Weak and variable relationships between environmental severity and small-scale co-occurrence in alpine plant communities

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Summary

1. The stress gradient hypothesis suggests a shift from predominant competition to facilitation along gradients of increasing environmental severity. This shift is proposed to cause parallel changes from prevailing spatial segregation to aggregation among the species within a community.

2. We used 904 1-m^2 plots, each subdivided into 100 10 × 10 cm, or 25 20 × 20 cm cells, respectively, from 67 European mountain summits grouped into 18 regional altitudinal transects, to test this hypothesized correlation between fine-scale spatial patterns and environmental severity.

3. The data were analysed by first calculating standardized differences between observed and simulated random co-occurrence patterns for each plot. These standardized effect sizes were correlated to indicators of environmental severity by means of linear mixed models. In a factorial design, separate analyses were made for four different indicators of environmental severity (the mean temperature of the coldest month, the temperature sum of the growing season, the altitude above tree line, and the percentage cover of vascular plants in the whole plot), four different species groups (all species, graminoids, herbs, and all growth forms considered as pseudospecies) and at the 10 × 10 cm and 20 × 20 cm grain sizes.

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4. The hypothesized trends were generally weak and could only be detected by using the mean temperature of the coldest month or the percentage cover of vascular plants as the indicator of environmental severity. The spatial arrangement of the full species set proved more responsive to changes in severity than that of herbs or graminoids. The expected trends were more pronounced at a grain size of 10×10 cm than at 20×20 cm.

5. *Synthesis*. In European alpine plant communities the relationships between small-scale co-occurrence patterns of vascular plants and environmental severity are weak and variable. This variation indicates that shifts in net interactions with environmental severity may differ among indicators of severity, growth forms and scales. Recognition of such variation may help to resolve some of the current debate surrounding the stress gradient hypothesis.

Introduction

During the last 15 years a renewed interest in facilitation has given rise to the hypothesis that most interactions among plants involve both negative and positive components (Callaway & Walker 1997; Holmgren *et al.* 1997). The net outcome of these opposing effects of neighbouring plants is proposed to vary along environmental gradients (Hunter & Aarssen 1988; Brooker & Callaghan 1998). In particular, the stress-gradient hypothesis (SGH; Bertness & Callaway 1994) suggests that the role of competition decreases and the role of facilitation increases with increasing environmental severity. In concurrence with this prediction, facilitation among plants has primarily been demonstrated in severe environments, such as arid ecosystems (e.g. Nobel & Franco 1989; Holzapfel & Mahall 1999; Tirado & Pugnaire 2005), salt marshes (e.g. Bertness & Shumway 1993; Callaway & Pennings 2000) and alpine grasslands (e.g. Carlsson & Callaghan 1991; Choler *et al.* 2001; Callaway *et al.* 2002). Furthermore, experimental tests of the SGH have demonstrated that neighbour removals may promote the growth of selected target species under benign conditions, indicating release from competition, but reduce growth in harsh environments, indicating a loss of facilitative effects (e.g. Bertness & Shumway 1993; Choler *et al.* 2001; Callaway *et al.* 2002).

In addition, recent studies have suggested that the assumed shifts in net interactions along severity gradients are linked to shifts in certain community properties, in particular the fine-scale spatial arrangement of species (Kikvidze *et al.* 2005; Tirado & Pugnaire 2005). Although the attribution of patterns to processes is generally problematic, these suggestions are in line with theoretical considerations and empirical evidence that small-scale spatial patterning is related to interactions among plants (e.g. Purves & Law 2002; Llambi

et al. 2004; Seabloom *et al.* 2005). In particular, increasing competition may lead to spatial segregation between species, whilst beneficial interspecific interactions may lead to species aggregation. As a corollary, if the SGH is correct, the fine-scale spatial arrangement of species should shift from prevailing interspecific segregation to aggregation along gradients of environmental severity (Kikvidze *et al.* 2005).

The SGH has, however, remained controversial (e.g. Olofsson *et al.* 1999; Maestre & Cortina 2004). In particular, two recent meta-analyses have produced contradictory results concerning the validity of its predictions (Maestre *et al.* 2005; Lortie & Callaway 2006; Maestre *et al.* 2006). This ambiguity may stem, at least in part, from unaccounted differences between the individual studies compiled for these meta-analyses. Whereas the use of different plant performance indicators, such as germination, growth or survival, is well known to have potentially profound effects on experimental outcomes (Goldberg *et al.* 1999; Maestre *et al.* 2005), more subtle differences among studies may also cause variability, but are often disregarded. Such differences include the supposed specificity of facilitative as well as competitive interactions to functional groups or species (Callaway 1998; Lortie & Callaway 2006), or the use of different proxies for the level of severity experienced by plants *in situ*, despite the fact that they are probably not equivalent representations of the same stress gradients (Lortie & Callaway 2006). Similar sources of variability may also be expected with regard to the predicted shift of fine-scale spatial patterns along environmental severity gradients. In addition, the ability to detect such trends may vary with the spatial scale of the investigation (e.g. Silander & Pacala 1985; Purves & Law 2002; Lortie *et al.* 2005). Moreover, spatial patterns in communities may not only arise from species interactions alone. Micro-habitat mosaics and dispersal processes may, for example, interfere

Table 1. Overview of the studied mountain regions with mean geographical latitude of the summits of each region. Summits: number of summits investigated within each region, with the number of those having at least one 1-m² plot suitable for co-occurrence analysis (= more than one species present) in brackets. Plots: number of 1-m² plots available for analysis. Altitude: difference between the altitude of the lowest and the highest summit of a region

