Linking small-scale topography with microclimate, plant species diversity and intra-specific trait variation in an alpine landscape

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Abstract

Background: Small-scale topographic complexity is a characteristic feature of alpine landscapes, with important effects on alpine plant distribution.

Aims: We investigated the links between small-scale topographic complexity and resultant microclimatic heterogeneity, vascular-plant species richness and beta diversity, and realised niche width and trait variation of some target species.

Methods: We recorded temperature and soil moisture within 10 sites (40 m x 40 m) of differing topographic complexity in alpine terrain at Finse, Norway (N 60° 36', E 7° 33'). Plant species occurrence and traits of target species was recorded in 16 sample plots at each site.

Results: Sites differed significantly in microclimatic heterogeneity, and topographically rough sites were always more heterogeneous than flatter ones. Greater species richness and turnover was associated with greater microclimatic heterogeneity, and rough sites contained 15-55% more species than flatter ones. Plant species had on average wider realised niches when growing at rough sites. Individuals of *Bistorta vivipara*, but not those of *Luzula spicata*, tended to exhibit greater phenotypic variation at rough sites.

Conclusions: Rough alpine terrains create small-scale variation in microclimate, promoting species richness and beta diversity. In the event of climate change, small-scale micro-climatic heterogeneity might allow plant species to escape from regional climate change by short-distance migration into local micro-refugia, This study suggests that the opportunity for such responses would be greater in topographically complex terrains.

Keywords: alpine plants; beta diversity; *Bistorta vivipara*; climate change; *Luzula spicata*; microclimatic heterogeneity; phenotypic variation; topography.

Introduction

Under a changing climate, plants and animals will often have to react to altered environmental conditions. For sessile organisms such as plants, this can be achieved either through migration of offspring to new suitable habitats (extending, contracting or displacing distributional ranges), or by staying where they are and physiologically adjusting or, across generations, genetically adapting to new conditions. The ability of plants to migrate in response to climate change has received considerable attention (e.g. Walther et al. 2005a; Walther et al. 2005b; Pearson 2006; Lenoir et al. 2008; Frei et al. 2010; Lenoir et al. 2010) and plant species have been shown to shift their range northwards (Walther et al. 2005b), upslope (Walther et al. 2005a; Lenoir et al. 2008) and downslope (Lenoir et al. 2010). The opportunity for plant populations to persist locally has, however, been less well studied. While some large-scale models have predicted tremendous losses of habitat and many local extinctions (e.g. Thomas et al. 2004; Thuiller et al. 2005; Dullinger et al. 2012; Gottfried et al. 2012), recent research points towards an important role of microclimatic heterogeneity and local refugia (e.g. Luoto and Heikkinen 2008; Randin et al. 2009; Scherrer and Körner 2011; Ashcroft et al. 2012; Lenoir et al. 2013, see also Edwards & Armbruster 1989).

Alpine plants have traditionally been seen as highly specialised to harsh environmental conditions (Körner 2003), and therefore particularly vulnerable to climate change (e.g. Theurillat and Guisan 2001). However, alpine landscapes are often topographically very complex, creating mosaics of diverse microclimates over short distances (Lloyd et al. 1994; Rae et al. 2006; Armbruster et al. 2007; Scherrer and Körner 2011). Topographically complex terrain should therefore contain a wide range of plant niches, and might be likely locations of climatic micro-refugia (Ashcroft 2010; Dobrowski 2011). Importantly, small-scale thermal variation has been shown to equal or exceed global climate warming predictions (Rae et al. 2006; Armbruster et al. 2007; Scherrer and Körner 2011; Graae et al. 2012; Lenoir et al.

2013). For predicting future changes to alpine plant communities, it is therefore important to consider the local variation in the environments of the resident plants, in addition to the mean values of the landscape (Armbruster et al. 2007). Complex alpine landscapes provide ideal natural experiments for understanding how small-scale topographic complexity translates into microclimatic heterogeneity, and how this, in turn, affects plant communities.

If plant communities occurring at topographically complex sites are subject to more climatic variation than those occurring at flatter sites, it can be expected that rough terrains generate greater variation both in species composition and in phenotypic traits within and among species (‘functional diversity’). The relationship between environmental heterogeneity and plant species diversity has been extensively studied, and there is now abundant evidence suggesting that an increase in habitat heterogeneity increases the number of coexisting species (reviewed in Lundholm 2009). A second, and less appreciated, aspect of habitat heterogeneity is that a greater number of unique micro-habitats within short distances might increase the potential for local reshuffling of plant communities through short-distance migration of resident species into local micro-refugia. When the environment varies at a small scale, it gives plants the opportunity to find new suitable habitats only short distances away when the climate changes, instead of moving long distances up mountain sides or towards the poles (Armbruster et al. 2007; Ackerly et al. 2010; Scherrer and Körner 2011; Spasojevic et al. 2013). Recent results from a long-term study in the Rocky Mountains suggested that plant communities in a heterogeneous alpine landscape were able to track fine-scale environmental variation while being under the influence of directional climate change (Spasojevic et al. 2013). To further understand the generality of this process, it is interesting to know the extent to which microclimatic heterogeneity differs among terrain types, combined with detailed information about the diversity and distribution of plant species inhabiting them.

