

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

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16

17 **Abstract**

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

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

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

27 **Results:** Sites differed significantly in microclimatic heterogeneity, and topographically
28 rough sites were always more heterogeneous than flatter ones. Greater species richness and
29 turnover was associated with greater microclimatic heterogeneity, and rough sites contained
30 15-55% more species than flatter ones. Plant species had on average wider realised niches
31 when growing at rough sites. Individuals of *Bistorta vivipara*, but not those of *Luzula spicata*,
32 tended to exhibit greater phenotypic variation at rough sites.

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

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

40 **Introduction**

41
42 Under a changing climate, plants and animals will often have to react to altered environmental
43 conditions. For sessile organisms such as plants, this can be achieved either through migration
44 of offspring to new suitable habitats (extending, contracting or displacing distributional
45 ranges), or by staying where they are and physiologically adjusting or, across generations,
46 genetically adapting to new conditions. The ability of plants to migrate in response to climate
47 change has received considerable attention (e.g. Walther et al. 2005a; Walther et al. 2005b;
48 Pearson 2006; Lenoir et al. 2008; Frei et al. 2010; Lenoir et al. 2010) and plant species have
49 been shown to shift their range northwards (Walther et al. 2005b), upslope (Walther et al.
50 2005a; Lenoir et al. 2008) and downslope (Lenoir et al. 2010). The opportunity for plant
51 populations to persist locally has, however, been less well studied. While some large-scale
52 models have predicted tremendous losses of habitat and many local extinctions (e.g. Thomas
53 et al. 2004; Thuiller et al. 2005; Dullinger et al. 2012; Gottfried et al. 2012), recent research
54 points towards an important role of microclimatic heterogeneity and local refugia (e.g. Luoto
55 and Heikkinen 2008; Randin et al. 2009; Scherrer and Körner 2011; Ashcroft et al. 2012;
56 Lenoir et al. 2013, see also Edwards & Armbruster 1989).

57 Alpine plants have traditionally been seen as highly specialised to harsh environmental
58 conditions (Körner 2003), and therefore particularly vulnerable to climate change (e.g.
59 Theurillat and Guisan 2001). However, alpine landscapes are often topographically very
60 complex, creating mosaics of diverse microclimates over short distances (Lloyd et al. 1994;
61 Rae et al. 2006; Armbruster et al. 2007; Scherrer and Körner 2011). Topographically complex
62 terrain should therefore contain a wide range of plant niches, and might be likely locations of
63 climatic micro-refugia (Ashcroft 2010; Dobrowski 2011). Importantly, small-scale thermal
64 variation has been shown to equal or exceed global climate warming predictions (Rae et al.
65 2006; Armbruster et al. 2007; Scherrer and Körner 2011; Graae et al. 2012; Lenoir et al.

66 2013). For predicting future changes to alpine plant communities, it is therefore important to
67 consider the local variation in the environments of the resident plants, in addition to the mean
68 values of the landscape (Armbruster et al. 2007). Complex alpine landscapes provide ideal
69 natural experiments for understanding how small-scale topographic complexity translates into
70 microclimatic heterogeneity, and how this, in turn, affects plant communities.

71 If plant communities occurring at topographically complex sites are subject to more
72 climatic variation than those occurring at flatter sites, it can be expected that rough terrains
73 generate greater variation both in species composition and in phenotypic traits within and
74 among species ('functional diversity'). The relationship between environmental heterogeneity
75 and plant species diversity has been extensively studied, and there is now abundant evidence
76 suggesting that an increase in habitat heterogeneity increases the number of coexisting species
77 (reviewed in Lundholm 2009). A second, and less appreciated, aspect of habitat heterogeneity
78 is that a greater number of unique micro-habitats within short distances might increase the
79 potential for local reshuffling of plant communities through short-distance migration of
80 resident species into local micro-refugia. When the environment varies at a small scale, it
81 gives plants the opportunity to find new suitable habitats only short distances away when the
82 climate changes, instead of moving long distances up mountain sides or towards the poles
83 (Armbruster et al. 2007; Ackerly et al. 2010; Scherrer and Körner 2011; Spasojevic et al.
84 2013). Recent results from a long-term study in the Rocky Mountains suggested that plant
85 communities in a heterogeneous alpine landscape were able to track fine-scale environmental
86 variation while being under the influence of directional climate change (Spasojevic et al.
87 2013). To further understand the generality of this process, it is interesting to know the extent
88 to which microclimatic heterogeneity differs among terrain types, combined with detailed
89 information about the diversity and distribution of plant species inhabiting them.