Region, mountain range/country	Abbreviation	Latitude (°)	Summits	Plots	Altitude (m)
Crete, Lefka Ori/Greece	LEO	35.28	4	38	675
Sierra Nevada/Spain	SNE	37.04	4	50	549
Central Apennines, Majella/Italy	CAM	42.07	4	64	332
Corsica, Monte Cinto/France	CRI	42.39	3 (2)	11	302
Central Caucasus, Kazbegi/Georgia	CAK	42.51	4	60	784
Central Pyrenees, Ordesa/Spain	CPY	42.65	4	38	780
Northern Apennines/Italy	NAP	44.23	4	64	256
SW-Alps, Mercantour/France	AME	44.31	4	59	523
W-Alps, Valais-Entremont/Switzerland	VAL	46.01	4 (3)	31	629
S-Alps, Dolomites/Italy	ADO	46.41	4	60	694
E-Carpathians, Rodnei/Romania	CRO	47.58	4	64	258
NE-Alps, Hochschwab/Austria	HSW	47.61	4	59	345
W-Carpathians, High Tatra/Slovakia	CTA	49.18	4	64	417
South Urals/Russia	SUR	54.82	4	51	456
Scotland, Cairngorms/UK	CAI	56.33	4	56	369
S-Scandes, Dovrefjell/Norway	DOV	62.30	4 (3)	37	490
Polar Urals/Russia	PUR	66.96	4 (3)	45	341
N-Scandes, Latnjajaure/Sweden	LAT	68.38	4	53	1068

with and confound interaction-driven patterns (e.g. Schoener & Adler 1991; Ulrich 2004; Bell 2005; Seabloom *et al.* 2005).

In this study, we use a combination of null-model and gradient analysis to test, first, if the predicted correlation between small-scale co-occurrence and environmental severity holds for a large standardized data set, and, secondly, if the detectability of such trends differs among different indicators of severity, for different species (sub)sets and at different scales of measurement of spatial patterning. The data set comprises 904 presence-absence matrices from 67 summits across all major mountain chains of Europe. We analysed these data by calculating a co-occurrence index for each matrix and correlating the standardized deviations of these indices from random simulations with several indicators of environmental severity. We expected a significant linear correlation representing a shift from interspecific segregation, indicating prevalent competition, to interspecific aggregation, indicating prevalent facilitation, with increasing environmental severity. All analyses were made separately at two scales of observation and for key species subgroups.

Methods

DATA COLLECTION

Species distribution data

Species data were obtained from permanent plots of 1 m² on 71 summits of 18 mountain regions across Europe (see Table 1), collected within the framework of a monitoring baseline project on climate change effects on high mountain floras (www.gloria.ac.at; Pauli *et al.* 2004). In each region, four summits (three in Corsica) were sampled along an altitudinal gradient

from the tree line ecotone to the nival zone, or to the highest suitable summit. On each summit, four 1-m² plots, separated by 1-m distance, were arranged at the four corners of a 3 × 3 m square (hereafter termed 'aspect groups'). This set-up was repeated in each cardinal compass direction at 5 m below the peak, giving a total of 16 sample plots on each summit. Plots were subdivided into 100 10 × 10 cm cells and the presence of vascular plant species was recorded in each cell. The 10 × 10 cm cells match the commonly used scale of neighbour removal experiments and co-occurrence analyses in alpine environments (e.g. Choler *et al.* 2001; Callaway *et al.* 2002; Kikvidze *et al.* 2005). In addition, a couple of covariates were recorded. In particular, the total cover of vascular plants, as well as the percentage cover of different substratum types (bare soil, scree, rock) were visually estimated for each 1-m² plot.

Indicators of environmental severity

Limitations on plant life at high elevations arise from a complex combination of factors, such as extreme temperatures, abrasion by snow and ice, or topsoil freezing with needle-ice formation, and restrictions upon tissue production due to overall low temperatures (Körner 1999). The complex nature of alpine stress justifies the common use of altitude *per se* as an integrative indicator of environmental severity (e.g. Choler *et al.* 2001; Callaway *et al.* 2002). In this paper, we represent the elevation gradient in terms of relative altitude (RA), which is the altitudinal distance of each summit to the estimated potential tree line in each of the 18 regions.

At any given altitude the conditions experienced at a particular plot will be modified by slope, aspect and local topographic variation. In addition to altitude, we

therefore used the total percentage cover of vascular plants per 1-m^2 plot (VC) as an integrative (plot-level) indicator of local site conditions. The productivity of a site, or more precisely its biomass, is thought to be closely linked to environmental severity (e.g. Grime 1973; Michalet *et al*. 2006). Although plant cover is not an optimal indicator of biomass because it disregards the vertical dimension of vegetation, it is likely to be well correlated with biomass in the commonly low-stature and open (mean VC of all 904 plots: 44%) alpine vegetation types studied here.

