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ORIGINAL ARTICLE

The rich sides of mountain summits – a pan-European view on aspect preferences of alpine plants

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ABSTRACT

Aim In the alpine life zone, plant diversity is strongly determined by local topography and microclimate. We assessed the extent to which aspect and its relatedness to temperature affect plant species diversity, and the colonization and disappearance of species on alpine summits on a pan-European scale.

Location Mountain summits in Europe's alpine life zone.

Methods Vascular plant species and their percentage cover were recorded in permanent plots in each cardinal direction on 123 summits in 32 regions across Europe. For a subset from 17 regions, resurvey data and 6-year soil temperature series were available. Differences in temperature sum and Shannon index as well as species richness, colonization and disappearance of species among cardinal directions were analysed using linear mixed-effects and generalised mixed-effects models, respectively.

Results Temperature sums were higher in east- and south-facing aspects than in the north-facing ones, while the west-facing ones were intermediate; differences were smallest in northern Europe. The patterns of temperature sums among aspects were consistent among years. In temperate regions, thermal differences were reflected by plant diversity, whereas this relationship was weaker or absent on Mediterranean and boreal mountains. Colonization of species was positively related to temperature on Mediterranean and temperate mountains, whereas disappearance of species was not related to temperature.

Main conclusions Thermal differences caused by solar radiation determine plant species diversity on temperate mountains. Advantages for plants on eastern slopes may result from the combined effects of a longer diurnal period of radiation due to convection cloud effects in the afternoon and the sheltered position against the prevailing westerly winds. In northern Europe, long summer days and low sun angles can even out differences among aspects. On Mediterranean summits, summer drought may limit species numbers on the warmer slopes. Warmer aspects support a higher number of colonization

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events. Hence, aspect can be a principal determinant of the pace of climate-induced migration processes.

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INTRODUCTION

In the absence of shading effects by trees and shrubs, the rugged terrain of alpine regions causes pronounced differences in the incident solar radiation and wind exposure. Hence, the aspect of mountain slopes is a driving factor contributing to the differentiation of topoclimates at high elevation, secondarily modulated by slope angle (Larson *et al.*, 2000; Huggett & Cheesman, 2002; Barry, 2008). The small-scaled mosaic resulting from contrasting micro-topographic and micro-climatic conditions creates a great variety of micro-habitats that differ significantly in species composition over short spatial distances (Scherrer & Körner, 2010; Körner, 2012), which strongly affects the distribution limits of species and of plant communities (Grabherr *et al.*, 2001; Crawford, 2008; Wipf *et al.*, 2013). Despite the obvious importance of aspect for plant life, however, the patterns of variation attributed to topography are not well documented, especially on the micro-scale (Moeslund *et al.*, 2013).

The thermal regimes determining plant growth differ among aspects (Moser *et al.*, 1977; Körner *et al.*, 2003). Differences in vegetation patterns in relation to slope

orientation have been described in detail in a number of studies (e.g., Grabherr, 1997, 2003; Theurillat *et al.*, 1998). Gottfried *et al.* (1998) and Pauli *et al.* (1999) have shown increasing elevation limits of alpine grassland from south-western to south-eastern slopes on Schrankogel in the central Eastern Alps. Increasing differences in plant species richness between northern and southern exposures with increasing elevation in the European Alps were observed by early botanists (Braun, 1913; Schröter, 1926). However, to date the role of aspect in determining small-scale plant species richness has only been analysed regionally, using subsets of the dataset we report here (Coldea & Pop, 2004; Stanisci *et al.*, 2005; Kazakis *et al.*, 2007; Gutiérrez-Girón & Gavilán, 2010; Vittoz *et al.*, 2010), and there are no known general patterns from continent-wide comparisons.

Analyses of large-scale patterns are particularly important because the effect of aspect may vary not only along elevation, but also along latitudinal gradients. The increase in radiation and the adiabatic decrease in air temperature with elevation cause more pronounced differences in topoclimates towards the summits (Geiger, 1950; Barry, 2008). The greatest difference in annual potential direct radiation between north- and

south-facing slopes in Europe can be observed in the temperate biome (i.e. from *c.* 45° N to 60° N; Holst *et al.*, 2005; Barry, 2008). As a consequence, the low-elevation limits of soil permafrost differ markedly, by around 600 m between the warmest (south-eastern) and coldest (north-western) aspects in the Alps (Haeberli, 1975; Boeckli *et al.*, 2012).

If aspect significantly influences the thermal input and thus the number of species on a mountain slope, it may also shape the pathways of upward migrating plants. In recent periods of amplified climate warming (Mountain Research Initiative E. D. W. Working Group, 2015), 'thermophilisation' of alpine vegetation (Gottfried *et al.*, 2012) and upward shifts of species ranges (Pauli *et al.*, 2012) have been observed. Thermally favourable slopes might preferably support both colonization, due to ameliorated climatic conditions, and disappearance of populations, e.g., due to increased competition, increasingly unsuitable temperature conditions and/or drought stress.

In the current study, we compared vascular plant diversity and its temporal changes among the four cardinal directions on mountain summits and related the diversity patterns to the respective soil temperature regime measured *in situ*. We used a unique, pan-European dataset derived from the GLORIA multi-summit design (**Gl**obal **O**bservation **R**esearch **I**nitiative in **A**lpine Environments; www.gloria.ac.at). Habitats near mountain summits are not or only marginally affected by shading from neighbouring land features and they include all aspects within a small area and, thus, share the same local species pool. Consequently, the European set of GLORIA summits provides the unique opportunity to answer the following questions on a continent-wide scale: (1) Are there differences in thermal conditions among aspects besides the obvious differentiation between northern and southern slopes? If so, are these patterns consistent across years? (2) Are thermal differences among aspects reflected in vascular plant diversity patterns? (3) Are aspect differences in thermal conditions and plant diversity more pronounced in the temperate biome compared to the biomes in southern and northern Europe? (4) Are colonization and disappearance of species more common at warmer aspects?

