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Topographic complexity and biotic resilience to climate change

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I bredegrus, i aur og stein
du stod so lysande og skein.
Ei dronning der i is og snjo
med drivkvit krune, glans og glo.

Olav H. Hauge

CONTENTS

ABSTRACT

Topographically complex alpine terrains create a mosaic of diverse microclimates over short distances. This study investigated the extent of small-scale variation in temperature and soil moisture using dense arrays of temperature loggers and moisture measurements, and how this microclimatic variation influenced vascular-plant species richness and intra-specific trait variation across five pairs of 40x40 m landscape plots of contrasting complexity in alpine tundra at Finse, Norway. Spatial variation in mean temperature within landscape plots was in the range of 2-4 °C, similar to what is expected across large altitudinal or latitudinal distances, suggesting an important "buffering capacity" of such landscapes in the event of climate warming. Rough landscapes contained more species than flatter ones, while patterns of within-species phenotypic variation were less clear and differed between species. These results suggest that local reshuffling and short-distance migration will be important biotic responses to climate change in this system, with assumed associated changes in biotic interactions and ecosystem function. The study also highlights the importance of mountains as target areas for biodiversity conservation.

Keywords: Alpine plants, *Bistorta vivipara*, Climate change, *Luzula spicata*, Microclimatic heterogeneity, Phenotypic plasticity, Soil moisture, Species richness, Temperature, Topographic complexity

SAMANDRAG

Topografisk komplekse alpine terreng skaper ein mosaikk av ulike mikroklima over korte distansar. Dette studiet undersøkte omfanget av variasjon i temperatur og jordvæte, og korleis slik mikroklimatisk variasjon påverkar artsrikdom og fenotypisk variasjon hos planter innanfor fem par 40x40 m store felt med varierande kompleksitet i alpint terreng ved Finse, Noreg. Temperaturvariasjon innanfor felta var i området 2-4 °C, som tilsvarar det ein ventar over store avstandar i høgdemeter eller breiddegrad, og indikerer ei "bufferevne" for slikt terreng mot global oppvarming. Komplekse landskap inneheldt fleire artar, medan mønster av fenotypisk variasjon var mindre klare. Dette tyder på at lokal omvelting og migrasjon over korte distansar vil vere viktige biotiske responsar til klimaendringar i dette systemet, med venta endringar i biotiske interaksjonar og økosystemfunksjon knytt til dette. Studiet kastar også lys på viktigheita av fjellterreng som målområde for bevaring av biodiversitet.

INTRODUCTION

With changing climate, plant species have to cope with new conditions for life. They can either migrate to new suitable habitats by shifting their ranges, or stay where they are and physiologically adjust or genetically adapt to new conditions. The ability of plants to migrate in response to climate change has received considerable attention (e.g. Walther et al. 2005a, b; Pearson 2006, Lenoir et al. 2008; 2010, Frei 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 plastic and adaptive capacities of plant populations under the same scenarios are, however, much less well studied. While some large-scale species distribution models of plant persistence under climate change have predicted tremendous losses of habitat and many local extinctions (e.g. Bakkenes et al. 2002; Thomas et al. 2004; Thuiller et al. 2005; Gottfried et al. 2012), recent developments point towards an important role of local refugia (e.g. Edwards & Armbruster 1989; Luoto & Heikkinen 2008; Randin et al. 2009; Willis & Bhagwat 2009; Scherrer & Körner 2011; Ashcroft et al. 2012; Lenoir et al. 2013).