Although much historical evidence points toward migration and community assembly processes (e.g. species sorting and reshuffling of local species) as leading forces in plant-community responses to climate change, the potential roles of phenotypic plasticity and adaptive evolution cannot be ignored (Davis and Shaw 2001; Ackerly 2003; Jump and Penuelas 2005; Stoecklin et al. 2009; Chevin et al. 2010). To understand the role of these processes in shaping plant communities, some studies have considered community-wide patterns of functional trait diversity based on mean values for each species in a given community or habitat (e.g. Onipchenko et al. 1998; Choler 2005; Spasojevic and Suding 2012; Spasojevic et al. 2013). Recently, however, attention has started to shift towards quantifying patterns of intra-specific trait variation, which has been shown to account for a large portion of community-wide trait diversity patterns (Albert et al. 2010; Jung et al. 2010; de Bello et al. 2011; Albert et al. 2012; Violle et al. 2012; Boucher et al. 2013; Jung et al. 2014; Sides et al. 2014). Regardless of the process by which it arises (genetic differentiation or phenotypic plasticity), intra-specific trait variation across a landscape might have consequences for the ability of plants to respond to climate change. Despite the potential of small-scale topographic complexity to drive microclimatic variation, there is still relatively little information about the extent of within-species trait variation at small scales across sites differing in topographic complexity (but see Albert et al. 2010; Boucher et al. 2013).

The hypothesis that small-scale topographic complexity will promote biotic resilience to climate change by creating opportunities for reshuffling of local species in the landscape, as well as potentially increasing adaptive and plastic capacities, depends on the link between topography, microclimate and plant communities. Consequently, the aim of this study was to investigate how small-scale topographic complexity translates into microclimatic heterogeneity, and how alpine plant communities respond to variation in microclimate. To achieve this, we measured the extent of variation in microclimate variables (temperature and soil moisture) within paired sites differing in small-scale topographic complexity. After testing if rough sites were more variable in microclimate than flatter sites, we investigated if the estimated microclimatic heterogeneity of each site was associated with the diversity of their local plant communities, and with within-species variation in phenotypic traits of two target species. Specifically, we predicted that topographically rough sites would contain greater microclimatic variation than flatter sites, and that sites with greater microclimatic variation supported both more plant species, and species exhibiting greater phenotypic variation. We also investigated whether plants growing at climatically more heterogeneous sites were able to utilise the greater number of different micro-habitats available, by estimating the realized niche widths of some common species in different terrain types.

Materials and methods

Field site

Fieldwork was conducted during the summer of 2012 near Finse at the Hardangervidda plateau in alpine southern Norway (N 60° 36.23', E 7° 33.40'; 1430 m above sea level; Figure 1). The study site is situated in the low to middle alpine zone, well above the climatic treeline at about 1000 m a.s.l. at Finse (Dahl 1986). The vegetation is low-growing alpine tundra in between rocky outcrops, dominated by lichens, dwarf shrubs (e.g. *Empetrum nigrum*, *Salix herbacea*), forbs (e.g. *Bistorta vivipara*, *Silene acaulis*) and graminoids (e.g. *Luzula spicata*, *Juncus trifidus*, *Carex bigelowii*). Mean summer (June-August) temperature and precipitation for Finse was 6.3 °C and 89 mm, respectively, during the period 1961-1990 (Norwegian Meteorological Institute 2013) . The site has been used for summer grazing by sheep.

Study design

In July 2012 we subjectively chose five areas, and located in each one ‘rough’ and one ‘flat’ site. The site pairs were chosen so that the two sites were as similar as possible in macro-exposure, altitude and vegetation type, and the intra-pair distance was less than the inter-pair distance (i.e. between areas). In each area, we took care to select sites that differed in micro-topography, although the flat site in one area might have been similar to the rough site in another. All sites were mainly south-facing and snow-free in early July, a period when much of the surrounding landscape was still snow-covered in the year of this study (2012). Hence, we assumed that the length of the growing season was about the same for all sites, although the date of snow-melt is probably more variable at the rough sites than at the flatter ones. Each site measured 40 m x 40 m, was divided into 16 sub-sites (10 x 10 m), and within each sub-site a 0.25 m^2 sample plot was placed, following a stratified random distribution (Figure 1).

In the south corner of each sample plot, we placed a temperature logger (iButtons, Maxim Integrated Products, Sunnyvale, CA, US) wrapped in matte green duct tape at the soil surface. Matte green tape was chosen in order to roughly approximate the reflective properties of leaves near the soil surface. Although the recorded temperatures might differ from the exact temperature of the plant canopy, we assumed that this approach would capture relevant variation in topographically controlled temperature conditions experienced by the plants and any deviation from canopy surface temperature would be consistent. The loggers were left in the plots for three weeks (11 Jul – 2 Aug 2012), taking one temperature measurement per hour. The resolution of the data is 0.5 °C, and includes mean, maximum and minimum temperature for each logger. Due to disturbance of temperature loggers by sheep, all data from the flat site in area 1 (1F) were excluded from the following analyses. Twelve additional loggers were classified as disturbed (by for example wind, water or animals) and 10 loggers were not found when returning to sites, leaving data from 122 loggers for the analyses. Apart from the excluded site, grazing pressure and disturbance by animals appeared to be low and similar across the study sites. We measured soil moisture with a hand-held moisture sensor (TRIME-PICO, IMKO GmbH, Ettlingen) in all sample plots on a humid day following some light drizzle in the morning.