MATERIALS AND METHODS

Study area and design

The complete dataset analysed in this study comprised 123 summits in 32 mountain regions across Europe covering the Mediterranean, temperate, boreal and polar biomes, surveyed between 2001 and 2012 (Fig. 1). At all sites a common protocol was used for recording species in permanent plots on four summits within a mountain region, representing an elevation gradient from the treeline ecotone to the highest summits where vascular plants still occurred (Pauli *et al.*, 2004, 2015). In five regions (1, 20, 21, 26, 30) only three suitable summits were found, and in two regions (13, 30) some aspects were not documented due to inaccessible terrain (see

Appendix S1 in Supporting Information). On each summit, the four corner 1 × 1 m quadrats of a 3 × 3 m grid were established as permanent plots in each cardinal direction (i.e. east, south, west, north) 5 m below the highest summit point. In each of the 1 × 1 m quadrats, we recorded all vascular plant species and the percent cover of each species was visually estimated following Pauli *et al.* (2004, 2015). In the centre of each 3 × 3 m grid a data logger (StowAway Tidbit v2; Onset Corporation, Bourne, MA, USA or GeoPrecision Mlog-5W, Ettlingen, Germany) recorded the soil temperature 10 cm below the surface at hourly intervals. Temperature series were available for 67 summits out of 17 regions which were established in 2001 and re-recorded in 2008 (see Appendix S1; Gottfried *et al.*, 2012). Analyses involving temperature indices and changes in species diversity were, therefore, restricted to this data subset.

Data analysis

Temperature sums

We computed temperature sums as a surrogate for the thermal input that potentially drives diversity patterns. As the threshold temperatures of photosynthetic activity and growth of vascular plants in alpine regions are not commonly agreed and are likely to differ among species (Körner, 2012), threshold values from 1–5 °C and two growing season lengths (June to August and May to September) were used (see Appendix S2). For each logger, hourly measurement values exceeding a given threshold during the given growing season were summed for each year of measurement (i.e., 2002–2007). Resulting temperature sums of each logger were divided by the highest temperature sum on the respective summit to rescale values between 0 and 1 (hereafter proportional temperature sum). This allows the comparison of the effect of aspect across regions. Within temperature series, gaps occurred in 98% of the loggers (e.g., because of battery change; see Appendix S3), which were filled based on the measurements of the remaining loggers in the same region using the function *amelia* of the R package 'Amelia II' (Honaker *et al.*, 2011) which applies an EM (expectation-maximisation)-algorithm on multiple bootstrapped samples of the incomplete original dataset. Imputation of missing values was repeated 30 times. Loggers whose data contained large gaps, which could not be filled through imputation, were removed prior to analyses (see Appendix S3).

The effect of cardinal directions on proportional temperature sums was modelled using linear mixed-effect models (LMMs) with cardinal direction, year and the interaction between them as fixed-effect predictors and a random intercept term for summits nested within regions. Parameters were estimated by restricted maximum likelihood using the function *lmer* of the R package 'lme4' (Bates *et al.*, 2015). To compare each pairwise combination of cardinal directions, we re-fitted the models with different cardinal directions as baseline level. LMMs were computed for each of the 30
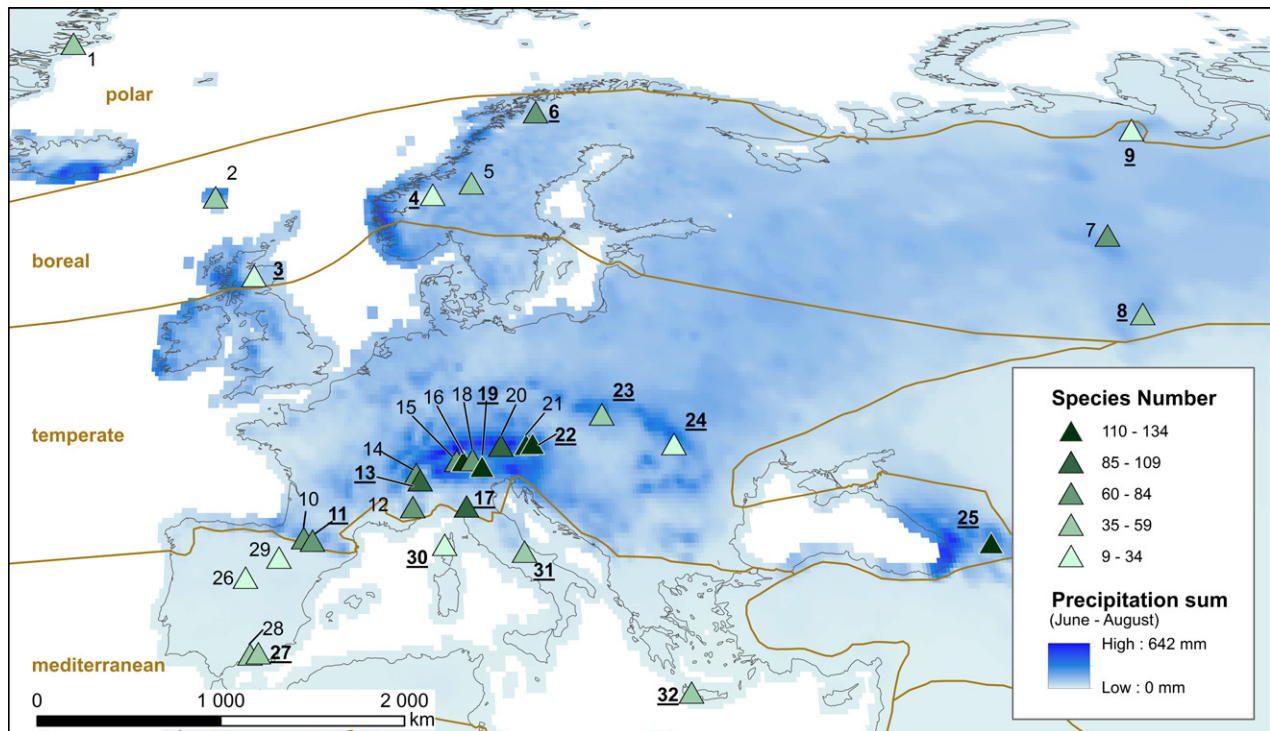
Figure 1 Geographic distribution of the 32 mountain regions (details see Appendix S1) representing 123 summits used to test for the effect of cardinal directions of slopes (east, south, west, north) on vascular plant species diversity sampled between 2001 and 2012. For regions indicated by bold and underlined numbers, soil temperature and species data for two surveys, conducted in 2001 and 2008 were available. The colours of symbols represent species richness on the regional level. The background map shows June/July/August precipitation sums (obtained from doi: 10.5676/DWD_GPCC/CLIM_M_V2015_025). Projection: Eckert IV.