In addition to these two integrative indicators of environmental severity, two climatic indices were derived from soil temperature measurements taken directly at the midpoint of each aspect group. A miniature temperature data logger (StowAway Tidbit; Onset Corporation, Bourne, Massachusetts, USA), buried at 10 cm below the soil surface, collected a 1-year temperature series (July 2001 to July 2002) at hourly intervals. Monthly temperature means were calculated from these hourly measurements. We used the mean of the coldest month (CM) as an indicator of stress because of low temperatures. Limitations to growth were accounted for by calculating growing season temperature sums (TS) from the measurement series. The growing season was defined as the snow-free period from spring to autumn. The snow-free period was extracted from the temperature series as follows: in a first step, days with a daily mean temperature ≥ 2 °C were selected. This was the average threshold daily mean where the diurnal temperature oscillation became large in spring, indicating snowmelt, or was dampened in autumn, indicating snow cover. However, at the beginning and the end of the growing season daily means may exceed or fall below the 2 °C threshold in a variable fashion, due to repeated cycles of snow fall and subsequent melting. For that reason, the temperature series over these transitional periods in spring and autumn were captured by sigmoidal models, and the dates of the start and end of the growing season were established where the fitted sigmoid curve crossed the mean of the modelled temperature range. Within the growing season, hourly temperature values above 2 °C were summed up to the growing season temperature sum.

DATA ANALYSIS

Null model analysis

Application of the full sampling design to the 71 summits would have yielded 1136 1-m^2 plots (64 in each of the 18 regions). However, of these 1136 plots, 139 had only one or no species and hence co-occurrence indices could not be calculated, 79 had no temperature data, and 14 had not been sampled at all, mostly owing to inaccessible terrain.

The remaining 904 plots were distributed across 67 summits (see Table 1). As the use of different co-occurrence indices may produce different results

(Gotelli 2000), we separately calculated two indices, the C-score and the variance ratio (cf. Gotelli 2000), for each of these plots. However, as both indices were nearly perfectly correlated (Pearson $r = -0.98$, $P < 0.0001$) across the 904 plots we undertook all subsequent analyses with the C-score only.

The C-score is a co-occurrence index based on the number of 'checkerboard units' in a species-by-sites presence-absence matrix. A checkerboard unit is an elementary combination of two species and two sites such that the occurrences of the species are mutually exclusive, i.e. a submatrix of the form:

	Species A	Species B
Site A	1	0
Site B	0	1

For the whole community represented by a species-by-sites presence-absence matrix (or for an individual 1-m^2 plot in our case), the C-score is the average number of checkerboard units across all possible species pairs (Stone & Roberts 1990). If competition mainly drives fine-scale co-occurrence patterns, the C-score should be larger (more checkerboard units = interspecific overdispersion) than expected by chance. It should be lower than random (fewer checkerboard units = interspecific aggregation) if facilitation is prevalent. The C-score was originally developed for analysing distribution patterns of birds across islands, but has since been successfully applied to various organisms at various spatial resolutions (e.g. Gotelli & McCabe 2002; Gotelli & Rohde 2002; Ribas & Schoereder 2002; Koide *et al*. 2005), including plants at very fine scales (Franzén 2004). Its power to successfully detect non-random co-occurrence patterns at arbitrary scales has been demonstrated by computer simulations (Gotelli 2000).

Positive or negative deviation of observed C-scores from randomness was evaluated with 1000 null models for each plot. Null models were generated by randomly re-shuffling species presences among the 100 (or 25 where four cells of 10 × 10 cm were aggregated into one 20 × 20 cm unit, see below and Table 2) cells (= sites) of a plot. For each of the randomized matrices C-scores were re-calculated and compared with the observed index. The randomization procedure was forced to hold the overall number of occurrences per plot, i.e. the empirical frequency, constant for each species, whereas the number of species per site (= cell) was not constrained by the original data. Such a 'fixed-rows-equiprobable-columns'-simulation scheme is suggested to be especially appropriate for standardized samples collected in homogenous habitats (Gotelli 2000).

Species richness and abundance distributions varied across the 904 plots, which affected observed C-scores and resulted in an uneven variance of the 1000 null-model simulations among the plots. To make the results for the individual plots comparable, the differences between observed and simulated C-scores were standardized for each plot as: (observed C-score – mean of

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Table 2. The species (sub)sets analysed. For each (sub)set, separate analyses were conducted at the 10×10 and 20×20 cm cell sizes. Plots: number of plots

Species (sub)set	Abbreviation	Plots
All species	SP10, SP20	904
Graminoids (Poaceae and Cyperaceae)	GR10, GR20	705
Rosette- and mat-forming perennial herbs	HB10, HB20	650
Growth forms as seven pseudo-species (graminoids, rosette- and mat-forming perennial herbs, dwarf shrubs, cushion plants, geophytes, succulents, annuals/biannuals)	GF10, GF20	876

simulated C-scores)/standard deviation of simulated C-scores. This scaling in standard deviation units delivers a measure of deviation from randomness that is centred around 0: it is positive where there are more checkerboard units (= less co-occurrence) than expected by chance and negative where there are fewer than random checkerboard units (= more frequent co-occurrence). As this metric is equivalent to effect size calculation in meta-analysis (Gurevitch & Hedges 2001) we henceforward call it standardized effect size in the sense that it describes the effect of (unknown) local conditions and processes on co-occurrence patterns. If competition regulates species' spatial patterning we would expect a positive effect size, but if facilitation is the dominant structuring process the effect size should be negative.

Standardized effect size and environmental severity

The SGH would predict a positive correlation between the standardized effect size and TS/CM/VC (= the warmer the microclimate/the more productive the vegetation, the more important the role of competition and hence the higher the number of checkerboard units) and a negative one between the standardized effect size and RA (because the environment becomes more severe with increasing altitude). However, a simple regression analysis was inappropriate with our data, as their structure did not allow for treating each plot as an independent sample. In fact, plots are clustered in aspect groups, aspect groups in summits, and summits in regions. In particular, the four summits of each of the 18 regions represent a separate gradient of environmental severity on their own. Hence we used a linear mixed-effects model (LMM) to test the hypothesized correlation within this hierarchical structure.