We chose to focus on temperature and soil moisture because these variables are known to be important drivers of plant species distribution and phenotypic trait variation, and they are expected to change with global warming and changes in precipitation regimes. Variation in temperature and moisture are also likely to be associated with variation in other important environmental factors, including snowpack, radiation load, pH, soil depth and soil nutrient levels. For example, topography affects snow-distribution by wind, and snowpack and rate of snow-melt has been shown to affect growing-season length, nutrient cycling, biomass production and species diversity (e.g. Litaor et al. 2008).

Vegetation sampling

Field sampling was carried out in August 2012. For each sample plot, we recorded all vascular plant species. A supplementary species list for each site was also compiled, by noting any additional species observed within each 10 m x 10 m sub-site. Plants were determined to species (or genus for *Alchemilla*, *Euphrasia*, *Hieracium* and *Taraxacum*). We calculated species richness at three scales: individual sample plots (‘plot richness’), cumulative species richness of the sample plots at each site (‘sample richness’) and the entire site (based on supplementary species lists, ‘site richness’). We chose to focus on species presence only, because we were mostly interested in species composition and turnover (‘beta diversity’) across sample plots and sites.

To investigate the extent of phenotypic variation of plants at the sites, the forb *Bistorta vivipara* (L.) Delarbre (Polygonaceae) and the graminoid *Luzula spicata* (L.) DC. (Juncaceae) were chosen as target species, based on their local abundance. For each sample plot, the shoots of each species closest to the centre of the plot were chosen, although these were not always within the sample plot. For these shoots we recorded the traits (1) plant height, (2) length and width of the largest leaf and (3) propagule number (bulbils for *Bistorta* and capsules for *Luzula)*. Plant height was measured in the field using a metre stick. The plant was then collected, stored in a plastic bag and transported to the laboratory. Leaf length and width were measured later the same day using digital calipers, and multiplied to obtain a measure of leaf area.

Statistical analyses

Topography per se is hard to quantify at small scales, especially in areas where high-resolution digital elevation models are not yet available. Therefore, we assumed that variation in the measured microclimate variables reflected the topographic complexity of the sites. To test if rough sites were indeed more heterogeneous than flatter ones, we derived a testable measure of microclimatic heterogeneity by estimating for each site the average Euclidean distance from centroids in multivariate space in terms of microclimate data (mean temperature, maximum temperature and soil moisture), standardised to zero mean and unit variance. Preliminary analyses showed that minimum temperature was little related to species richness and distribution, and this variable was therefore not used in the analysis. We tested the null-hypothesis of homogeneity of multivariate dispersions by applying permutation tests (Anderson 2006). Similarly, we derived a measure of beta diversity by estimating for each site the average multivariate dispersion of sample plots in community space, using the Jaccard index of community dissimilarity as a measure of compositional distance between sample plots (Anderson et al. 2006).

To investigate the relationship between microclimate and plot richness, we fitted a mixed-effects Poisson regression model with species richness of the sample plots as the dependent variable, and microclimate variables as possible explanatory variables. To account for the structure of the data (sites nested within areas), site and area was entered as random factors. At the among-site scale (using each site as an observation unit), we used regression analysis to test for relationships between the previously derived measures of microclimatic heterogeneity, beta diversity and species richness.

To investigate the habitat utilisation of plant species at the sites, we estimated the realised niche width of some common species in the two site topography classes. A total of 45 species occurred in the sample plots in both topography classes, and hence comprised the common species pool. Of these, 16 species with a sufficiently high frequency (>10 sample plots in both topography classes) were chosen for detailed analysis. To quantify the realised niche widths of these species we took two approaches. First, as an abiotic approach, we calculated for each topography class the range of mean and maximum temperatures among sample plots in which the focal species occurred, averaged over sites. Hence, this represents an estimate of the microclimatic preferences of each species. Second, as a biotic approach, we used recently developed methods (Fridley et al. 2007; Manthey and Fridley 2009) to estimate the width of each species' realised niche based on co-occurrence data. This method estimates realised niche width as the beta diversity, in this case the multi-site Simpson dissimilarity index, among a random sample of plots in which the focal species occurs. The multi-site Simpson index was chosen because it has been shown to be robust against variation in species richness and plot abundances (Manthey and Fridley 2009). Greater values of this index for a given species indicate a greater turnover in co-existing species among plots. The sampling procedure was repeated 100 times for each species.

Relationships between microclimate variables and phenotypic traits were tested using mixed-effect models, where site nested within area was entered as random factors and microclimate variables as possible explanatory variables. We partitioned the variance in phenotypic traits into between topography-class, among-site within topography-class and within-site components by fitting mixed-effects models with site nested within topography-class as random factors. To be able to compare the variation of traits when the means differed, we calculated the coefficient of variation (CV) for each trait and site, to produce a proportional measure of variation. We then used permutational multivariate analysis of variance (PERMANOVA; Anderson 2001) to test for differences in CV values between flat and rough sites. All statistical analyses were carried out in R, version 3.0.2 (R Core Team 2014), using the packages lme4 (Bates et al. 2014) and vegan (Oksanen et al. 2013).

