

experiment lasted only one growing season. At the start of experiment, the number of leaves for each target and control individual were counted. Plots were not weeded during the first growing season since re-growth was very slow and weeding would only disturb the sites. For experiments lasting two seasons, plots were weeded in spring of year 2. At the end of the experimental period, the numbers of leaves were re-counted, flowers and fruits counted, and survival recorded. Finally, all aboveground parts of targets and controls were harvested. Samples were oven dried for 3 days at 70°C and mass was recorded. These biomass accumulation data were used as a measure of plant performance. At the Caucasus high site, only leaf number was available, but relative changes in this measure corresponded to biomass differences.

Plant interactions were calibrated using the “relative interaction index” (RII, Armas et al. 2004). This index represents neighbour effects as a continuum from competitive to facilitative, and is calculated as

$$\text{RII} = (C - T)/(C + T),$$

where T and C correspond to the biomass accumulated, respectively, by isolated (without neighbours) and control (with neighbours) individuals. The values between 0 and 1 indicate positive neighbour interactions (facilitation) and values between 0 and -1 indicate negative neighbour interactions (competition). We calculated mean values of several plant species’ RII per plot from the means obtained for each species to characterize plant–plant interaction on the given plot.

Community structure data were derived from the presence/absence of all vascular species recorded in 300 randomly placed, 10 cm \times 10 cm quadrats, at each of our sites except Banff. The size of small quadrats was selected for analyses of micro-scale spatial patterns (Kikvidze et al. 2005, see also below). The total area sampled varied in size (25–50 m²) covering the same communities as the experimental plots. Diversity indices such as Inverse of Simpson’s dominance index and Evenness (based on Simpson’s index) were also calculated:

$$D = \sum_{i=1}^S p_i^2$$

where p_i is the proportion of a given i th species (based on the frequency of occurrence in 10 cm \times 10 cm quadrats), and S is species richness (Magurran 2004). Evenness was calculated as

$$E = (1/D)/S.$$

In addition, we calculated Shannon’s index (Magurran 2004). However, the behaviour of species richness was not distinguishable from those of the reciprocal of Simpson’s dominance or Shannon’s index. We found that Evenness declined gradually with increase of species richness, which

is not an unexpected result (not shown). We picked species richness as the diversity measure to present our results, since it is simple and biologically meaningful, and most commonly used in large-scale studies (e.g. Kluth and Bruehlheide 2004).

To quantify spatial relationships among species, the observed variance in species number per small (10 cm \times 10 cm in our case) quadrat can be compared to the variance expected from a random distribution of species (Schluter 1984; Palmer 1987; Gotelli 2000), using either the ratio or the difference of variances. The variance ratio (RV) has been used to describe spatial relationships in many different types of communities (Schluter 1984; Palmer 1987; Gotelli 2000; Wilson et al. 2000). The difference between variances, however, is more explicitly related to covariance because

$$V_{\text{obs}} = \sum \text{var} + 2 \sum \text{cov},$$

where $\sum \text{var}$ is the sum of variances of each species frequencies, and $\sum \text{cov}$ is net covariance, or the sum of covariance values obtained for all possible pairs of species in a given matrix. When net covariance is zero according to the null model, then the expected variance becomes merely the sum of variance of each species’ frequencies (Palmer 1987); hence, the difference between the observed and expected variances actually measures net covariance: $\sum \text{cov} = (V_{\text{obs}} - V_{\text{exp}})/2$. Covariance was selected for measurements of spatial pattern because it is symmetric around zero (unlike RV, which is constrained to values of zero and above), and because the interpretation of covariance is more straightforward (Wagner 2003). We calculated the observed and expected variances from the community matrices and used the equation above to calculate net spatial covariance. The values of net covariance close to zero indicate random dispersion of species over space. Positive net covariance values show clumping (since species absences and presences co-vary—often this aggregated spatial pattern results in patchy vegetation). Negative net covariance values point to over-dispersed pattern (since a species presence coincides with absence of other species and vice versa).

We analysed links between predictors (climate variables, latitude, principal components and composite variables) and response variables (RII, net spatial covariance, species richness) with regression analyses. For these and other statistical analyses (descriptive statistics, t test, PCA, correlation), we used the package Statistix 9 (Analytical Software, Tallahassee, FL, USA).