imputations of the incomplete temperature sums dataset. Their marginal coefficients ($\pm$ SE) and *t*-values were averaged over these repetitions and *P*-values were derived from the mean *t*-value. Differences in proportional temperature sums among cardinal directions were similar across temperature sum thresholds and growing season lengths (see Appendix S2), therefore only the results for the intermediate temperature sum threshold 3 °C and growing season from May to September are shown.

Plant diversity

We computed two indices describing plant diversity patterns (species richness and Shannon index) for the dataset encompassing 123 summits. Only the first inventory of each region was used, as second survey data were available only for a subset of 17 regions. To account for the uneven species numbers among summits (ranging from 0 to 102 species; see Appendix S1) we used proportional species richness, i.e., the number of species in a 3 × 3 m grid divided by the number of species at the summit, instead of the absolute number of species.

To analyse the effects of cardinal direction on plant species richness, we applied binomial generalised linear mixed-effects models (GLMMs) using the logit-link, where the occurrence of species in a 3 × 3 m grid was regarded as a binary variable with each species out of a local species pool (i.e., all species found on a given summit) either occurring or not in a

given 3 × 3 m grid (see Appendix S4a). Cardinal direction was the only fixed-effect predictor and hierarchical random intercept terms were estimated for summits nested within regions. Parameters were estimated by the Laplace approximation using the function *glmer* as implemented in the R package 'lme4' (Bates *et al.*, 2015).

As an additional measure of diversity which does not rely solely on presence/absence, but takes into account abundances of species, the Shannon index (Hill, 1973) was calculated for each cardinal direction of each summit as:

$$H' = -\sum_{i=1}^{s}(p_i \ln p_i),$$

where p_i is the cover of the *i*th species (averaged over the four permanent 1 × 1 m quadrats of each 3 × 3 m grid), using the R package 'vegan' (Oksanen *et al.*, 2015).

The effects of cardinal directions on the Shannon index were modelled using LMMs as described above for temperature sums, but with cardinal direction as the only fixed-effect predictor.

Colonization and disappearance of species

Two indices indicating changes in diversity patterns (proportional colonization and proportional disappearance of residents relative to the local species pool) between 2001 and

2008 for the data subset encompassing 67 summits were computed.

The effect of cardinal direction on the binary variables colonization and disappearance was modelled using binomial GLMMs with the same settings as described for plant species richness above. Similar to species richness, colonization and disappearance were regarded as binary variables, where each species out of a local species pool colonizes or disappears from a 3×3 m grid or not. The species pool for disappearance was defined as all species found in the respective 3×3 m grid in 2001 (see Appendix S4c). For colonization the species pool was defined as all species found on a summit in at least one of the observation years, minus the species already present in the respective 3×3 m grid in 2001 (see Appendix S4b).

Thermal input and plant diversity

To analyse the effect of thermal input on plant diversity, GLMMs with binomially coded species richness, and LMMs with Shannon diversity index as dependent variables, proportional temperature sum (threshold 3 °C, growing season May–September) as fixed effect and summit nested in region as random intercepts were applied. GLMMs and LMMs were computed for each of the 30 imputations of the incomplete temperature sums dataset. Their marginal coefficients ($\pm$ SE) and *t*-values were averaged over these repetitions and *P*-values were derived from the mean *t*-value.

All GLMMs and LMMs were fitted for each biome separately, except for the polar biome, which was represented by only one region and therefore pooled with the boreal regions. As the contribution of each data point to the degrees of freedom (d.f.) is still under discussion in LMMs, we used a conservative approach and calculated d.f. for *t*-tests as the number of observations minus the number of fixed effects, minus the number of random effects, plus the number of random terms.

Two summits without any vascular plant species in the sample plots were excluded from analyses involving diversity indices. All analyses were carried out by using R 3.1.1 (R Development Core Team, 2015). Graphs were drawn using SigmaPlot 12.0 (Systat Software Inc., San José, California, USA).

RESULTS

Proportional temperature sums averaged across years were significantly higher in the east and south than in the north, with west being intermediate, on European summits in all biomes (Fig. 2, see Appendix S5). Differences among cardinal directions were most pronounced in the temperate biome, and smaller in the Mediterranean and boreal biomes, respectively (LMMs; Fig. 2, see Appendix S5). These differences in temperature sums among cardinal directions were consistent across years (Table 1).