90 Although much historical evidence points toward migration and community assembly
91 processes (e.g. species sorting and reshuffling of local species) as leading forces in plant-
92 community responses to climate change, the potential roles of phenotypic plasticity and
93 adaptive evolution cannot be ignored (Davis and Shaw 2001; Ackerly 2003; Jump and
94 Penuelas 2005; Stoecklin et al. 2009; Chevin et al. 2010). To understand the role of these
95 processes in shaping plant communities, some studies have considered community-wide
96 patterns of functional trait diversity based on mean values for each species in a given
97 community or habitat (e.g. Onipchenko et al. 1998; Choler 2005; Spasojevic and Suding
98 2012; Spasojevic et al. 2013). Recently, however, attention has started to shift towards
99 quantifying patterns of intra-specific trait variation, which has been shown to account for a
100 large portion of community-wide trait diversity patterns (Albert et al. 2010; Jung et al. 2010;
101 de Bello et al. 2011; Albert et al. 2012; Violle et al. 2012; Boucher et al. 2013; Jung et al.
102 2014; Sides et al. 2014). Regardless of the process by which it arises (genetic differentiation
103 or phenotypic plasticity), intra-specific trait variation across a landscape might have
104 consequences for the ability of plants to respond to climate change. Despite the potential of
105 small-scale topographic complexity to drive microclimatic variation, there is still relatively
106 little information about the extent of within-species trait variation at small scales across sites
107 differing in topographic complexity (but see Albert et al. 2010; Boucher et al. 2013).

108 The hypothesis that small-scale topographic complexity will promote biotic resilience
109 to climate change by creating opportunities for reshuffling of local species in the landscape, as
110 well as potentially increasing adaptive and plastic capacities, depends on the link between
111 topography, microclimate and plant communities. Consequently, the aim of this study was to
112 investigate how small-scale topographic complexity translates into microclimatic
113 heterogeneity, and how alpine plant communities respond to variation in microclimate. To
114 achieve this, we measured the extent of variation in microclimate variables (temperature and

115 soil moisture) within paired sites differing in small-scale topographic complexity. After
116 testing if rough sites were more variable in microclimate than flatter sites, we investigated if
117 the estimated microclimatic heterogeneity of each site was associated with the diversity of
118 their local plant communities, and with within-species variation in phenotypic traits of two
119 target species. Specifically, we predicted that topographically rough sites would contain
120 greater microclimatic variation than flatter sites, and that sites with greater microclimatic
121 variation supported both more plant species, and species exhibiting greater phenotypic
122 variation. We also investigated whether plants growing at climatically more heterogeneous
123 sites were able to utilise the greater number of different micro-habitats available, by
124 estimating the realized niche widths of some common species in different terrain types.

125

126 **Materials and methods**

127 *Field site*

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

137 *Study design*

138 In July 2012 we subjectively chose five areas, and located in each one ‘rough’ and one ‘flat’
139 site. The site pairs were chosen so that the two sites were as similar as possible in macro-
140 exposure, altitude and vegetation type, and the intra-pair distance was less than the inter-pair
141 distance (i.e. between areas). In each area, we took care to select sites that differed in micro-
142 topography, although the flat site in one area might have been similar to the rough site in
143 another. All sites were mainly south-facing and snow-free in early July, a period when much
144 of the surrounding landscape was still snow-covered in the year of this study (2012). Hence,
145 we assumed that the length of the growing season was about the same for all sites, although
146 the date of snow-melt is probably more variable at the rough sites than at the flatter ones.
147 Each site measured 40 m x 40 m, was divided into 16 sub-sites (10 x 10 m), and within each
148 sub-site a 0.25 m² sample plot was placed, following a stratified random distribution (Figure
149 1).