Alpine plants have traditionally been seen as highly specialized to harsh environmental conditions (Körner 2003), and therefore especially vulnerable to climate change (e.g. Theurillat & Guisan 2001). It is important to remember, however, that mountains are usually topographically very complex, creating mosaics of diverse microclimates (e.g. surface temperature and soil moisture) over short distances (Armbruster et al. 2007; Scherrer & Körner 2011). Topographically complex landscapes will therefore make room for a wider range of plant niches, and might be likely locations of climatic microrefugia (Ashcroft 2010; Dobrowski 2011). Recent studies using both microloggers and thermal imagery (Scherrer & Körner 2010, 2011; Scherrer et al. 2011) confirm that topographic variation together with atmospheric decoupling of alpine vegetation creates a diverse set of life conditions in such landscapes, giving plants the opportunity to find a new suitable habitat just a short distance away, instead of moving long distances up mountain sides or towards the poles (Armbruster et al. 2007; Ackerly et al. 2010; Scherrer & Körner 2011). Small-scale thermal variation has also been shown to equal or exceed global climate warming predictions (Rae et al. 2006; Scherrer & Körner 2011; Graae et al. 2012, Lenoir et al.

2013). If we are to predict future changes to alpine plant communities, it is therefore important to consider the local variation in the environments of the resident plants, not only the mean values of the landscape (Armbruster et al. 2007). Complex landscapes provide good natural experiments to study this variation.

Local topographic variation implies that plant communities are subjected to more climatic variation than those in a more homogeneous environment (Körner 2003). It can therefore be assumed that such rough landscapes generate higher variation both in species composition and within-species phenotypic traits. The relationship between environmental heterogeneity and plant species diversity has been studied for a wide range of environments and measures of heterogeneity, including topography. Lundholm (2009) reviewed studies on this topic up to 2007, and found that 34 out of 41 observational studies that measured some aspect of heterogeneity and the corresponding species richness found a positive relationship between environmental heterogeneity and species diversity. The same pattern has also been found in experimental studies including manipulation of micro-topography (e.g. Vivian-Smith 1997).

One interesting question is whether migration or local adaptation will dominate as the biotic response to a warming climate. Although much historical (including palaeoecological) evidence point towards migration and community assembly processes being most important, the potential for adaptive evolution cannot be overlooked (Ackerly 2003). Phenotypic trait variation across a landscape, for example within-species variation in plant height, leaf area or propagule number, should reflect responses to local differences in life conditions, maximizing the fitness of an individual in a particular environment (Ackerly 2003). Rough landscapes can in this way be seen as producing a "geographic selection mosaic", with different phenotypes of a given species being favoured at different, yet nearby places (Thompson 2005).

It must be noted that phenotypic variation across a landscape might arise from non-heritable phenotypic plasticity or heritable genetic differentiation ("ecotypic differentiation", Turesson 1925), or some combination of the two. In landscapes where the scale of environmental variation is small relative to typical dispersal distances of its plant species, adaptive phenotypic plasticity is expected (Alpert & Simms 2002; Sultan & Spencer 2002;

Baythavong 2011). Also on a somewhat larger scale, plasticity is expected to be adaptive as long as some gene flow occurs between sub-populations (Sultan & Spencer 2002). Armbruster and co-workers (2007) suggest that with high microclimatic heterogeneity, small changes in species composition would indicate local adaptation as an important factor, while large changes would indicate local replacement of species. Before an attempt can be made to disentangle the possible causes of phenotypic variation, however, the extent of phenotypic variation across landscapes of contrasting topographic complexity must first be established.

The aim of this study is to investigate if plant communities are more diverse and plant phenotypes are more variable within species in topographically heterogeneous mountain landscapes than in more homogeneous ones, and how this variation is related to microclimatic variation. Both patterns would then point in the direction of higher adaptive capacity in mountainous areas, thereby improving the resilience of such communities to climate change. If this is true, it will be important knowledge for both basic climate change research, and not least for future conservation efforts. Specifically, it is predicted that rough landscapes (1) show higher microclimatic variation (temperature and moisture), (2) contain more plant species and (3) contain plants that show higher within-species phenotypic variation in selected traits than flatter landscapes.