In the mixed model a linear relationship between the standardized effect size and, alternatively, TS, CM, RA and VC, was defined as the fixed effect. Random effects at the three cluster levels, including the respective intercepts, were evaluated by first establishing four different models for each severity indicator: the first model involved no structure, i.e. it was an ordinary linear least-squares model, the second one involved a grouping by region, the third one a grouping by summit within regions, and the fourth one a grouping by aspect group within summits within regions. The structured models allowed for heteroscedasticity at the region level, i.e. for

among-region differences in the variances of standardized effect sizes. The fit of the four models was then compared by means of the Akaike information criterion (AIC) and a likelihood ratio test for nested models. The best fitting models were used to evaluate the fixed effects of the respective severity indicators.

The null model simulations used to calculate the standardized effect sizes were based on the assumption that all 100, or 25, cells, respectively, of each plot are approximately homogeneous in abiotic conditions. Despite the small extent of the plots, this assumption represents a simplification. In particular, microsites that are *a priori* unsuitable for vascular plant life may occur in many of the plots. If the proportion of such sites increases along severity gradients, co-occurrence patterns will appear more aggregated under high severity conditions because of a reduction of available space. To account for such space effects causing apparent co-occurrence-severity relationships, we additionally included an indicator of the amount of suitable area per plot into the LMM analysis. Among the data available for each individual 1-m^2 plot we considered the percentage cover of rock substratum as the most reliable indicator of suitable area, because bare rocks lack the soil substratum required by rooting vascular plants and are hence largely uncolonizable except for small fissures. Following this rationale, all LMMs were re-calculated as multiple models combining the respective indicator of severity and percentage rock cover as predictors.

Spatial scales and growth forms

In order to assess variation in detected co-occurrence-severity relationships due to plant growth form and sampling scale, each analysis was run for four different species (sub)sets and at two different grain sizes in a factorial design (Table 2). Species sets included (i) all vascular plant species (= all species present in a plot, SP10); (ii) two subgroups comprising all species belonging to the two most important growth forms of European alpine vegetation, namely graminoids (Poaceaea, Cyperaceae, and Juncaceae) and perennial rosette- or mat-forming herbs (GR10 and HB10); and (iii) a combination of all growth forms represented in the plots (graminoids, perennial rosette or mat forming herbs, dwarf shrubs, cushion plants, geophytes, succulents, annuals/biannuals) considered as pseudo-species
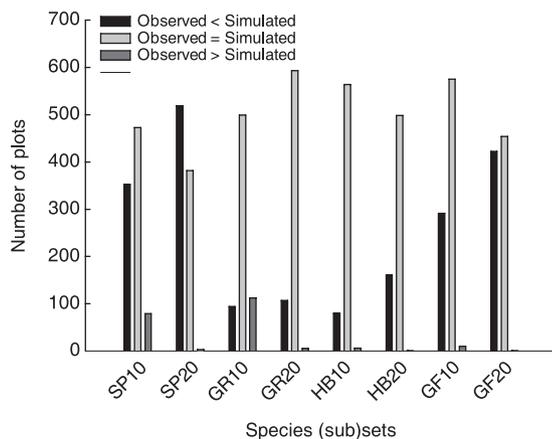
Fig. 1. Number of plots where observed C-scores were significantly larger, smaller, or not significantly different from the mean C-score of the randomized data (1000 simulations). Differences were considered significant if observed values fell within the upper or lower 2.5%-tails of the distribution of the 1000 simulated C-scores. For definition of species (sub)sets see Table 2.

Fig. 2. Box plots of standardized deviations from random co-occurrence for each of the eight species (sub)sets. Central lines represent the 95%-confidence intervals around the median values, boxes the second and third quartiles, i.e. the middle half of the data, and horizontal lines indicate outliers. For definition of species (sub)sets see Table 2.

(GF10). The number of plots available for these group-specific analyses varied according to the frequency and distribution of the species belonging to the respective groups.

The two grain sizes considered were 10×10 cm, the original sampling scale, and 20×20 cm. Data for the latter resolution were derived by aggregating every four neighbouring 10×10 cm cells, i.e. producing 25 20×20 cm sites per 1-m² plot (SP20, GR20, HB20 and GF20).

We used ECOSim (Gotelli & Entsminger 2004) for C-score calculations and null model simulations and S-Plus 2000 (MathSoft 1999) for all other statistical analyses.