Results

Topography and microclimatic heterogeneity

The overall mean temperature of all sample plots was 9.4 °C (SD = 0.96, range = 7.2 - 11.5 °C). Mean values (Table 1) did not differ significantly between flat and rough sites (ANOVA, $P = 0.92$ for mean temperature and $P = 0.19$ for soil moisture). Within-site differences in mean temperatures varied between 2 and 4 °C (Table 1). Microclimatic heterogeneity differed significantly among sites ($P = 0.02$), and was consistently greater for rough sites than for flatter sites in all four areas (significantly so only for area 2, Table 2).

Topography and species diversity

Sixty-four species of vascular plants were found in the sample plots, and a total of 85 at the 10 sites. As predicted, there was greater plant species richness at all four rough sites compared to paired flat sites, with rough sites containing 15-55% more species than their paired flat sites (Table 1). For sample richness, the difference was less pronounced. Beta diversity differed significantly among sites ($P = 0.015$), and was consistently greater at rough sites (significantly so for area 2 and 3, Table 2).

At the sample-plot scale, there was a positive relationship between logger mean temperature and corresponding plot richness (*GLMM*, $P < 0.001$), and mean temperature was strongly positively correlated with maximum temperature (*R = 0.75, P < 0.001*). The model estimated the species richness of a sample plot with an average mean temperature (9.4 °C) to 8.75 species, while an increase in temperature of one standard deviation (0.96 °C) increased the estimated species richness by 1.14 species. At the among-site level, there were significant positive relationships between microclimatic heterogeneity and species richness both for sample richness (Figure 2a) and site richness (Figure 2b). Considering the relationship between microclimatic heterogeneity and beta diversity (Figure 3), flat sites clustered below and to the left of rough sites, indicating on average less dispersion of sample plots both in microclimatic space and in community space than for rough sites. Secondly, when considered pair-wise, rough sites were in all cases located above and to the right of their paired flat sites, hence they were more variable along both axes. Finally, there was a positive trend of increasing beta diversity with increasing microclimatic heterogeneity.

Realised niche width

Most species were found in plots spanning a greater range of temperatures, and with a greater diversity of co-existing species, at rough sites (Table 3). Hence, they displayed wider realised niches, suggesting that these species were able to utilise the increased range of different microhabitats, and co-existing species, found at rough sites. Mean and maximum temperatures of the sample plots were strongly correlated, and the results for these two variables were qualitatively similar. Therefore, only results for mean temperatures are shown in Table 3. The abiotic and biotic measures of realised niche width yielded qualitatively similar results, although there was somewhat more inter-specific variation for the abiotic measure (Table 3). Interestingly, the two measures were significantly correlated (*R = 0.37, P = 0.03*), suggesting that the biotic approach based on co-existence yield results that can be interpreted in terms of microclimatic preferences.

Phenotypic traits

While all measured traits of *Bistorta* were related significantly to at least one of the measured microclimate variables, only plant height did so for *Luzula* (Table S1). The largest component of variation in all traits occurred within sites (73–94%; Table S2). After correcting for differences in trait means among sites, proportional trait variation (CV) tended to increase at rough sites compared to flat sites for most traits (Figure 4). Overall, however, this trend was not statistically significant (PERMANOVA, $P = 0.12$ for *Bistorta* and $P = 0.59$ for *Luzula*).

Discussion

Small-scale topographic complexity is a characteristic feature of alpine landscapes, and this has important consequences for alpine plant life. For example, variation in slope and aspect over a few metres influence patterns of radiation load, snow distribution and water runoff, hence creating variation in microclimate (Körner 2003). This variation subsequently influences which species can co-exist, and creates variation in selection pressures. As expected, we found that microclimatic heterogeneity differed among sites. Although these differences were often not statistically significant for individual site-pairs (areas), topographically complex sites were consistently more variable in microclimate than flatter sites for all areas. In the following, we discuss the implications of microclimatic heterogeneity for alpine plant-community responses to climate change.

Effects of topographic complexity on microclimate

Among sample plots within the 40 m x 40 m sites, mean temperatures recorded during three weeks of the growing season differed by between 2 and 4 °C, comparable to global warming scenarios for the next century (IPCC 2007), as well as to results from previous field and modelling studies (Rae et al. 2006; Armbruster et al. 2007; Scherrer and Körner 2011; Graae et al. 2012; Lenoir et al. 2013). Hence, there are microclimatic differences within 40 m x 40 m sites similar to what is expected over an altitudinal range of between 350 and 700 m (assuming a standard lapse rate of 5.5 K km^{-1}; Körner 2007), or a latitudinal range of between 308 and 616 km (2.7 and 5.5 degrees, respectively, assuming a lapse rate of 0.73 K per degree latitude; De Frenne et al. 2013). Our measure of microclimatic heterogeneity, which in addition to variation in mean temperatures also incorporates variation in soil moisture and extreme temperatures, also suggested greater overall variation in microclimate at rough sites. These results illustrate the importance of local variation in microclimate, and lead one to be cautious when interpreting large-scale models based on mean values (Armbruster et al. 2007; Lenoir et al. 2013).