150 In the south corner of each sample plot, we placed a temperature logger (iButtons,
151 Maxim Integrated Products, Sunnyvale, CA, US) wrapped in matte green duct tape at the soil
152 surface. Matte green tape was chosen in order to roughly approximate the reflective properties
153 of leaves near the soil surface. Although the recorded temperatures might differ from the
154 exact temperature of the plant canopy, we assumed that this approach would capture relevant
155 variation in topographically controlled temperature conditions experienced by the plants and
156 any deviation from canopy surface temperature would be consistent. The loggers were left in
157 the plots for three weeks (11 Jul – 2 Aug 2012), taking one temperature measurement per
158 hour. The resolution of the data is 0.5 °C, and includes mean, maximum and minimum
159 temperature for each logger. Due to disturbance of temperature loggers by sheep, all data
160 from the flat site in area 1 (1F) were excluded from the following analyses. Twelve additional
161 loggers were classified as disturbed (by for example wind, water or animals) and 10 loggers

162 were not found when returning to sites, leaving data from 122 loggers for the analyses. Apart
163 from the excluded site, grazing pressure and disturbance by animals appeared to be low and
164 similar across the study sites. We measured soil moisture with a hand-held moisture sensor
165 (TRIME-PICO, IMKO GmbH, Ettlingen) in all sample plots on a humid day following some
166 light drizzle in the morning.

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

175 *Vegetation sampling*

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

185 To investigate the extent of phenotypic variation of plants at the sites, the forb *Bistorta*
186 *vivipara* (L.) Delarbre (Polygonaceae) and the graminoid *Luzula spicata* (L.) DC. (Juncaceae)

187 were chosen as target species, based on their local abundance. For each sample plot, the
188 shoots of each species closest to the centre of the plot were chosen, although these were not
189 always within the sample plot. For these shoots we recorded the traits (1) plant height, (2)
190 length and width of the largest leaf and (3) propagule number (bulbils for *Bistorta* and
191 capsules for *Luzula*). Plant height was measured in the field using a metre stick. The plant was
192 then collected, stored in a plastic bag and transported to the laboratory. Leaf length and width
193 were measured later the same day using digital calipers, and multiplied to obtain a measure of
194 leaf area.

195 *Statistical analyses*

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

210 To investigate the relationship between microclimate and plot richness, we fitted a
211 mixed-effects Poisson regression model with species richness of the sample plots as the

212 dependent variable, and microclimate variables as possible explanatory variables. To account
213 for the structure of the data (sites nested within areas), site and area was entered as random
214 factors. At the among-site scale (using each site as an observation unit), we used regression
215 analysis to test for relationships between the previously derived measures of microclimatic
216 heterogeneity, beta diversity and species richness.

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

234 Relationships between microclimate variables and phenotypic traits were tested using
235 mixed-effect models, where site nested within area was entered as random factors and
236 microclimate variables as possible explanatory variables. We partitioned the variance in

237 phenotypic traits into between topography-class, among-site within topography-class and
238 within-site components by fitting mixed-effects models with site nested within topography-
239 class as random factors. To be able to compare the variation of traits when the means differed,
240 we calculated the coefficient of variation (CV) for each trait and site, to produce a
241 proportional measure of variation. We then used permutational multivariate analysis of
242 variance (PERMANOVA; Anderson 2001) to test for differences in CV values between flat
243 and rough sites. All statistical analyses were carried out in R, version 3.0.2 (R Core Team
244 2014), using the packages lme4 (Bates et al. 2014) and vegan (Oksanen et al. 2013).

245 **Results**

246 *Topography and microclimatic heterogeneity*

247 The overall mean temperature of all sample plots was 9.4 °C (SD = 0.96, range = 7.2 - 11.5
248 °C). Mean values (Table 1) did not differ significantly between flat and rough sites (ANOVA,
249 $P = 0.92$ for mean temperature and $P = 0.19$ for soil moisture). Within-site differences in
250 mean temperatures varied between 2 and 4 °C (Table 1). Microclimatic heterogeneity differed
251 significantly among sites ($P = 0.02$), and was consistently greater for rough sites than for
252 flatter sites in all four areas (significantly so only for area 2, Table 2).

253 *Topography and species diversity*

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

260 At the sample-plot scale, there was a positive relationship between logger mean
261 temperature and corresponding plot richness (*GLMM*, $P < 0.001$), and mean temperature was

262 strongly positively correlated with maximum temperature ($R = 0.75$, $P < 0.001$). The model
263 estimated the species richness of a sample plot with an average mean temperature (9.4 °C) to
264 8.75 species, while an increase in temperature of one standard deviation (0.96 °C) increased
265 the estimated species richness by 1.14 species. At the among-site level, there were significant
266 positive relationships between microclimatic heterogeneity and species richness both for
267 sample richness (Figure 2a) and site richness (Figure 2b). Considering the relationship
268 between microclimatic heterogeneity and beta diversity (Figure 3), flat sites clustered below
269 and to the left of rough sites, indicating on average less dispersion of sample plots both in
270 microclimatic space and in community space than for rough sites. Secondly, when considered
271 pair-wise, rough sites were in all cases located above and to the right of their paired flat sites,
272 hence they were more variable along both axes. Finally, there was a positive trend of
273 increasing beta diversity with increasing microclimatic heterogeneity.