Results

GENERAL PATTERNS OF CO-OCCURRENCE

A plot-wise comparison of observed C-scores against the distribution of the 1000 simulated C-scores revealed that a majority of the plots had co-occurrence patterns not significantly different from randomness for all species (sub)sets except SP20 (Fig. 1). However, among those plots where non-random patterns could be detected, significant interspecific aggregation (= observed C-scores significantly smaller than mean of simulated C-scores) was much more frequent than non-random segregation of species (= observed C-scores significantly larger than mean of simulated C-scores) for seven out of eight species sets; only for GR10 were the numbers of plots with aggregated and segregated patterns approximately balanced. As a consequence, the medians of the standardized effect sizes across all plots were slightly negative for all subsets except GR10 (Fig. 2).
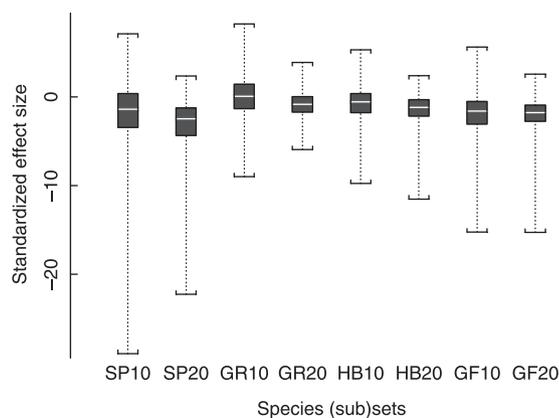
RELATIONSHIPS OF CO-OCCURRENCE PATTERNS AND SEVERITY INDICATORS FOR THE DIFFERENT SPECIES SETS AT THE 10×10 CM SCALE

The effect of environmental severity on co-occurrence patterns was variable among species sets and severity indicators (Table 3a). The LMMs revealed significant effects in the hypothesized direction for all four species sets when using the percentage cover of vascular plants (VC) as an indicator, and for SP10, GR10 and GF10 along a gradient of the mean temperature of the coldest month (CM). With respect to TS and RA, co-occurrence patterns did not show any significant trend in any of the species sets, although with the latter indicator marginally non-significant trends were detected for the same groups that responded to CM (SP10, GR10 and GF10).

As suggested by *t*-values and associated probabilities, co-occurrence among all vascular plant species of the community was more responsive to gradients of environmental severity than co-occurrence among subsets of species with the same growth form (Table 3a,b). Using all seven growth forms as pseudo-species delivered results similar to that for the complete species set. Focusing on the two main growth forms of European alpine grasslands, severity-driven shifts in co-occurrence patterns were more detectable for graminoid species than for perennial herbs.

Including percentage rock cover into the LMMs did not alter these results qualitatively although fixed effect estimates of the severity indicators slightly decreased (Table 3a). This decrease suggests that a small part of the detected co-occurrence-severity relationships may indeed be due to covariance of severity and the area available for colonization in each plot. Percentage rock cover itself was highly significantly correlated with co-occurrence patterns of all species sets, indicating that it is indeed a useful indicator of available space.

Table 3. Fixed effects (FE) of linear mixed models relating deviations from random co-occurrence at the (a) 10×10 cm and (b) 20×20 cm grain to indicators of environmental severity and to the combination of indicators of environmental severity and percentage rock cover, respectively. CM, mean temperature of the coldest month; RA, altitude above the treeline; TS, temperature sum of the growing season; VC, percentage cover of vascular plants per 1-m² plot; d.f. are denominator degrees of freedom, *t*-values the ratios of fixed effects and their standard errors with the associated *P*-values from *t*-distributions. FE-rock are fixed effects of percentage rock-cover in the bivariate LMMs. Asterisks indicate significance: ***0.001, **< 0.01, *< 0.05. For abbreviations of species (sub)sets see Table 2.

	d.f.	FE	t	P	FE-rock	FE	t	P
(a)								
	Predictor: CM				Predictor: CM + rock cover			
SP10	176	0.219	3.82	**0.0002**	**−0.048*****	0.185	3.47	**0.0006**
GR10	138	0.065	2.41	**0.0169**	**−0.025*****	0.064	2.31	**0.0219**
HB10	131	0.031	1.18	0.2381	**−0.010****	0.018	0.73	0.4647
GF10	170	0.078	2.90	**0.0038**	**−0.030*****	0.052	1.99	**0.0473**
	Predictor: RA				Predictor: RA + rock cover			
SP10	48	−0.0021	−1.84	0.0709	**−0.053*****	−0.0009	−0.99	0.324
GR10	37	−0.0012	−1.69	0.0993	**−0.028*****	−0.0008	−1.09	0.279
HB10	41	0.00004	0.12	0.9050	**−0.010*****	0.0001	0.36	0.718
GF10	48	−0.0016	−2.00	0.0507	**−0.032*****	−0.0006	−1.08	0.282
	Predictor: TS				Predictor: TS + rock cover			
SP10	176	0.007	1.23	0.218	**−0.067*****	0.010	1.45	0.146
GR10	138	0.003	0.84	0.397	**−0.027*****	0.002	0.62	0.532
HB10	131	0.001	0.86	0.390	**−0.010*****	0.001	1.16	0.248
GF10	170	0.002	1.20	0.229	**−0.032*****	0.001	0.38	0.702
	Predictor: VC				Predictor: VC + rock cover			
SP10	658	0.055	6.41	**< 0.0001**	**−0.033*****	0.044	4.83	**< 0.0001**
GR10	507	0.021	4.94	**< 0.0001**	**−0.021*****	0.014	3.25	**0.0012**
HB10	457	0.008	4.12	**< 0.0001**	**−0.008***	0.006	2.56	**0.0106**
GF10	636	0.024	5.58	**< 0.0001**	**−0.024*****	0.015	3.46	**0.0006**
(b)								
	Predictor: CM				Predictor: CM + rock cover			
SP20	176	0.026	0.63	0.524	**−0.019*****	0.008	0.20	0.838
GR20	138	0.024	0.64	0.518	**−0.010*****	0.0141	0.35	0.722
HB20	131	−0.053	−1.45	0.149	−0.004	−0.057	−1.50	0.134
GF20	170	−0.004	−0.19	0.842	**−0.008*****	−0.007	−0.35	0.720
	Predictor: RA				Predictor: RA + rock cover			
SP20	48	0.000005	0.004	0.996	**−0.020*****	0.0007	0.98	0.329
GR20	37	0.0002	0.60	0.550	**−0.009****	0.0004	0.96	0.341
HB20	41	0.0008	1.90	0.063	−0.001	0.0008	1.92	0.061
GF20	48	0.0002	0.28	0.772	−0.004	0.0003	0.86	0.389
	Predictor: TS				Predictor: TS + rock cover			
SP20	176	−0.006	−2.04	**0.042**	**−0.021*****	−0.008	−1.84	0.067
GR20	138	−0.001	−0.49	0.622	**−0.007****	−0.001	−0.56	0.571
HB20	131	−0.004	−0.96	0.333	−0.002	−0.004	−0.98	0.324
GF20	170	0.0007	0.31	0.752	**−0.009*****	0.001	0.34	0.727
	Predictor: VC				Predictor: VC + rock cover			
SP20	658	0.012	2.40	**0.016**	**−0.018*****	0.006	1.16	0.244
GR20	507	0.004	1.53	0.125	**−0.008****	0.0009	0.30	0.760
HB20	457	−0.003	−1.33	0.183	−0.003	−0.004	−1.68	0.092
GF20	636	0.0007	0.29	0.767	**−0.008*****	−0.002	−0.88	0.378