Results

Our earlier publications showed that simple climate variables such as temperature and precipitation could predict

Table 2 Pearson's coefficients of correlation between PCA principal components and geographical/climatic variables

Variables	PC1	PC2	PC3
$T1_{min}$	0.714***	-0.483*	0.383
$T6_{max}$	0.859***	0.410	-0.155
$T7_{max}$	0.919***	0.219	-0.251
$T7_{min}$	0.260	-0.916***	-0.066
Pr	0.114	0.258	0.942***
Latitude, °N	-0.766***	-0.114	0.008
$UE = Pr \times T7_{max}$	0.497*	0.386	0.721***
$EP = Pr/(T7_{max} + 10)^\circ$	-0.149	0.140	0.957***
RII	0.510*	0.139	0.050
Net spatial covariance	-0.183	-0.027	-0.124
Species richness, S	0.3551	0.273	0.523*

$T1_{min}$ January minimum temperature (°C), $T6_{max}$ June maximum temperature (°C), $T7_{max}$ July maximum temperature (°C), $T7_{min}$ July minimum temperature (°C), Pr precipitation during growing season (mm), EP Effective Precipitation, UE Utilizable Energy, RII Relative Interaction Index

* $P < 0.05$, *** $P < 0.001$

RII, productivity, spatial patterns and diversity (Callaway et al. 2002; Kikvidze et al. 2005). The present re-analysis extracted additional information. Three principal components (PC) accounted for 93.1% of between-site variance in climate. The first, second and third components were responsible for 43.5, 27.1 and 22.5% of variance, respectively. PC1 was most strongly related to the January minimum, June and July maximum temperatures, and to latitude; PC1 correlated also significantly with UE and RII (Table 2). PC2 correlated strongly with July minimum temperature, and weakly but still significantly with January minimum temperature. PC3 correlated with precipitation during the growing season, the composite variables (EP, UE), and species richness (Table 2). Net spatial covariance did not correlate with any of these variables except PC4 that explained only 5.3% of variation ($R = 0.610$, $P < 0.01$). PC4 also correlated with latitude ($R = 0.532$, $P < 0.05$).

Plant responses to neighbour removal behaved remarkably differently at low versus high sites along the latitudinal gradient. The RII index measured at low sites showed a clear trend of decreasing intensity of competitive interactions with increasing latitude, whilst RII index measured at high sites was more constant and did not correlate with latitude (Fig. 1a). Similarly, net spatial covariance of species at low sites showed a declining trend with increasing latitude, whilst latitude could not predict change in spatial pattern of high sites (Fig. 1b). One site, however, behaved as a clear outlier—the Sierra Nevada of Spain, where competitive effects were not detected at all. Although we included it in Fig. 1, this site was excluded from the trend analysis along the latitudinal gradient. The peculiarity of Sierra Nevada is

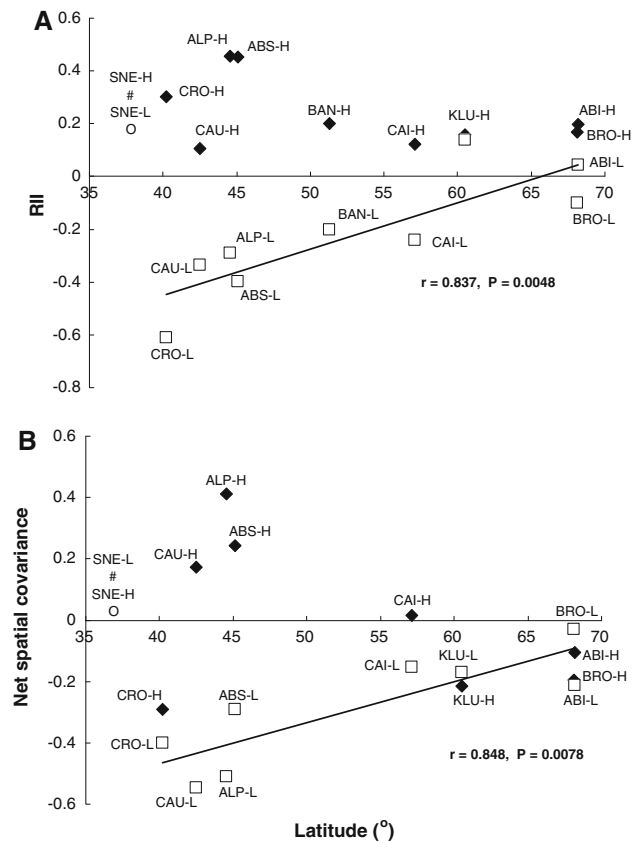


Fig. 1 Trends along the latitudinal gradient of **a** RII and **b** net spatial covariance of species at low (*empty squares*) and high altitudes (*filled diamonds*). RII (Relative Interaction Index) was used to quantify the response of target plants to neighbour removal; each point represents a mean of 5–10 species with 10 replicates. Net spatial covariance was used to quantify patterns of species distribution at a localized spatial scale (neighbour species within $10 \times 10 \text{ cm}^2$). See Table 1 for plot location abbreviations

that it represents a very arid zone within the Mediterranean region, and it is not surprising that net plant interactions shifted to facilitation at both low and high sites (see also Callaway et al. 2002).