METHODS

Field site

The study was conducted at a site near Finse at the Hardangervidda plateau in alpine southern Norway (N 60° 36.23', E 7° 33.40'). The site is situated in the low to middle alpine zone (centre around 1430 meters above sea level), well above the climatic treeline at about 1000 m.a.s.l. at Finse (Dahl 1986). The total area of the site encompassing the plots is about 3×10^5 m^2. 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 normal period 1961-1990 (Norwegian Meteorological Institute 2012).

Study design

In July 2012 five landscape pairs, each consisting of one "rough" and one "flat" landscape, were subjectively placed in the terrain at the site. The landscape pairs were chosen so that the two landscapes were as similar as possible in macro-exposure, altitude and general community type, and the intra-pair distance was lower than the inter-pair distance (Fig. 1). The landscapes were all early melt-off sites (snow-free in early July), and mostly south-facing. Each landscape plot measured 40x40 m, was parted into 16 quadrants and within each quadrant a 0.25 m^2 sample plot was placed, following a stratified random distribution (Fig. 1).
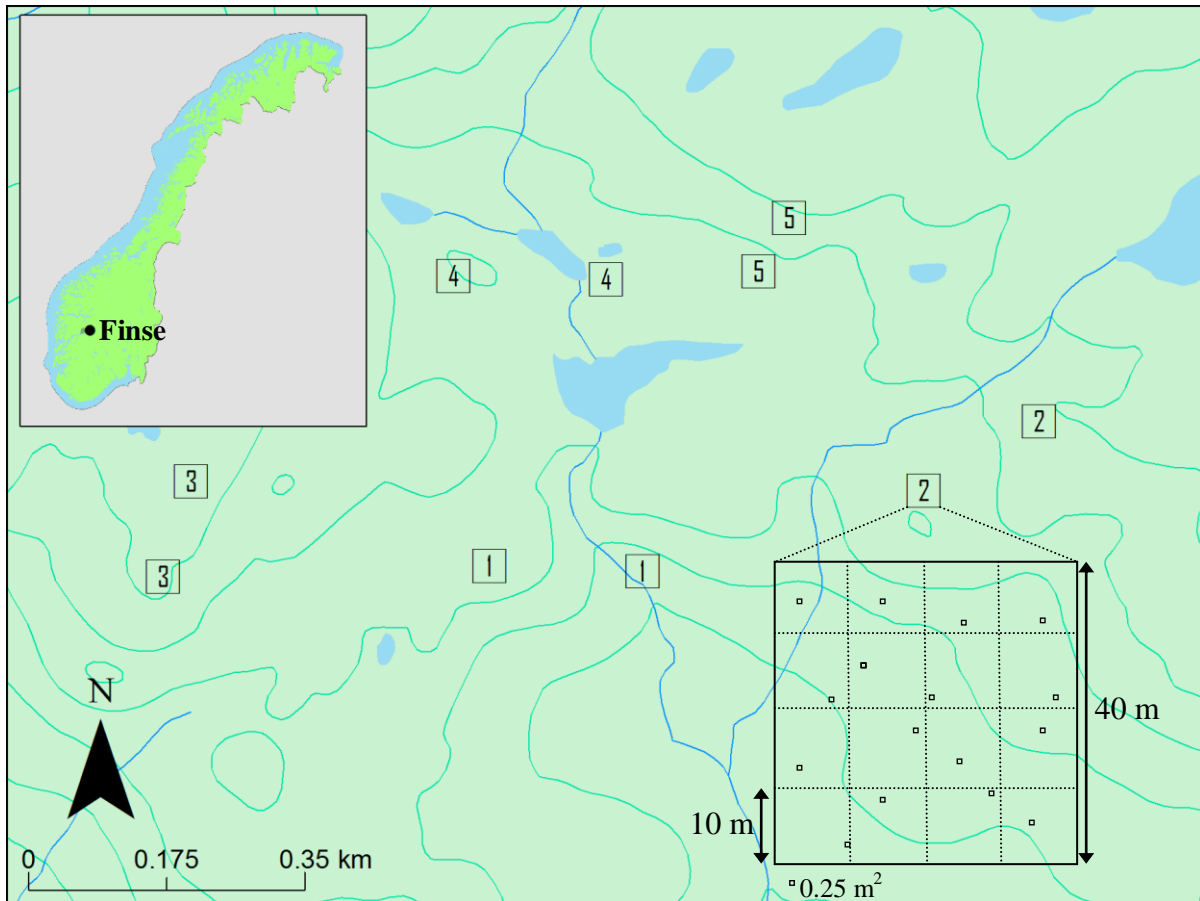
Fig. 1. Map of the study site at Finse. Each square shows the position of a landscape plot at the site, with numbers inside squares denoting the landscape pair number. The upper left insert shows the location of Finse, and the lower right insert shows the sampling design for one landscape plot, with sample plots placed within landscape plots following a stratified random distribution.