EFFECTS OF GRAIN SIZE

The hypothesized shifts in co-occurrence patterns were less likely to be observed at the 20×20 cm grain size than at 10×10 cm (Table 3b). At the larger grain, significant trends could only be detected for combinations of SP20 with TS and VC. However, the effect of TS on SP20 was actually opposite to the one expected, i.e. standardized effect sizes increased (= co-occurrence decreased) with decreasing temperature sums. Moreover, including rock cover into the LMMs for the 20×20 cm data rendered both detected trends non-significant.

Rock cover itself was significantly correlated to co-occurrence in SP20, GR20 and GF20, but not in HB20.

REGIONAL VARIATION IN DETECTED TRENDS

For all combinations of severity indicators and species sets, likelihood ratio tests demonstrated that fully structured models, i.e. those that allowed for random effects at all levels of grouping (region, summit, aspect), fitted the data significantly better than simpler structured ones (cf. Table S1 in Supplementary Material). However, improvement of fit (in terms of AIC and LR)

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was consistently most pronounced when switching from an unstructured model (an ordinary linear least-squares model) to a mixed model with random effects for region. Additional increase in fit by allowing for random effects of summit and exposition was much lower throughout. These results were not affected by whether or not rock cover was included as a covariate into the LMMs.

In line with the model improvement achieved by including random effects for the different mountain ranges, regional variation in the effect of environmental severity on co-occurrence patterns was indeed pronounced, even where fixed effects in the LMMs were highly significant, as in combinations of SP10 with VC and CM (Fig. 3). Not only did the regression slopes vary between regions, the relationships even shifted from positive to negative in some cases. This variation was generally not related to the length of the environmental severity gradient sampled within each region. Tests of correlations between region-specific linear-regression slopes and gradient length were non-significant in 38 out of 40 cases (4 indicators × 5 species sets × 2 scales). The scatter around the regression lines in Fig. 3, moreover, demonstrates that even where the hypothesized shifts in co-occurrence patterns along severity gradients are detectable, the models explain only a limited amount of the variance in the data.

Discussion

Overall, our analysis suggests that there are trends in small-scale co-occurrence patterns among alpine plants that are consistent with predictions of the SGH. However, there is considerable scatter around these trends and their detectability depends on the environmental stress indicator applied, the group of species considered, and on the spatial scale of the analysis.

REGIONAL VARIATION IN DETECTED TRENDS

With respect to regional variation and the large scatter around the detected trends, at least three non mutually exclusive factors may have contributed to confound the hypothesized correlations. First, heterogeneity in site conditions may probably codetermine species pattern even at microscales in alpine environments. Although we statistically accounted for the amount of unavailable area per plot by including percentage rock cover into the LMMs, non-rock sites may still vary in abiotic conditions, especially on rugged microrelief. Such heterogeneity may promote spatial segregation of species with different habitat affinities (e.g. Schoener & Adler 1991), but may also foster interspecific aggregation in relatively benign microsites under generally severe conditions.

Secondly, dispersal processes may interfere with interaction-driven patterning (Franzén 2004; Ulrich 2004; Bell 2005). Indeed, small-scale disturbances that may open gaps are frequent in alpine habitats (e.g.

Chambers 1995) and co-occurrence patterns could hence partly reflect small-scale extinction and recolonization dynamics. However, as reproduction from seeds is generally considered to play a minor role in alpine environments compared with clonal propagation of the mostly long-living perennial plants (Bliss 1971; Körner 1999), seed dispersal-driven patterns may be less important in high-mountain plant communities than in grasslands of lower altitudes (van der Maarel & Sykes 1993).

Thirdly, co-occurrence of vascular plants and cryptogams has not been accounted for (because cryptogam species data was not recorded). Mosses and lichens usually gain in abundance with environmental severity, especially in boreal and temperate mountains (Virtanen *et al.* 2003; Björk & Molau 2007), and hence the importance of interactions with cryptogams is likely to increase along severity gradients. Such interactions may have both positive and negative effects on the vital rates of vascular plants in cold environments (Erschbamer *et al.* 2003; Van der Waal & Brooker 2004), or even be highly species-specific as suggested by results from arid ecosystems (Escudero *et al.* 2007). Like interactions among vascular plants, they will probably translate into non-random segregation or aggregation of vascular plant and cryptogam species. Disregarding this component of overall co-occurrence patterns will hence probably confound the hypothesized co-occurrence severity correlation.