Previous research identified significant links between plant–plant interactions and spatial patterns at micro-scale (nearest neighbours within $10 \times 10 \text{ cm}^2$): competition at low sites coincided with over-dispersed patterns, whilst facilitation at high sites coincided with aggregated patterns (Kikvidze et al. 2005). This re-analysis now shows that latitude is a predictor for both competition and spatial over-dispersion of plant species (Fig. 2) particularly since the former probably generates the latter. We could not detect any significant correlation between the composite variables EP and UE with RII or net spatial covariance.

Generally, low sites were more species-rich than high sites, yet the difference was not significant ($P = 0.148$ by one-tailed paired t test). Richness at both high and low sites decreased with increasing latitude, yet the trends were not

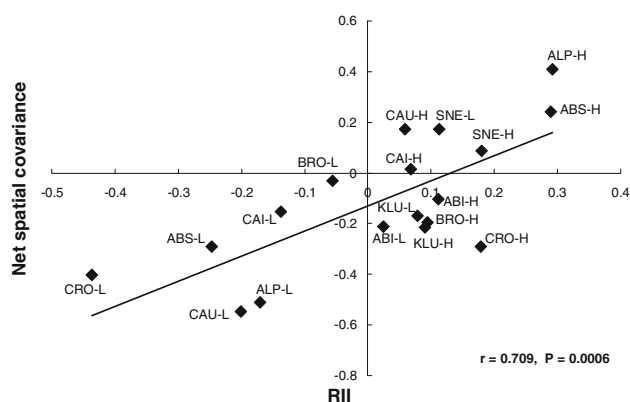


Fig. 2 Dependence of net spatial covariance on neighbour effects quantified by RII (Relative Interaction Index); see Table 1 for plot location abbreviations

statistically significant (not shown). However, species richness increased strongly with increasing UE (Fig. 3), whilst EP did not show a significant trend with richness. Three sites visibly deviate and thus drive the observed trend (Fig. 3). High variability is not unusual in ecological data, especially from such a wide geographical range, where unknown factors may contribute to variability. However, although quantitatively these data may lack precision, qualitatively they appear reasonably exact since it is improbable that 3 out of 18 points were outliers, especially when two of the most extreme data indicating to the same direction are from two different sites (low sites from the Alps and the Caucasus).

Discussion

PCA produced a split pattern of relations between meteorological data, plant interactions, and species richness. PC1

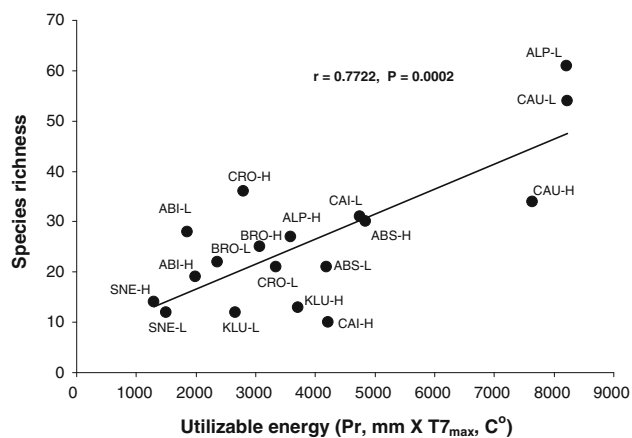


Fig. 3 Dependence of species richness in plant communities on Utilizable Energy. Utilizable Energy was quantified as a product of July maximum temperature ($T7_{max}$) and precipitation during the growing season (Pr). See Table 1 for plot location abbreviations