Species richness on Mediterranean summits tended to be highest on the west-facing and lowest on the east- and north-facing summit slopes. However, these differences among cardinal directions were not significant (GLMMs: Fig. 3a, see Appendix S6a). Species richness on temperate summits was significantly higher on the east- and south-facing slopes than in the west- and north-facing ones (GLMMs: Fig. 3b, see Appendix S6a). On boreal/polar summits, east- and south-facing slopes both had a higher species richness than north-facing ones, but west-facing slopes were not significantly different from those facing north and south (GLMMs: Fig. 3c, see Appendix S6a). Differences among cardinal directions in the Shannon diversity index showed a similar pattern as species richness except for northern slopes: (1) differences among cardinal directions were not significant on Mediterranean summits, (2) on temperate summits east and south had significantly higher Shannon index values than west and north, (3) on boreal/polar summits only east and west differed significantly (LMMs; Fig. 3d–f, see Appendix S6b).

Proportional temperature sum and species richness were significantly positively correlated in the Mediterranean and temperate biomes, but not in the boreal biome (GLMMs: Table 2a). Shannon index and proportional temperature sums were significantly positively correlated only in the temperate biome (LMMs: Table 2b).

Colonization between 2001 and 2008 was higher in the east and south than in the west and north on temperate and Mediterranean summits. These differences among cardinal directions were statistically significant except for east versus west on Mediterranean summits (GLMMs: Fig. 4a–b, see Appendix S7a). In contrast, colonization events were evenly distributed among cardinal directions on boreal summits (GLMMs: Fig. 4c, see Appendix S7a). Significant differences among cardinal directions in disappearance of species were only observed on temperate summits, with higher species losses on eastern slopes than on southern and western slopes (GLMMs: Fig. 4e, see Appendix S7b). On Mediterranean and boreal summits, disappearance of species was highest in the north and the south, respectively, however, these differences were not statistically significant (GLMMs: Fig. 4d,f, see Appendix S7b).

Raw data means and confidence intervals of proportional temperature sum, proportional species richness, Shannon index, proportional colonization and proportional disappearance of species in the four cardinal directions (Table 3) were similar to the GLMM and LMM model estimates illustrated in Figs 2–4.

DISCUSSION

The warmest aspect on mountain slopes

Temperature sums differed significantly among cardinal directions on mountain summits from treeline ecotone to alpine/nival elevations, with east and south exposures showing higher values than west and north. It is common knowledge that, in the Northern Hemisphere, south exposed slopes provide a warmer microclimate than northern ones at the same elevation. In addition, we found eastwardly oriented areas to be thermally more favourable than westerly exposed

ones, and no significant difference between east and south (Fig. 2). These patterns were stable across years (Table 1), similar to snow distribution patterns in relation to topography (Keller *et al.*, 2005). Three climatic features could have caused the higher thermal input at eastern compared to western slopes. Firstly, an important factor is likely the time of the day when direct radiation is received (compare Vittoz *et al.*, 2010). On western slopes cool or cold night conditions
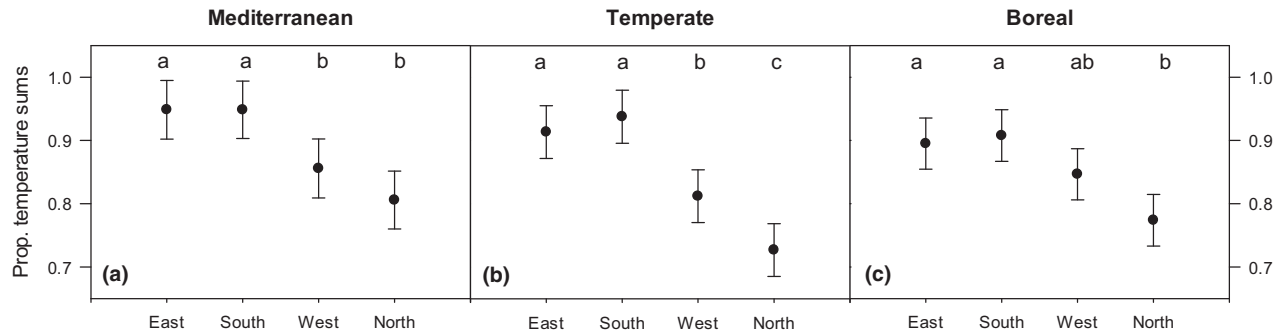
Figure 2 Thermal input compared among cardinal directions of 67 European mountain summits in the Mediterranean (a), temperate (b), and boreal (c) biomes. Temperature sums were calculated by summing hourly measurements of soil temperature exceeding a threshold value of 3 °C during the growing season (May to September) in the years 2002–2007. Proportional temperature sums were calculated by dividing temperature sums for each cardinal direction by the highest value for the respective summit. Model estimates ± 95% confidence interval of proportional temperature sums at each cardinal direction are given. Different letters refer to significant differences according to linear mixed-effects models with cardinal direction, year and their interaction as fixed effects (see Appendix S5).

Table 1 Fixed effects of linear mixed-effects models comparing soil temperature sums at 10-cm depth among cardinal directions and years on European mountain summits in the (a) Mediterranean (number of regions N_{reg} = 4, number of summits N_{sum} = 15), (b) temperate (N_{reg} = 8, N_{sum} = 32), and (c) boreal biomes (N_{reg} = 5, N_{sum} = 20). Temperature sums represent values of hourly measurements summed up above a threshold of 3 °C during the growing season (May to September). Gaps in temperature measurement series were filled through imputation. This process was repeated 30 times. Models for each of the 30 imputed datasets and mean estimates ± standard error (SE) and *t*-values were calculated (for details see text). *P*-values are derived from the mean *t*-value, *P*-values below 0.05 are given in bold. For the categorical variables cardinal direction and year, the first level (i.e., 'East' for cardinal direction, and '2002' for year) is treated as the base level and all remaining levels are compared with the base level.