Topography and plant communities

Topographically complex sites were more species-rich than flatter ones, but like previous studies (reviewed in Lundholm 2009), the strength of the relationship depended on the scale of investigation, and the pattern was most readily observed when considering all species found at the 40 m x 40 m sites (Table 1, Figure 2). This may be because the rough sites often contained ‘rare’ species (e.g. *Draba* spp., *Saxifraga cernua, Arabis alpina),* typically found growing in special microsites, such as small crevices, rocky outcrops or shady north-facing spots, and therefore often detected in the site surveys but not in the sample plots. Some of this diversity might be an effect of habitat heterogeneity, driven by factors not directly related to microclimate. The strong association between our measure of microclimatic heterogeneity and the total number of species found at each site suggests, however, that species richness in this system is correlated with variation in microclimate.

Mean temperature emerged as a good predictor of plot species richness, with plot richness increasing linearly with increasing mean temperature. In this relatively low-productive environment, this probably reflects an increase in available energy as a result of an increased radiation load (Virtanen et al. 2013). Across sites, microclimatic heterogeneity was positively correlated both with species richness and species turnover (beta diversity). The increase in beta diversity, which measures the dissimilarity among sample plots within a site, further supports the idea that increased small-scale variation in microclimate positively affects community diversity. The relative roles of available energy (mean supply of limiting resources) and heterogeneity (variation in limiting resources) as drivers of species richness has been debated (e.g. Stevens and Carson 2002; Lundholm 2009). Our measure of microclimatic heterogeneity was in fact positively correlated with maximum temperatures measured at the sites, and some caution should therefore be taken in interpreting their effects.

The realised niche represents the habitat-space occupied by a species in the presence of co-existing species (Hutchinson 1957). On the small scale of this study, it is unlikely that differences in niche width among sites reflect fundamental niche expansion. Instead, it provides a measure of the habitat utilisation of a species. While estimated niche widths were on average greater at rough sites, these sites also contained greater variation in microclimate. These species therefore appear to have tolerance ranges that allow them to exploit the increased niche space available at rough sites. Note that this analysis, in order to provide reasonably accurate estimates, was restricted to the most common local species, and that less common species might have narrower habitat preferences.

Topography and trait variation

Traits of alpine plant species has been shown to vary along topographic gradients (e.g. Kudo et al. 2001; Albert et al. 2010; Boucher et al. 2013). In topographically complex terrains such gradients can be expected to occur on a small scale, and we therefore expected to see increased intra-specific trait variation at rough sites. We found that trait responses to microclimate differed between species, and *Bistorta* appeared to respond more directly to variation in the measured microclimatic variables than *Luzula* did (Table S1). Across sites, we found no significant difference in overall trait variation between rough sites and less heterogeneous, flatter sites for either species. For *Bistorta*, though, the trend was towards greater trait variation at rough sites (Figure 4). Within-species trait variation across a landscape might arise from heritable genetic differentiation (‘ecotypic differentiation’) , non-heritable phenotypic plasticity, or some combination of the two. In rough alpine terrains we may assume that the scale of environmental variation is small relative to typical dispersal distances of many species, so that propagules will often develop in a micro-environment different from that of its mother. In this case, genotype x environment-correlations are unlikely to emerge, and phenotypic plasticity is assumed to be an adaptive response to environmental variation (Alpert and Simms 2002). A complementary common-environment study of plasticity in *Bistorta* originating from the same sites used in the present study revealed significant plastic responses to variation in soil moisture for all traits measured. However, we found no significant difference in the degree of plasticity between individuals originating from rough and flat sites (Ø. H. Opedal et al., unpublished data). Therefore, it seems that across the alpine landscape studied here, this species responds to microclimatic heterogeneity, at least in part, through non-genetic phenotypic adjustment. As suggested by Stoecklin et al. (2009), phenotypic plasticity may provide alpine plants with the flexibility needed to persist in a highly variable habitat. In support of this, a recent study suggested that intra-specific trait variability contributed to mediating the response of alpine grassland communities to an experimental drought event (Jung et al. 2014).

Intra-specific phenotypic variation has also been suggested to correlate positively with the species’ niche width, by increasing the range of micro-habitats and community types where the species can persist (Jung et al. 2010; Sides et al. 2014). For example, intra-specific variation in specific leaf area were found to often be associated with greater elevation ranges across 21 species of alpine plants (Sides et al. 2014). Our data on only two species and a limited range of microclimatic conditions precludes any direct test of this hypothesis, but we note that *Bistorta*, which exhibited a clearer trend towards greater trait variation at rough sites than *Luzula* (Figure 4), also occupied a wider realised niche at rough sites (Table 3).