274 *Realised niche width*

275 Most species were found in plots spanning a greater range of temperatures, and with a greater
276 diversity of co-existing species, at rough sites (Table 3). Hence, they displayed wider realised
277 niches, suggesting that these species were able to utilise the increased range of different
278 microhabitats, and co-existing species, found at rough sites. Mean and maximum
279 temperatures of the sample plots were strongly correlated, and the results for these two
280 variables were qualitatively similar. Therefore, only results for mean temperatures are shown
281 in Table 3. The abiotic and biotic measures of realised niche width yielded qualitatively
282 similar results, although there was somewhat more inter-specific variation for the abiotic
283 measure (Table 3). Interestingly, the two measures were significantly correlated ($R = 0.37$, P
284 $= 0.03$), suggesting that the biotic approach based on co-existence yield results that can be
285 interpreted in terms of microclimatic preferences.

286 *Phenotypic traits*

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

293 **Discussion**

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

304 *Effects of topographic complexity on microclimate*

305 Among sample plots within the 40 m x 40 m sites, mean temperatures recorded during three
306 weeks of the growing season differed by between 2 and 4 °C, comparable to global warming
307 scenarios for the next century (IPCC 2007), as well as to results from previous field and
308 modelling studies (Rae et al. 2006; Armbruster et al. 2007; Scherrer and Körner 2011; Graae
309 et al. 2012; Lenoir et al. 2013). Hence, there are microclimatic differences within 40 m x 40 m

310 sites similar to what is expected over an altitudinal range of between 350 and 700 m
311 (assuming a standard lapse rate of 5.5 K km^{-1} ; Körner 2007), or a latitudinal range of between
312 308 and 616 km (2.7 and 5.5 degrees, respectively, assuming a lapse rate of 0.73 K per degree
313 latitude; De Frenne et al. 2013). Our measure of microclimatic heterogeneity, which in
314 addition to variation in mean temperatures also incorporates variation in soil moisture and
315 extreme temperatures, also suggested greater overall variation in microclimate at rough sites.
316 These results illustrate the importance of local variation in microclimate, and lead one to be
317 cautious when interpreting large-scale models based on mean values (Armbruster et al. 2007;
318 Lenoir et al. 2013).

319

320 *Topography and plant communities*

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

332 Mean temperature emerged as a good predictor of plot species richness, with plot
333 richness increasing linearly with increasing mean temperature. In this relatively low-
334 productive environment, this probably reflects an increase in available energy as a result of an

335 increased radiation load (Virtanen et al. 2013). Across sites, microclimatic heterogeneity was
336 positively correlated both with species richness and species turnover (beta diversity). The
337 increase in beta diversity, which measures the dissimilarity among sample plots within a site,
338 further supports the idea that increased small-scale variation in microclimate positively affects
339 community diversity. The relative roles of available energy (mean supply of limiting
340 resources) and heterogeneity (variation in limiting resources) as drivers of species richness
341 has been debated (e.g. Stevens and Carson 2002; Lundholm 2009). Our measure of
342 microclimatic heterogeneity was in fact positively correlated with maximum temperatures
343 measured at the sites, and some caution should therefore be taken in interpreting their effects.

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

353 *Topography and trait variation*

354 Traits of alpine plant species has been shown to vary along topographic gradients (e.g. Kudo
355 et al. 2001; Albert et al. 2010; Boucher et al. 2013). In topographically complex terrains such
356 gradients can be expected to occur on a small scale, and we therefore expected to see
357 increased intra-specific trait variation at rough sites. We found that trait responses to
358 microclimate differed between species, and *Bistorta* appeared to respond more directly to
359 variation in the measured microclimatic variables than *Luzula* did (Table S1). Across sites, we