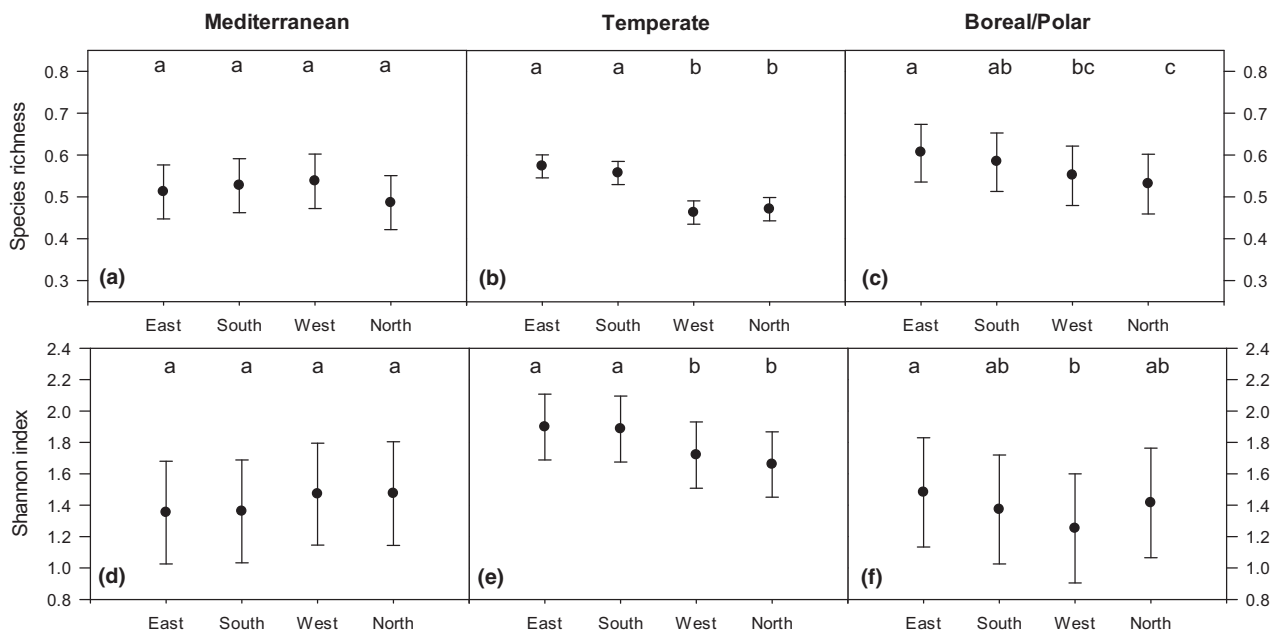|	(a) Mediterranean			(b) Temperate			(c) Boreal		
	Estimate (± SE)	*t*-value	*P*-value	Estimate (± SE)	*t*-value	*P*-value	Estimate (± SE)	*t*-value	*P*-value
(Intercept)	0.96 ± 0.03	27.65	**< 0.001**	0.92 ± 0.03	31.41	**< 0.001**	0.90 ± 0.03	26.43	**< 0.001**
North	−0.15 ± 0.04	−3.83	**< 0.001**	−0.16 ± 0.03	−5.21	**< 0.001**	−0.14 ± 0.04	−3.21	**0.001**
South	−0.01 ± 0.04	−0.28	0.781	0.02 ± 0.03	0.58	0.561	0.00 ± 0.04	−0.02	0.983
West	−0.10 ± 0.04	−2.55	**0.011**	−0.08 ± 0.03	−2.67	**0.008**	−0.07 ± 0.04	−1.58	0.114
Year 2003	−0.03 ± 0.04	−0.66	0.508	−0.02 ± 0.03	−0.61	0.543	0.00 ± 0.04	0.10	0.917
Year 2004	−0.01 ± 0.04	−0.14	0.885	−0.02 ± 0.03	−0.55	0.584	−0.01 ± 0.04	−0.34	0.738
Year 2005	−0.01 ± 0.04	−0.20	0.839	−0.02 ± 0.03	−0.50	0.619	−0.01 ± 0.04	−0.23	0.819
Year 2006	0.00 ± 0.04	−0.11	0.910	0.01 ± 0.03	0.26	0.795	0.00 ± 0.04	0.01	0.993
Year 2007	−0.01 ± 0.04	−0.22	0.830	0.01 ± 0.03	0.17	0.862	−0.02 ± 0.04	−0.44	0.660
North: Year 2003	0.03 ± 0.05	0.55	0.583	−0.04 ± 0.04	−0.83	0.407	0.02 ± 0.06	0.26	0.798
South: Year 2003	0.04 ± 0.05	0.72	0.473	0.01 ± 0.05	0.33	0.740	0.00 ± 0.06	0.00	0.998
West: Year 2003	0.04 ± 0.06	0.68	0.498	−0.02 ± 0.04	−0.35	0.728	0.02 ± 0.06	0.28	0.781
North: Year 2004	0.01 ± 0.05	0.17	0.867	−0.05 ± 0.04	−1.24	0.216	0.01 ± 0.06	0.21	0.833
South: Year 2004	0.01 ± 0.05	0.20	0.838	0.02 ± 0.05	0.49	0.622	0.01 ± 0.06	0.24	0.811
West: Year 2004	0.01 ± 0.06	0.24	0.809	−0.02 ± 0.04	−0.45	0.649	0.02 ± 0.06	0.42	0.678
North: Year 2005	0.00 ± 0.05	−0.05	0.958	−0.01 ± 0.05	−0.13	0.895	0.01 ± 0.06	0.17	0.868
South: Year 2005	0.01 ± 0.05	0.14	0.888	0.00 ± 0.05	0.07	0.947	0.00 ± 0.06	0.08	0.934
West: Year 2005	0.00 ± 0.06	0.09	0.931	−0.03 ± 0.05	−0.73	0.463	0.02 ± 0.06	0.31	0.756
North: Year 2006	0.00 ± 0.05	0.00	0.998	−0.02 ± 0.04	−0.42	0.677	0.02 ± 0.06	0.33	0.739
South: Year 2006	0.01 ± 0.05	0.12	0.903	−0.01 ± 0.05	−0.14	0.892	0.02 ± 0.06	0.32	0.746
West: Year 2006	0.00 ± 0.06	−0.03	0.976	−0.02 ± 0.04	−0.37	0.712	0.02 ± 0.06	0.26	0.795
North: Year 2007	−0.01 ± 0.05	−0.09	0.925	−0.02 ± 0.04	−0.45	0.652	0.04 ± 0.06	0.62	0.533
South: Year 2007	0.00 ± 0.05	−0.01	0.994	0.00 ± 0.05	−0.01	0.993	0.04 ± 0.06	0.73	0.468
West: Year 2007	−0.01 ± 0.06	−0.19	0.848	−0.02 ± 0.04	−0.49	0.621	0.03 ± 0.06	0.58	0.561