Despite the potential impacts of these confounding factors, we could detect trends in line with the predictions of the SGH and we propose changes in net interactions, which have repeatedly been demonstrated by neighbour removals in high mountain environments (Choler *et al.* 2001; Callaway *et al.* 2002), as the most plausible and parsimonious explanation for these trends.

VARIATION AMONG SEVERITY INDICATORS

The four proxies of environmental severity are only loosely to moderately correlated ($r < \pm 0.5$ for all possible pairs of these four indicators). They are hence not equivalent indicators of the same severity gradient. Of the two measured climatic variables, TS should mainly influence biomass production, whereas CM, as measured in the topsoil, i.e. below an eventual protective snow cover, indicates the extent of exposure to the destructive forces of high-mountain winter conditions. Hence, facilitative interactions among plants may affect different vital rates at low levels of CM and TS, respectively. At low levels of TS, plant growth may benefit from favourable microclimatic conditions created by neighbours (e.g. Carlsson & Callaghan 1991), whereas provision of shelter against potentially lethal damage may be more important along gradients of CM. The more pronounced response of co-occurrence patterns to CM may therefore result from the fact that effects of neighbours on survival are more important
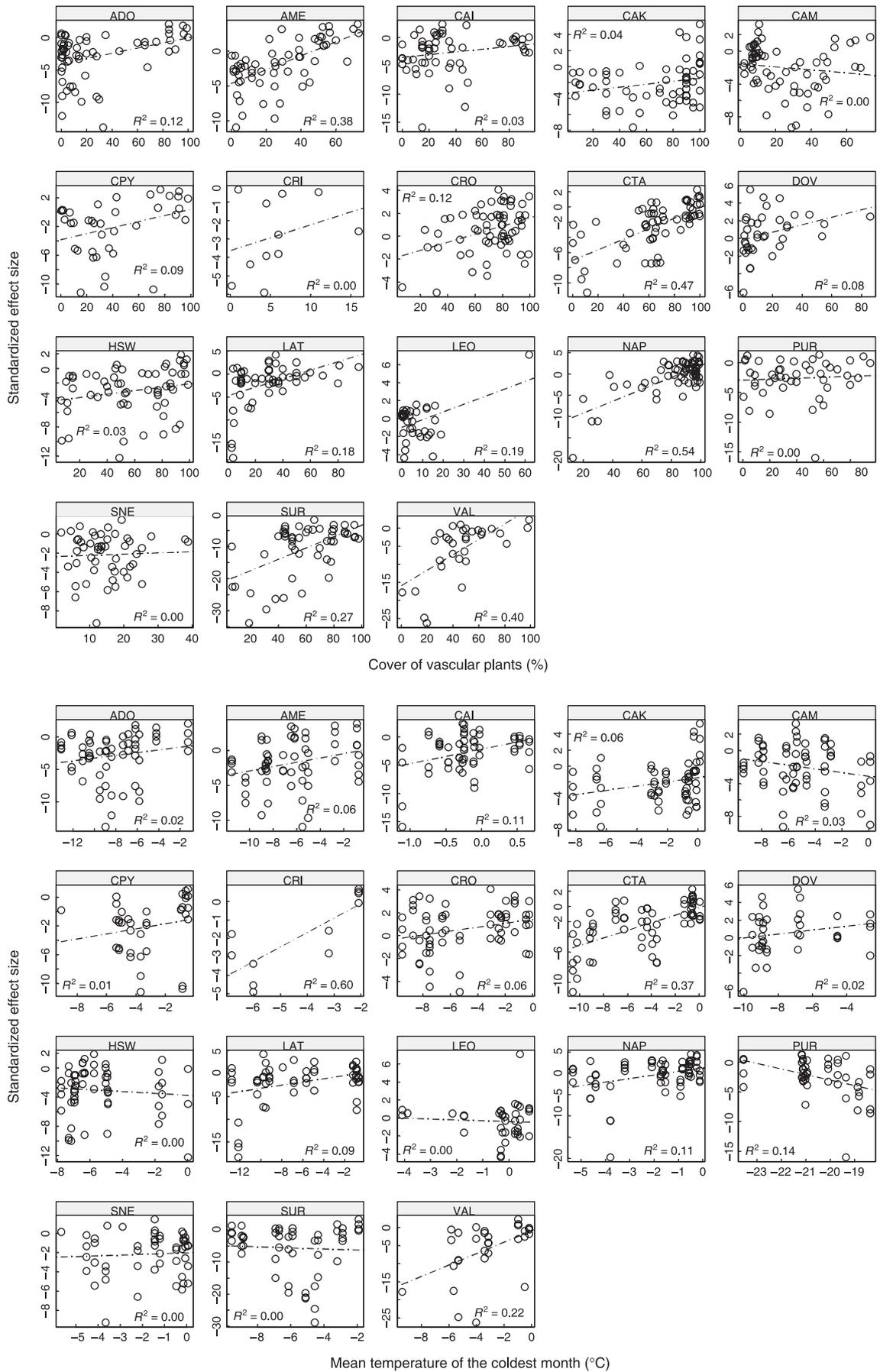
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Standardized effect size

Cover of vascular plants (%)

Standardized effect size

Mean temperature of the coldest month (°C)

Fig. 3. Scatter plots of standardized deviations from random co-occurrence against the mean cover of vascular plants per 1-m^2 plot (upper panel) and the mean temperature of the coldest month (lower panel) for each of the 18 European mountain regions studied. Dashed lines indicate linear least squares regression slopes and R^2-values are the associated coefficients of determination. For abbreviations of regions see Table 1.

for the spatial arrangement of species than effects on growth rates (Wilson *et al.* 2000; Llambi *et al.* 2004). This is especially plausible as co-occurrence indices are based on presence–absence data and do not include any measure of biomass or abundance.