Insights into biotic response to climate change

The observation that micro-climatically more diverse sites support a greater number of plant species does not directly imply that local reshuffling occur more readily in such terrains. However, this study demonstrated that an increased range of microhabitats were available at rough sites. These sites also contained a greater number of plant species, and there were often greater turnover of species across microhabitats (beta diversity) than at flatter sites. Many common species seems able to utilise this increased range of microhabitats available at rough sites. This can be achieved, for example, by being phenotypically plastic. Taken together, these features might allow species to persist locally under regional climate change, instead of migrating long distances to track climatic niches, and the possibility for such persistence would be greater in topographically complex terrain. While migration over long distances along elevation or latitude might be precluded by dispersal limitations, this is much less of an issue for local species reshuffling through short distance migration. Indeed, vegetation plots in the Rocky Mountains were found to transition back and forth among ‘community types’, assumingly in response to inter-annual variation in climate (Spasojevic et al. 2013). We follow these authors and others (Armbruster et al. 2007; Scherrer and Körner 2011; Lenoir et al. 2013) in suggesting that topographically complex terrain might have the potential to buffer alpine plant communities against the effects of climate change. If, in addition, topographic complexity selects for phenotypic plasticity and/or genetic differentiation, this can create communities that are diverse both within and among species (functional diversity). We further suggest that such multi-level diversity, if it exists, might increase the capacity of alpine plant communities to persist locally under environmental change.

Conclusions

Accumulating evidence suggests that rough alpine terrains create small-scale variation in microclimate. Our observations of the plant communities occurring at sites of differing topographic complexity supports the hypothesis that, in the event of climate change, the opportunity for local persistence of alpine plant species through migration into local micro-refugia might be greater in topographically more complex terrains. We encourage further studies comparing the phenotypic plasticity and genetic diversity of plant species growing in alpine terrains of contrasting topographic complexity.

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Table 1. Diversity and microclimate data recorded during the summer of 2012 within nine 40 m x 40 m sites in alpine tundra at Finse, Norway.

Site	Plot richness ± SE	Sample richness	Site richness	n	Temperature (°C)				Moisture (%)	
					Mean ± SE	Min	Max	Range	Mean ± SE	Range
1R	8.88 ± 0.89	33	57	10	9.49 ± 0.27	-1.0	47.5	2.6	25.81 ± 1.55	20.2
2F	8.13 ± 0.72	29	42	13	9.25 ± 0.19	0.5	37.5	2.5	28.67 ± 1.36	22.8
2R	9.13 ± 0.91	42	65	16	8.95 ± 0.31	0.0	44.5	3.9	29.33 ± 1.59	28.5
3F	4.00 ± 0.49	13	37	13	8.33 ± 0.18	0.5	36.0	2.4	32.99 ± 2.13	31.1
3R	6.31 ± 0.68	24	46	16	9.27 ± 0.16	-0.5	40.0	2.2	28.65 ± 2.75	37.2
4F	9.56 ± 0.63	32	46	15	9.58 ± 0.22	0.5	43.5	2.8	32.07 ± 209	33.7
4R	9.81 ± 0.78	34	53	13	9.63 ± 0.21	-1.5	41.5	2.4	29.96 ± 1.97	32.9
5F	14.63 ± 0.83	45	56	11	10.40 ± 0.18	-2.0	43.0	1.9	35.85 ± 2.74	49.2
5R	11.44 ± 0.89	42	66	15	9.65 ± 0.24	0.0	48.5	2.9	37.36 ± 3.86	71.7

Sites are annotated by the area number followed by a letter indicating rough (R) and flat (F) sites. Sample size (n) is the number of undisturbed temperature loggers within each site. Range is the difference between the highest and lowest mean value recorded within each site.

Table 2. P-values from permutation tests for homogeneity of multivariate dispersions. The overall test represents the null-hypothesis of homogeneity of multivariate dispersions, and the contrasts represents pair-wise comparisons.

	Microclimatic heterogeneity	Beta diversity
Overall	0.020	0.015
2F - 2R	0.004	0.013
3F - 3R	0.127	0.003
4F - 4R	0.516	0.348
5F - 5R	0.214	0.597

Table 3. Estimated realised niche width of plant species growing at flat and rough alpine sites at Finse, southern Norway..

Growth form	Species	Niche width (Abiotic)			Niche width (Biotic)		
		Flat	Rough	Difference	Flat	Rough	Difference
Dwarf shrub	*Empetrum nigrum*	1.29	2.45	1.16	0.654	0.657	0.003
Dwarf shrub	*Salix herbacea*	1.89	2.46	0.57	0.628	0.719	0.091
Dwarf shrub	*Vaccinium vitis-idaea*	1.5	2.22	0.72	0.603	0.624	0.021
Forb	*Antennaria dioica*	2.15	2.59	0.44	0.688	0.698	0.010
Forb	*Bartsia alpina*	1.61	1.41	-0.20	0.709	0.681	-0.028
Forb	*Bistorta vivipara*	2.28	2.78	0.50	0.696	0.721	0.025
Forb	*Hieracium* spp.	1.82	2.32	0.50	0.670	0.699	0.029
Forb	*Saussurea alpina*	1.87	2.54	0.67	0.672	0.678	0.006
Forb	*Thalictrum alpinum*	1.69	2.47	0.78	0.680	0.697	0.017
Cushion plant	*Silene acaulis*	1.95	1.81	-0.14	0.673	0.671	-0.002
Graminoid	*Anthoxantrum odoratum*	1.16	1.48	0.32	0.665	0.670	0.005
Graminoid	*Carex bigelowii*	1.92	2.63	0.71	0.630	0.689	0.059
Graminoid	*Festuca ovina*	1.57	2.75	1.18	0.653	0.679	0.026
Graminoid	*Juncus trifidus*	1.94	1.44	-0.50	0.649	0.658	0.009
Graminoid	*Luzula spicata*	2.02	1.25	-0.77	0.689	0.691	0.002
Spikemoss	*Selaginella selaginoides*	2.24	1.39	-0.85	0.672	0.678	0.006
	Mean	1.81	2.12	0.32	0.66	0.68	0.02
	P	0.098			0.005		