persist longer during the day compared to eastern slopes, which receive direct solar radiation early in the morning. Secondly, convective cloud formation is a common phenomenon, especially in temperate mountains, which occurs most frequently after midday (Geiger, 1950; Hoeck, 1952). It disproportionally reduces the daily direct radiation on the western slopes compared to eastern ones. Thirdly, in most European mountains, the western to north-western sides of mountains are exposed to the main weather system and, therefore, experience windier conditions, causing stronger evaporative cooling (Barry, 2008) than eastern to south-eastern aspects.

The warmer, the richer . . .

Here, we provide a first pan-European view on relationships of alpine vascular plant species diversity at different aspects and their climatic conditions. We show that east- and south-exposed mountain slopes favour local-scale species richness, compared to the western and northern sides of the same mountains (Fig. 3a), which largely confirms the results of regional summit studies (Coldea & Pop, 2004; Stanisci et al., 2005; Gutiérrez-Girón & Gavilán, 2010; Vittoz et al., 2010). This pattern, however, is not consistent across the continent. On temperate mountains the strong positive relation between plant diversity and temperature (Table 2) is consistent with the species-energy hypothesis (Wright, 1983) and other temperature-related diversity hypotheses (Currie et al., 2004), suggesting temperature-driven processes as decisive determinants of vascular plant species richness. A number of studies

and reviews (Allen et al., 2002; Francis & Currie, 2003; Willig et al., 2003; Clarke & Gaston, 2006; O'Brien, 2006; Hawkins et al., 2007; Kreft & Jetz, 2007; Whittaker et al., 2007; Hurlbert & Jetz, 2010; Gillman et al., 2015) discussed temperature, solar radiation, water and potential evapotranspiration as underlying determinants of species richness along large-scale, mostly latitudinal gradients. Moser et al. (2005) found that climatic variables such as temperature and potential evapotranspiration were by far the most important predictors of vascular plant species richness on a country-wide scale in the Austrian Alps. Elevation gradients in species richness have also been associated with climatic gradients and particularly gradients of solar energy received, as well as with species–area relationships, since the available area decreases with increasing elevation (Grabherr et al., 1995; Lomolino, 2001; Grytnes, 2003; Theurillat et al., 2003, 2011; Bruun et al., 2006).

The strong match between patterns of thermal input and plant species diversity in the temperate biome (Table 2) might be related to the growing season that usually starts around the summer solstice in the alpine zone. As morning irradiation starts in the north-east at summer solstice, the advantage in growing on an eastern slope is obvious and especially pronounced when night-time temperature falls close to or below the threshold for plant growth and when afternoon radiation is reduced through convective cloud formation. Diurnal periods of low temperature, which are detrimental to plant growth or other biotic processes may, thus, be shorter on eastern than on western, northern and even on southern slopes.
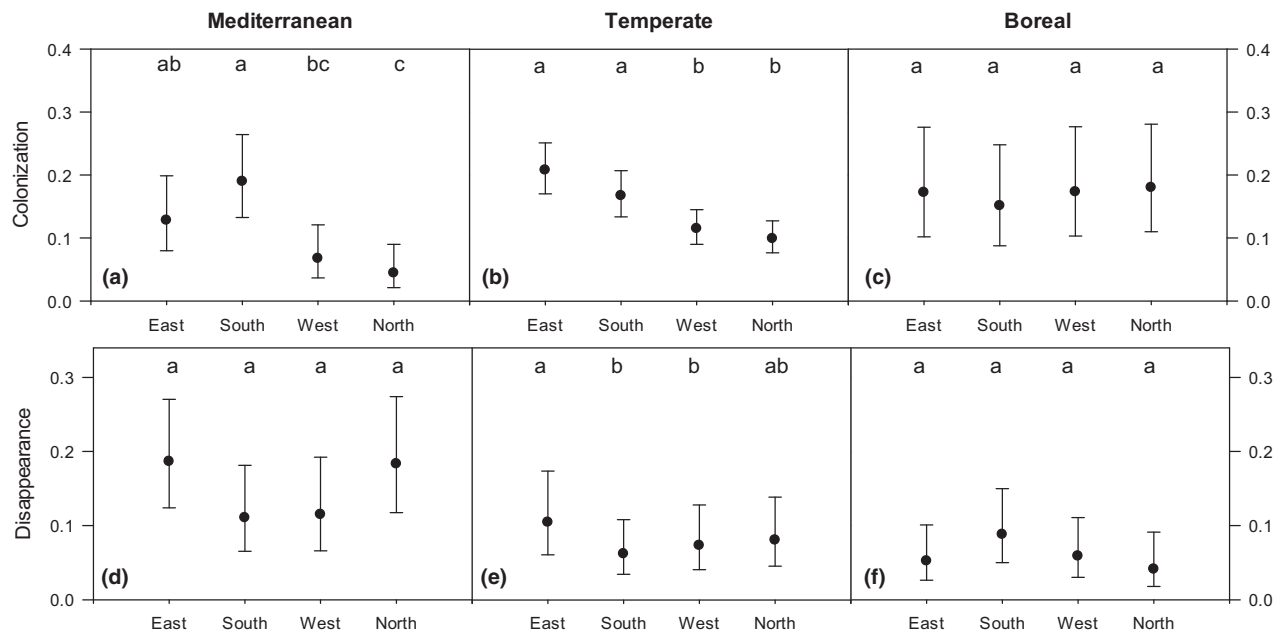