360 found no significant difference in overall trait variation between rough sites and less
361 heterogeneous, flatter sites for either species. For *Bistorta*, though, the trend was towards
362 greater trait variation at rough sites (Figure 4). Within-species trait variation across a
363 landscape might arise from heritable genetic differentiation ('ecotypic differentiation'), non-
364 heritable phenotypic plasticity, or some combination of the two. In rough alpine terrains we
365 may assume that the scale of environmental variation is small relative to typical dispersal
366 distances of many species, so that propagules will often develop in a micro-environment
367 different from that of its mother. In this case, genotype x environment-correlations are
368 unlikely to emerge, and phenotypic plasticity is assumed to be an adaptive response to
369 environmental variation (Alpert and Simms 2002). A complementary common-environment
370 study of plasticity in *Bistorta* originating from the same sites used in the present study
371 revealed significant plastic responses to variation in soil moisture for all traits measured.
372 However, we found no significant difference in the degree of plasticity between individuals
373 originating from rough and flat sites (Ø. H. Opedal et al., unpublished data). Therefore, it
374 seems that across the alpine landscape studied here, this species responds to microclimatic
375 heterogeneity, at least in part, through non-genetic phenotypic adjustment. As suggested by
376 Stoecklin et al. (2009), phenotypic plasticity may provide alpine plants with the flexibility
377 needed to persist in a highly variable habitat. In support of this, a recent study suggested that
378 intra-specific trait variability contributed to mediating the response of alpine grassland
379 communities to an experimental drought event (Jung et al. 2014).

380 Intra-specific phenotypic variation has also been suggested to correlate positively with
381 the species' niche width, by increasing the range of micro-habitats and community types
382 where the species can persist (Jung et al. 2010; Sides et al. 2014). For example, intra-specific
383 variation in specific leaf area were found to often be associated with greater elevation ranges
384 across 21 species of alpine plants (Sides et al. 2014). Our data on only two species and a

385 limited range of microclimatic conditions precludes any direct test of this hypothesis, but we
386 note that *Bistorta*, which exhibited a clearer trend towards greater trait variation at rough sites
387 than *Luzula* (Figure 4), also occupied a wider realised niche at rough sites (Table 3).

388 *Insights into biotic response to climate change*

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

410

411 Conclusions

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

419

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426

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437

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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 \pm SE	Sample richness	Site richness	n	Temperature ($^{\circ}$ C)				Moisture (%)	
					Mean \pm SE	Min	Max	Range	Mean \pm SE	Range
1R	8.88 \pm 0.89	33	57	10	9.49 \pm 0.27	-1.0	47.5	2.6	25.81 \pm 1.55	20.2
2F	8.13 \pm 0.72	29	42	13	9.25 \pm 0.19	0.5	37.5	2.5	28.67 \pm 1.36	22.8
2R	9.13 \pm 0.91	42	65	16	8.95 \pm 0.31	0.0	44.5	3.9	29.33 \pm 1.59	28.5
3F	4.00 \pm 0.49	13	37	13	8.33 \pm 0.18	0.5	36.0	2.4	32.99 \pm 2.13	31.1
3R	6.31 \pm 0.68	24	46	16	9.27 \pm 0.16	-0.5	40.0	2.2	28.65 \pm 2.75	37.2
4F	9.56 \pm 0.63	32	46	15	9.58 \pm 0.22	0.5	43.5	2.8	32.07 \pm 2.09	33.7
4R	9.81 \pm 0.78	34	53	13	9.63 \pm 0.21	-1.5	41.5	2.4	29.96 \pm 1.97	32.9
5F	14.63 \pm 0.83	45	56	11	10.40 \pm 0.18	-2.0	43.0	1.9	35.85 \pm 2.74	49.2
5R	11.44 \pm 0.89	42	66	15	9.65 \pm 0.24	0.0	48.5	2.9	37.36 \pm 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	<i>Empetrum nigrum</i>	1.29	2.45	1.16	0.654	0.657	0.003
Dwarf shrub	<i>Salix herbacea</i>	1.89	2.46	0.57	0.628	0.719	0.091
Dwarf shrub	<i>Vaccinium vitis-idaea</i>	1.5	2.22	0.72	0.603	0.624	0.021
Forb	<i>Antennaria dioica</i>	2.15	2.59	0.44	0.688	0.698	0.010
Forb	<i>Bartsia alpina</i>	1.61	1.41	-0.20	0.709	0.681	-0.028
Forb	<i>Bistorta vivipara</i>	2.28	2.78	0.50	0.696	0.721	0.025
Forb	<i>Hieracium</i> spp.	1.82	2.32	0.50	0.670	0.699	0.029
Forb	<i>Saussurea alpina</i>	1.87	2.54	0.67	0.672	0.678	0.006
Forb	<i>Thalictrum alpinum</i>	1.69	2.47	0.78	0.680	0.697	0.017
Cushion plant	<i>Silene acaulis</i>	1.95	1.81	-0.14	0.673	0.671	-0.002
Graminoid	<i>Anthoxantrum odoratum</i>	1.16	1.48	0.32	0.665	0.670	0.005
Graminoid	<i>Carex bigelowii</i>	1.92	2.63	0.71	0.630	0.689	0.059
Graminoid	<i>Festuca ovina</i>	1.57	2.75	1.18	0.653	0.679	0.026
Graminoid	<i>Juncus trifidus</i>	1.94	1.44	-0.50	0.649	0.658	0.009
Graminoid	<i>Luzula spicata</i>	2.02	1.25	-0.77	0.689	0.691	0.002
Spikemoss	<i>Selaginella selaginoides</i>	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
	<i>P</i>		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.