Niche width (Abiotic) is defined as the range of mean temperatures of plots in which the species occur, averaged across sites. Niche width (Biotic) is multi-site Simpson dissimilarity among plots in which the species occur. The last row gives p-values from Mann-Whitney U-tests between species values for flat and rough sites.

Figure 1. Map of the study sites used to investigate the relationships between small-scale topographic complexity, microclimatic heterogeneity and alpine plant communities at Finse, southern Norway. Sites are annotated by the area number followed by a letter indicating rough (R) or flat (F) sites. The lower right insert shows the design of each 40 m x 40 m study site, with 0.25 m^2 sample plots placed within the sites following a stratified random distribution. Equidistance is 20 m. Coordinates are on the UTM grid, in zone 32V.

Figure 2. Relationships between average Euclidian distance to centroid for standardised environmental data (± SE; 'Microclimatic heterogeneity') and cumulative sample richness (a) and total site richness (b), respectively, for nine 40 x 40 m sites of two topography classes (F, Flat; R, Rough). Regression lines are drawn from GLMs with Poisson-distributed errors

Figure 3. Relationship between average Jaccard dissimilarity for community data (± SE; 'beta diversity') and average Euclidian distance to centroid for standardised environmental data (± SE; 'Microclimatic heterogeneity') across 16 sample plots within each of nine 40 x 40 m sites of two topography classes (F, Flat; R, Rough)

Figure 4. Proportional trait variation (CV) in *Bistorta vivipara* and *Luzula spicata* within nine 40 m x 40 m sites of two topography classes (F, Flat; R, Rough). Error bars represent ± 1 SE. N =16 plants within each site.

Fig 1.

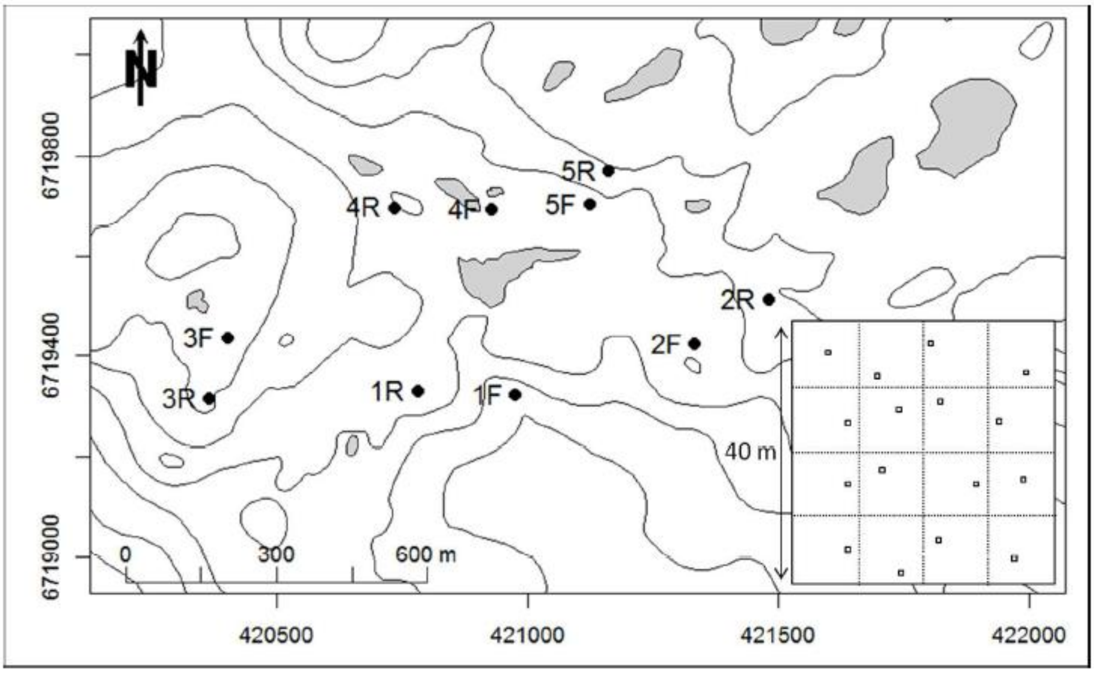

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Fig. 2.