In the south corner of each sample plot, a temperature logger (iButtons, Maxim Integrated Products, Sunnyvale, CA, USA) wrapped in matte green duct tape (http://www.greenducttape.com) was placed at the soil surface. The loggers were left in the plots for three weeks (11th of July to 2nd of August), taking one temperature measurement per hour for a total of 505 measurements per logger. The resolution of the data is 0.5 °C, and includes mean, maximum and minimum temperature for each logger. For each landscape, spatial temperature range (ΔTmean) is defined as the difference between the on average warmest and coldest sample mean (i.e. logger mean) within each landscape. All temperature data are given in degrees Celsius (°C).

Soil moisture was measured in all sample plots on the 10th of August, a humid day following some light drizzle in the morning. Moisture was measured using a soil moisture sensor (TRIME-PICO, IMKO GmbH, Ettlingen, Germany). Moisture data are treated the same way as temperature, and given as moisture percent in the soil.

Field data

Field sampling was carried out between the 1st and 10th of August 2012. For each sample plot, all vascular plant species were recorded. A supplementary species list for each landscape was also compiled, by noting any additional species observed within each of the 16 10x10 m quadrants of each landscape. Species richness of the landscapes was calculated at two different scales, namely for sample plots (cumulative species richness of the sample plots, "sample richness") and for the entire landscape (based on supplementary species lists, "landscape richness"). Nomenclature for vascular plants follows Elven (2005).

To investigate the phenotypic variation of plants in the landscapes, the forb *Bistorta vivipara* (L.) Delarbre (Polygonaceae) and the graminoid *Luzula spicata* (L.) DC. (Juncaceae) were chosen as target species based on local abundance. For these species the traits (1) plant height, (2) length and width of the longest leaf and (3) propagule number (bulbils for *Bistorta* and capsules for *Luzula)* were recorded. For each sample plot, the shoot of each species closest to the center of the plot were chosen, but not necessarily within the sample plot. Plant height was measured in the field using a meter stick. The plant was then collected, stored in a plastic bag and taken back to the lab. Leaf length and width was measured using a digital caliper, and leaf length x leaf width was calculated as a measure of leaf area.

STATISTICAL ANALYSES

Paired comparisons between landscape types were done using paired t-tests. Due to the relatively low number of comparisons, however, p-values from these tests should be interpreted with care, and focus should be on effect sizes and biological significance (Yoccoz 1991).

Diversity

The relationship between microclimatic variables and species richness was modeled both within (at sample plot level) and between (at landscape plot level) landscapes. At the within-landscape level, a mixed-effects Poisson regression model (Generalized Linear Mixed-Effects Model with Poisson distributed errors, package lme4 [Bates et al. 2012]) was fitted with species richness of the sample plots as the dependent variable, and microclimatic variables as possible explanatory variables (Table 1). To account for the structure of the data (landscapes nested within landscape pairs), landscape and landscape pair was entered as random factors. Model simplification was done by stepwise removal of non-significant terms until the minimum adequate model was reached (Crawley 2007).