621 Figure 1. Map of the study sites used to investigate the relationships between small-scale topographic
622 complexity, microclimatic heterogeneity and alpine plant communities at Finse, southern Norway.
623 Sites are annotated by the area number followed by a letter indicating rough (R) or flat (F) sites. The
624 lower right insert shows the design of each 40 m x 40 m study site, with 0.25 m² sample plots placed
625 within the sites following a stratified random distribution. Equidistance is 20 m. Coordinates are on
626 the UTM grid, in zone 32V.

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

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

635 Figure 4. Proportional trait variation (CV) in *Bistorta vivipara* and *Luzula spicata* within nine 40 m x
636 40 m sites of two topography classes (F, Flat; R, Rough). Error bars represent \pm 1 SE. N =16 plants
637 within each site.

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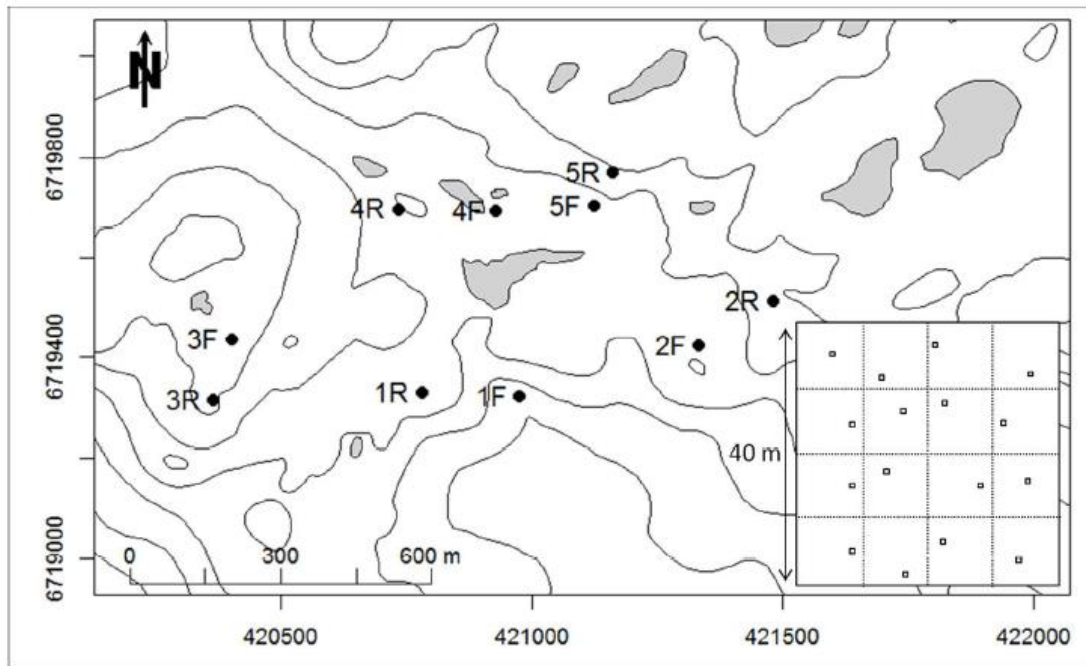
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647 Fig 1.