Figure 3 Vascular plant species diversity on alpine summits in Mediterranean (a, d), temperate (b, e), and boreal/polar (c, f) Europe recorded between 2001 and 2012. Model estimates (± 95% confidence interval) are given for species richness as proportion of the local species pool (upper panel) and Shannon index (lower panel) at each cardinal direction. Different letters refer to significant differences according to generalised linear mixed models (GLMMs) with a binomial error distribution and logit link (upper panel, see Appendix S6a); and linear mixed-effect models (lower panel, see Appendix S6b).

Table 2 The influence of soil temperature on (a) species richness, and (b) the values of Shannon index on European mountain summits in the Mediterranean (number of regions N_{reg} = 4, number of summits N_{sum} = 15), temperate (N_{reg} = 8, N_{sum} = 32), and boreal/polar biomes (N_{reg} = 5, N_{sum} = 20). Given are fixed effects of (a) generalised linear mixed-effects models with species richness coded as a binomial variable (estimates are given on both the logit scale and the scale of the response variable, i.e., the probability scale), and (b) linear mixed-effects models. Temperature sums represent values of hourly measurements above a threshold of 3 °C summed up during the growing season (May to September) and averaged for the years 2002–2007. Temperature sums of each cardinal direction were divided by the highest temperature sum on the respective summit to rescale values between 0 and 1. Gaps in temperature measurement series were filled through imputation. This process was repeated 30 times. Models for each of the 30 imputed datasets and mean parameter estimates were calculated (for details see text); *P*-values below 0.05 are given in bold.

	(a) Species richness				(b) Shannon index		
	Estimate (probability scale)	Estimate ± SE (logit scale)	*z*-value	*P*-value	Estimate ± SE	*t*-value	*P*-value
Mediterranean							
(Intercept)		−1.86 ± 0.64	−2.90	**0.004**	1.13 ± 0.54	2.09	**0.045**
Temperature sum	0.050	2.12 ± 0.67	3.15	**0.002**	0.40 ± 0.54	0.75	0.460
Temperate							
(Intercept)		−1.19 ± 0.19	−6.15	**< 0.001**	1.06 ± 0.28	3.74	**< 0.001**
Temperature sum	0.040	1.56 ± 0.22	7.10	**< 0.001**	0.83 ± 0.29	2.86	**0.005**
Boreal/Polar							
(Intercept)		−0.20 ± 0.42	−0.47	0.635	1.46 ± 0.36	4.04	**< 0.001**
Temperature sum	0.015	0.61 ± 0.44	1.39	0.164	−0.35 ± 0.37	−0.95	0.348

Figure 4 Colonization and disappearance of resident species on alpine summits in Mediterranean (a, d), temperate (b, e), and boreal (c, f) Europe between 2001 and 2008. Model estimates (± 95% confidence interval) are given for colonization (upper panel) and disappearance (lower panel) as proportion of the local species pool at each cardinal direction. Different letters refer to significant differences according to generalised linear mixed models (GLMMs) with a binomial error distribution and logit link (see Appendix S7).

...but not in all biomes

The pattern of the warmest conditions on eastern and southern aspects compared to western and northern ones was clearly more distinct in temperate than in Mediterranean and boreal mountain regions of Europe (Fig. 2). This is in concordance with latitude-dependent differences in direct solar radiation being most pronounced among aspects at temperate latitudes (Barry, 2008). In boreal and polar biomes diurnal differences in solar radiation and thus in temperature sums among aspects, are generally reduced due to long day lengths at low sun angles. In contrast to temperate regions, thermal differences on Mediterranean mountains between east and south versus west and north slopes are not or only

Table 3 Indices for thermal input, plant species diversity, colonization and disappearance of species compared among cardinal directions of Mediterranean, temperate and boreal/polar European mountain summits. Given are raw data means and 95% confidence intervals (CI) of (a) proportional temperature sums (i.e., temperature sums of each cardinal direction divided by the highest temperature sum on the respective summit), (b) proportional species richness, (c) Shannon index, (d) proportional colonization, and (e) proportional disappearance of resident species. Proportional in (b)–(e) means relative to the local species pool. For details on the definition of local species pool and computation of indices see text and Appendix S4.