With respect to RA, a lack of accuracy in representing the conditions that plants experience *in situ* may have contributed to confound relationships with co-occurrence. Altitudinal gradients in local site conditions are strongly modified by topography in alpine landscapes (Geiger 1965; Körner 1999) and hence plots of the same RA but in different topographic positions may vary considerably in environmental conditions. The importance of local topography for alpine plant interactions was also indicated by the results of neighbour removal experiments in sheltered vs. exposed sites at the same altitudes (Choler *et al.* 2001).

The hypothesized shifts in co-occurrence patterns were most clearly correlated with VC. In contrast to CM and TS, VC is not only related to climatic constraints but may integrate all potential stressors, including, for example, drought or mineral nutrient deficiencies. Moreover, VC can be taken to represent the long-term average gradient of site conditions as the majority of species are slow-growing long-lived perennials, whereas CM and TS were only measured over the course of a single year and inter-annual variability may cause considerable deviations between the conditions in a particular year and the long-term average. The clear trends for VC are in line with reported correlations between spatial co-occurrence patterns, net interactions and biomass (Kikvidze *et al.* 2005), and with theoretical models assuming a close relationship between biomass, or productivity, and environmental severity in herbaceous vegetation (Grime 1973; Michalet *et al.* 2006).

EFFECTS OF SCALE

Variation in co-occurrence-severity relationships among scales of observation suggests that co-occurrence is driven by different processes at these two spatial resolutions and, in particular, that species interactions are less important at the larger grain. A highly restricted spatial domain of species interactions is in line with studies that demonstrated that interactive neighbourhoods are often as small as just a few centimetres in herbaceous vegetation (Mack & Harper 1977; Silander & Pacala 1985; Purves & Law 2002) and interactions are irrelevant for spatial structures at larger scales (Molofsky 1999). Of course, neighbourhood size depends on the size of the species involved and cell sizes smaller than the average individual are generally not appropriate for detecting co-occurrence patterns, irrespective of the driving force. The optimal scale of observation will hence depend on the system studied. Alpine species are mostly small, and the fact that there were on average more than two species per 10×10 cm cell (and more than three when empty cells are

excluded) suggests that this grain was large enough to study eventual segregation or aggregation in this system. It may, however, be assumed that differences in average plant size may affect the detected differences in standardized effect sizes among species of different growth forms, and in particular be responsible for the comparatively less clumped pattern of graminoid species. However, the putatively smaller herbs were also less clumped than the overall species set, which, besides graminoids, mainly includes species of other probably larger growth forms such as dwarf shrubs and cushion plants. We hence consider it unlikely that plant size-cell size relationships play a major role in explaining differences in co-occurrence patterns among growth forms in our data.

VARIATION AMONG SPECIES (SUB)SETS

The more pronounced trends found for SP10 suggest that interactions among species of different growth forms are at least as important for spatial structuring as those among species belonging to the same growth form. Indeed, non-random co-occurrence indicative of facilitative relationships in high-mountain environments has mostly been reported between species of different growth forms (Carlsson & Callaghan 1991; Cavieres *et al.* 2002; Kalin-Arroyo *et al.* 2003; Klanderud 2005). In the high alpine to subnival belts, cushion plants are particularly important nurse plants for species of other growth forms (Cavieres *et al.* 2002, 2005, 2006; Kalin-Arroyo *et al.* 2003), probably because they are efficient heat-traps, store considerable amounts of nutrients and moisture and stabilize the soil (Körner 1999). At somewhat lower elevations, prostrate or mat-forming dwarf shrubs may act as the most important benefactors (Carlsson & Callaghan 1991; Klanderud 2005). As a consequence, if facilitative interactions in severe alpine environments largely involve species of different growth forms, species patterning driven by shifts in net interactions should be less detectable when focusing on individual growth forms only.

Conclusions

In conclusion, fine-scale species arrangements in plant communities on European alpine summits tend to be correlated with environmental severity in a manner consistent with predictions of the SGH, but these relationships are weak and show a high degree of variability. The large scatter around the trends probably stems from other processes that may confound the translation of net interactions into spatial patterns. Variation among severity indicators, scales and species sets, however, supports the proposition that detection of trends predicted by the SGH will not only depend on the measure of plant performance used (Goldberg *et al.* 1999; Maestre *et al.* 2005) but on a variety of additional factors (Lortie & Callaway 2006). Recognition of such variation may help to resolve some of the

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current debate surrounding the SGH, and emphasizes the need to carefully define a given experimental or observational design to arrive at consistent conclusions about the validity of the SGH (Maestre *et al.* 2006).

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Supplementary material

The following supplementary material is available for this article.

Table S1 Akaike information criterion and likelihood-ratio tests for comparison among differently structured linear mixed models.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/abs/10.1111/j.1365-2745.2007.01288.x
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