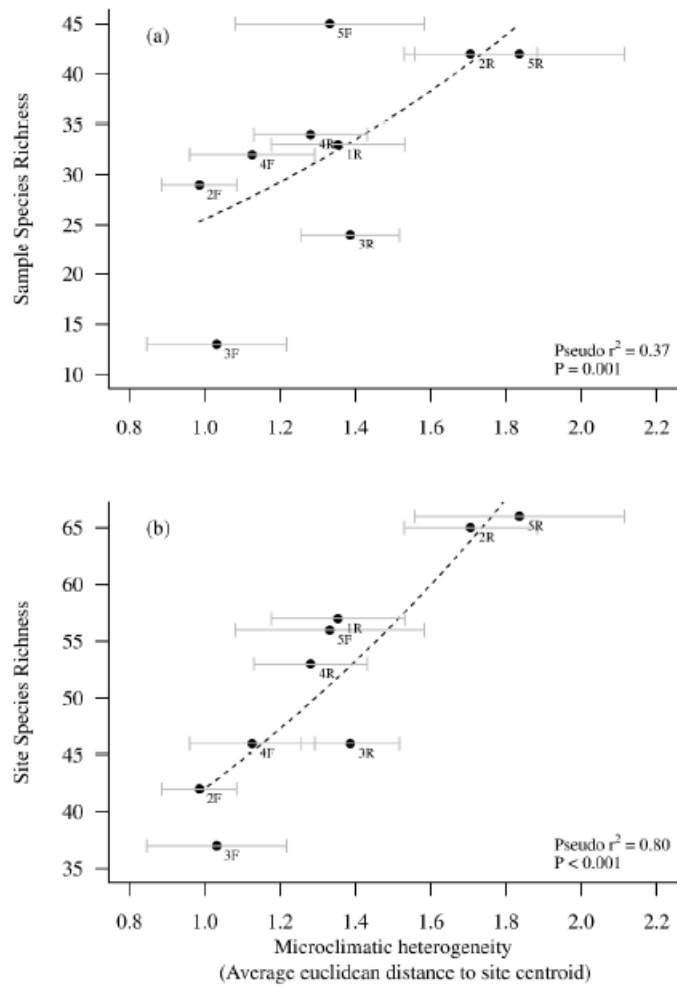


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650 Fig. 2.

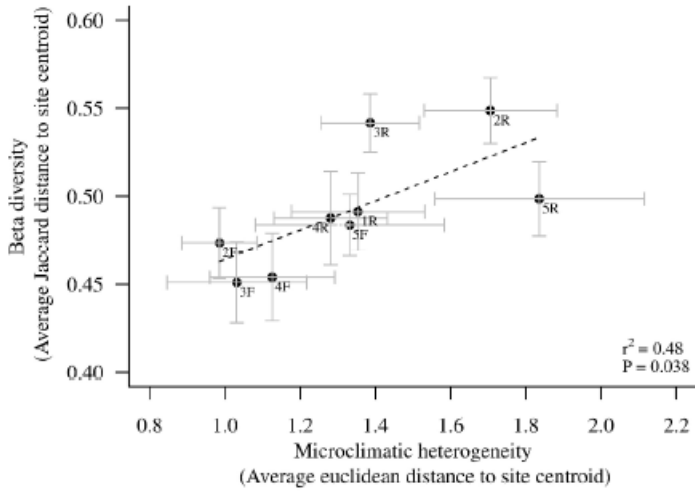


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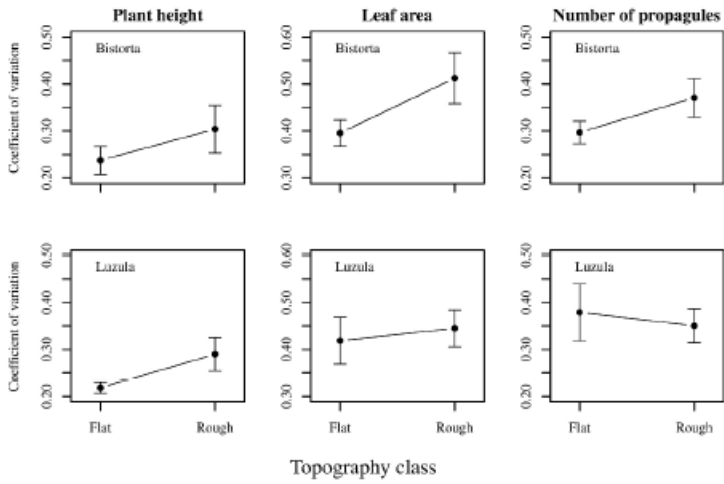
654 Fig. 3.



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657 Fig. 4.



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