	Cardinal direction	Mean (95% CI)		
		Mediterranean	Temperate	Boreal/Polar
(a) Temperature sum	East	0.940 (0.925–0.956)	0.910 (0.893–0.926)	0.891 (0.870–0.912)
	South	0.937 (0.915–0.960)	0.928 (0.914–0.942)	0.904 (0.873–0.934)
	West	0.841 (0.815–0.867)	0.809 (0.788–0.831)	0.846 (0.816–0.876)
	North	0.804 (0.768–0.841)	0.723 (0.697–0.750)	0.772 (0.744–0.801)
(b) Species richness	East	0.467 (0.364–0.570)	0.582 (0.531–0.633)	0.594 (0.506–0.682)
	South	0.517 (0.424–0.610)	0.546 (0.493–0.599)	0.580 (0.506–0.654)
	West	0.560 (0.490–0.630)	0.448 (0.397–0.500)	0.560 (0.474–0.645)
	North	0.488 (0.388–0.587)	0.459 (0.412–0.505)	0.537 (0.445–0.630)
(c) Shannon index	East	1.408 (1.068–1.749)	1.923 (1.762–2.085)	1.510 (1.260–1.760)
	South	1.422 (1.131–1.712)	1.900 (1.722–2.078)	1.394 (1.133–1.655)
	West	1.519 (1.283–1.755)	1.754 (1.581–1.927)	1.279 (1.027–1.531)
	North	1.531 (1.279–1.784)	1.656 (1.466–1.846)	1.492 (1.280–1.704)
(d) Colonization	East	0.140 (0.048–0.232)	0.263 (0.167–0.360)	0.236 (0.119–0.353)
	South	0.220 (0.073–0.366)	0.169 (0.127–0.211)	0.160 (0.080–0.241)
	West	0.083 (0.004–0.161)	0.130 (0.096–0.165)	0.228 (0.103–0.354)
	North	0.066 (−0.023–0.154)	0.122 (0.070–0.174)	0.143 (0.047–0.238)
(e) Disappearance	East	0.142 (0.057–0.227)	0.142 (0.088–0.195)	0.059 (0.022–0.096)
	South	0.100 (0.029–0.171)	0.106 (0.037–0.174)	0.054 (0.013–0.095)
	West	0.135 (0.030–0.239)	0.084 (0.038–0.129)	0.084 (0.020–0.147)
	North	0.187 (0.007–0.368)	0.085 (0.049–0.121)	0.058 (−0.003–0.120)

weakly mirrored by plant diversity (Figs 2 & 3; Table 2; compare with Kazakis *et al.*, 2007), most likely due to interfering effects of low water availability during the growing season in the Mediterranean (Fig. 1; Köppen & Geiger, 1936). Summer drought in Mediterranean mountains can act as a filter preventing a number of species to grow in the warmest habitats that are likely to suffer from increased evapotranspiration (O'Brien, 2006; Giménez-Benavides *et al.*, 2007; Gutiérrez-Girón & Gavilán, 2013; Li *et al.*, 2013). A further reason for inconsistent results at the Mediterranean sites might lie in regional idiosyncrasies regarding the onset and length of the dry summer period, which can lead to a differing severity of drought effects. Finally, the lower number of sites in the Mediterranean and boreal/polar biomes and the lower species numbers may have contributed to less significant differences among aspects.

The magnitude of species colonization

Observed species colonization was not evenly distributed among cardinal directions on temperate and Mediterranean summits. Colonizations were more frequently observed at warmer eastern and southern sides than at northern or western exposed slopes (Fig. 4a,b). This pattern is consistent with observations on Piz Linard, Switzerland, during the past six decades (Pauli *et al.*, 2003; Wipf *et al.*, 2013). Disappearances of species on the European GLORIA summits were less

common (see Appendix S1 and S7) and more randomly distributed among aspects than observed colonizations (Fig. 4), probably due to the short period of observation with respect to the longevity of alpine plants. Similarly, species turnover on the majority of historical summit observation sites in the Alps has been attributed to colonization rather than to local extinction of species (Matteodo *et al.*, 2013), although factors that are not directly temperature-related may also be relevant for the upward shift observed in comparison with historical data from European summits (Grytnes *et al.*, 2014). Our results, however, show that climatically amenable mountain slopes support stronger migration dynamics through suitable habitat conditions and, probably, also through stronger convective winds on warmer mountain slopes, which may promote diaspore propagation. Topography in high-mountain environments, thus, can be a crucial determinant of the velocity of climate change-induced migration processes.

CONCLUSIONS

Differences in plant species richness appear to be strongly related to a thermal gradient caused by incident solar radiation. The general pattern of higher species numbers on eastern sides, compared to western ones, could result from combined effects of a longer solar exposure and wind sheltering in a leeward position. Differences in species numbers and temperature sums, however, are mainly observed in mesic

temperate mountains, whereas boreal/polar as well as Mediterranean mountains showed no relationship, probably due to a more even diurnal radiation or because of unfavourable aridity at the warmer sides, respectively. Colonization of species was more frequent at the warmest sides of temperate mountain peaks, indicating that thermal patterns on mountain slopes are determinants of the pathways and of the magnitude of species migration. Thus, aspect may strongly influence the persistence of populations and most likely the pace and dynamics of thermophilisation (Gottfried *et al.*, 2012), and the time lag until extinction debts will be paid-off (Jackson & Sax, 2010; Dullinger *et al.*, 2012) under amplifying climate warming conditions (Mountain Research Initiative E. D. W. Working Group, 2015).

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SUPPORTING INFORMATION

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

Appendix S1 Characteristics of summits in 32 European mountain regions.
Appendix S2 Temperature sum thresholds and growing season lengths.
Appendix S3 Gaps in soil temperature measurements.
Appendix S4 Species pool definition.
Appendix S5 Soil temperature sums among cardinal directions.
Appendix S6 Plant diversity among cardinal directions.
Appendix S7 Species colonization and disappearance among cardinal directions.

BIOSKETCH

The authors represent the European chapter of the international long-term monitoring network GLORIA (www.gloria.ac.at). The network was established at the beginning of the century and currently comprises over 400 summit sites in more than 120 mountain regions globally. The purpose of GLORIA is to detect short- and long-term impacts of climate change on biodiversity and habitat stability in high mountain environments.

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