representing primarily maximum temperatures of June and July correlated with RII, whilst PC3 representing primarily precipitation correlated with species richness. Introduction of latitude and UE clarified further these findings. First, our results clearly show that the intensity of competitive interactions prevailing at low, relatively benign sites decreased with latitude. Conversely, at stressful high sites, the intensity of facilitative interactions did not depend on latitude. The tight correlation of latitude with PC1 shows that latitude as a complex variable primarily represents a gradient in temperature, which therefore ultimately can be interpreted as a gradient of energy (e.g. Moles et al. 2009). At benign sites decreasing energy probably translates into less intense competition, possibly because of decreasing soil weathering and thus community productivity (Michalet et al. 2002). In contrast, high sites may consistently suffer from abiotic stress derived from energy imbalances caused by direct strong irradiation, mechanical movements of soil, wind, and frequent unpredictable frost. These consistent high levels of stress may differ little in the way they are ameliorated by benefactor (nurse) species and hence facilitation intensity does not depend on latitudinal decrease of energy. The finding that competition decreases with latitude may have implications for the hypotheses that incorporate biotic interactions as important variables. For example, the “Speciation rate hypothesis” postulates that stronger biotic interactions increase the opportunity for evolutionary diversification in some regions (Currie et al. 2004; Moya-Laraño 2010). This corresponds with the slight decrease in species richness along latitudinal gradient observed in our study.

We selected at each site the most common species for the experiments, irrespective of their life form. In theory, some information on species-specific responses to neighbour removal could be obtained from a posteriori comparison of the observed responses to the species characteristics. For instance, one might predict that less tolerant species such as forbs were facilitated more often than tolerant species such as graminoids (see also Choler et al. 2001; Brooker et al. 2008). However, since the life forms, altitudinal distribution and tolerance ranges of species co-varied, we were not yet able to analyse this trend properly. Importantly, however, within sites, between-species variation did not mask the between-site trend described above.

Another important finding of our re-analysis is that species richness but not plant interactions correlated strongly with a composite variable that combines precipitation and maximum temperature in summer—UE. Probably, UE also reflects the “water–energy balance” (sensu Hawkins et al. 2003; Field et al. 2009), particularly in alpine systems across climate types and continents. High levels of available water and energy can be interpreted as a proxy of plant primary productivity. Therefore, our results show that plant species

richness increases monotonically with productivity at a cross-continental scale. This finding agrees also with the results of an earlier meta-analysis on the productivity–diversity relationships (Mittelbach et al. 2001), which found monotonically increasing richness along productivity gradients typically at large spatial scales across climates, whilst at smaller scales within the same climate zone the relationship is known to be mostly unimodal (Michalet et al. 2002, 2006). At the same time, we found no evidence for the hypothesis that the intensity of facilitative interactions wanes at the most extreme levels of abiotic stress (Michalet et al. 2006). However, this may be due to not having sites sufficiently close to the edge of the severity gradient. In contrast, in a study carried out in extremely arid conditions at high elevations in the Chilean Andes, where cushion plants dominate the vegetation and facilitate many other non-cushion species, Cavieres and Badano (2009) found a humped-back pattern of species richness along a wide latitudinal gradient.

Overall, our finding that competition intensity in alpine communities declines with increasing latitude can be considered a novel contribution to the SGH indicating specific effects of temperature. Importantly, micro-scale spatial patterns followed the same trend, indicating that plant–plant interactions generate these spatial patterns (see also Kikvidze et al. 2005). However, inclusion of the dependence of species richness on water–energy balance into the SGH does not seem as straightforward since we could not detect relationships between plant interactions and composite water–energy indices. Yet these processes can be still related indirectly, via other consequences of plant interactions such as non-random spatial distribution of species at the micro-scale: e.g. competition can generate over-dispersed patterns, in which strongly competing species are spatially segregated, thus helping to avoid competitive exclusion at the community scale (Kikvidze et al. 2005). These effects of local spatial patterns may decouple the link between plant interactions and diversity. To clarify these possibilities, further studies of the SGH might focus on the importance of water–energy relations for the dynamic balance of facilitation and competition. Such developments can evidently benefit from cross-scale studies conducted in alpine environments.

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Appendix 1: Calculations of temperature data

Temperature values were corrected for altitudinal differences among sites by applying a linear lapse rate of

$-0.6^{\circ}\text{C}/100\text{ m}$, a typical value used at regional-to-continental scale when no real weather station data are available (Cramer and Leemans 1993; Woodward 1987). We used the formula below: $T_{\text{site}} = T_{\text{stat}} - [(\text{alt}_{\text{site}} - \text{alt}_{\text{stat}})/100] \times 0.6$, where T_{site} is maximum June temperature of the experimental site, T_{stat} is maximum June temperature of the local weather station and alt_{site} and alt_{stat} are elevations of the experimental site and local weather station, respectively. Weather stations were chosen from local climatic databases in order to be in the direct geographical vicinity of experimental sites, and to have at least 20 years of records between 1960 and 1990.

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