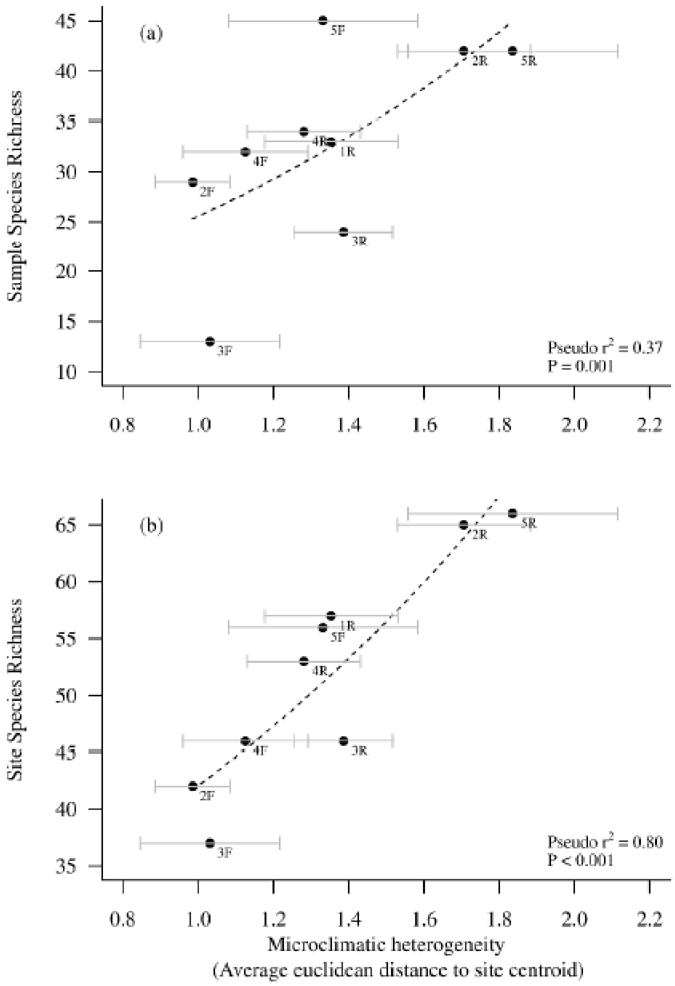

(a)
Sample Species Richness
45
40
35
30
25
20
15
10
5F
2R
5R
4R
1R
4F
2F
3R
3F
Pseudo $r^2 = 0.37$
P = 0.001
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
(b)
Site Species Richness
65
60
55
50
45
40
35
5R
2R
1R
5F
4R
4F
3R
2F
3F
Pseudo $r^2 = 0.80$
P < 0.001
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
Microclimatic heterogeneity
(Average euclidean distance to site centroid)

Fig. 3.

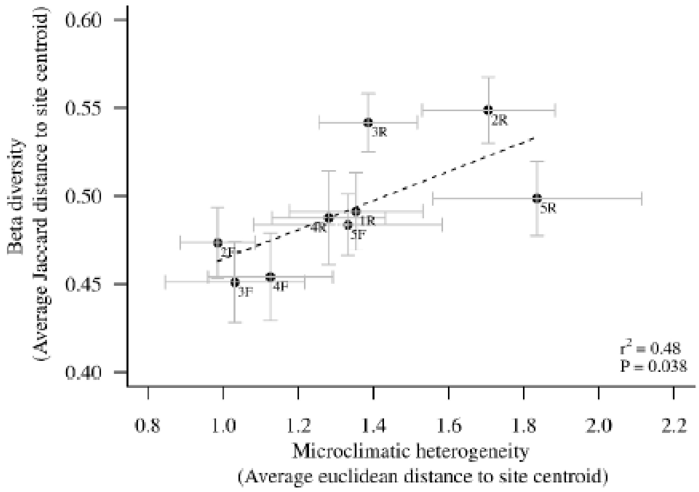
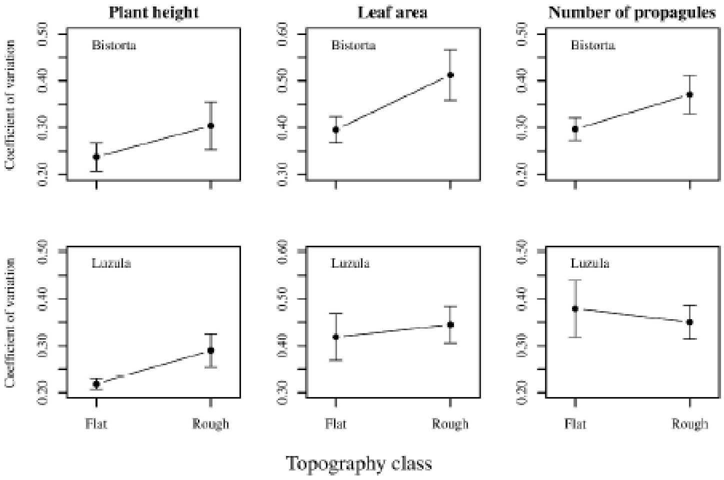

Beta diversity
(Average Jaccard distance to site centroid)
0.60
0.55
0.50
0.45
0.40
3R
2R
5R
4R
1R
5F
2F
3F
4F
r² = 0.48
P = 0.038
0.8
1.0
1.2
1.4
1.6
1.8
2.0
2.2
Microclimatic heterogeneity
(Average euclidean distance to site centroid)

Fig. 4.


Plant height
Leaf area
Number of propagules
Bistorta
Luzula
Coefficient of variation
0.20
0.30
0.40
0.50
0.60
Flat
Rough
Topography class