Table 1. Microclimatic variables measured within 40x40 m landscape plots and fitted as possible explanatory variables in statistical models of trait responses and species richness within and between landscapes. sp = sample plot

Variable		Description
Within landscapes (sample plot level)		
Mean temperature	T(sp)	Logger mean temperature
Min temperature	Tmin(sp)	Logger minimum temperature
Max temperature	Tmax(sp)	Logger maximum temperature
Moisture	M(sp)	Moisture sensor measurement
Between landscapes (landscape level)		
Mean temperature	T	Mean of logger means within each landscape
Min temperate	Tmin	Lowest logger minimum within each landscape
Max temperature	Tmax	Highest logger maximum within each landscape
Temperature range	ΔTmean	Difference between highest and lowest logger mean
Mean T variance	var (T)	Variance of logger means within each landscape
Max T variance	var (Tmax)	Variance of logger maxima within each landscape
Moisture	M	Mean of moisture measurements within each landscape
Moisture range	ΔM	Difference between wettest and driest sample
Moisture variance	var (M)	Variance of moisture measurements within each landscape

At the between-landscape level similar models were fitted, but with different microclimatic variables (Table 1). Separate models were fitted for total landscape richness and sample richness. The effect of landscape pair was considered and found to have no significant effect at this level, and was therefore not included in the final models. Model comparison were based on AICc, the finite-sample corrected Akaike Information Criterion, due to low sample size (n=9) at this scale (Burnham & Anderson 2002).

To investigate correlations between explanatory variables, path analyses (Shipley 2000; see Lloyd et al. 1994; Rae et al. 2006 for some applications to ecological data) were conducted with variables chosen from the models above. All explanatory variables were standardized to unit variance (SD=1), to be able to compare effects. In contrast to traditional path analysis/structural equation modeling, non-linear relationships between variables and non-normal errors were allowed. Hence, the response variable (SR, which is a count) was not standardized, as this allowed fitting Poisson models as above.

Phenotypic traits

To be able to compare the variation of traits when the means differed, two approaches were taken. For each trait/landscape the coefficient of variation (CV, $SD(X)/\bar{x}$) was calculated, to produce a relative measure of variation. To test for significant differences in variance, trait data were log-transformed before applying Fishers F-Test of homogeneity of variances.

Relationships between microclimatic parameters and traits were tested using linear mixed-effects models (package nlme [Pinheiro et al. 2012]), where landscape nested within pair was entered as random effects, and microclimatic variables (Table 1) were entered as possible explanatory variables. Model simplifications were done as for models of species richness.

All statistical analyses were performed in the statistical software R, version 2.15.2 (R Core Team 2013).

RESULTS

Due to heavy disturbance caused by sheep, through trampling, breaking marking sticks and moving temperature loggers, all data from the flat landscape belonging to the first pair (F1) are excluded from all analyses. The following results are therefore based upon the four remaining landscape pairs, while the data from the rough landscape from the first pair are included in statistical models.

Microclimatic variation

In addition to the disturbed loggers in the excluded flat landscape, 12 other loggers were classified as disturbed and 10 loggers were not found when returning to the field site, leaving data from 122 loggers for the following analyses (Table 2).

The overall mean temperature of the study site was 9.37 °C (SD=0.96, range=7.17-11.54 °C). The spatial range of the two microclimatic parameters was higher in the rough landscape in most cases (Fig. 2), though not statistically significant (*Paired T-test, P=0.24* for temperature range and *P=0.18* for moisture range). The pattern of within-pair contrasts was quite similar for the two variables (Fig. 2), indicating similar responses to roughness.

Additional microclimatic data are given in table 2. Variation in temperature and moisture was generally higher in the rough landscapes than in the corresponding flat ones, while mean values were more similar across landscapes. Maximum temperatures also tended to be higher in rough landscapes.
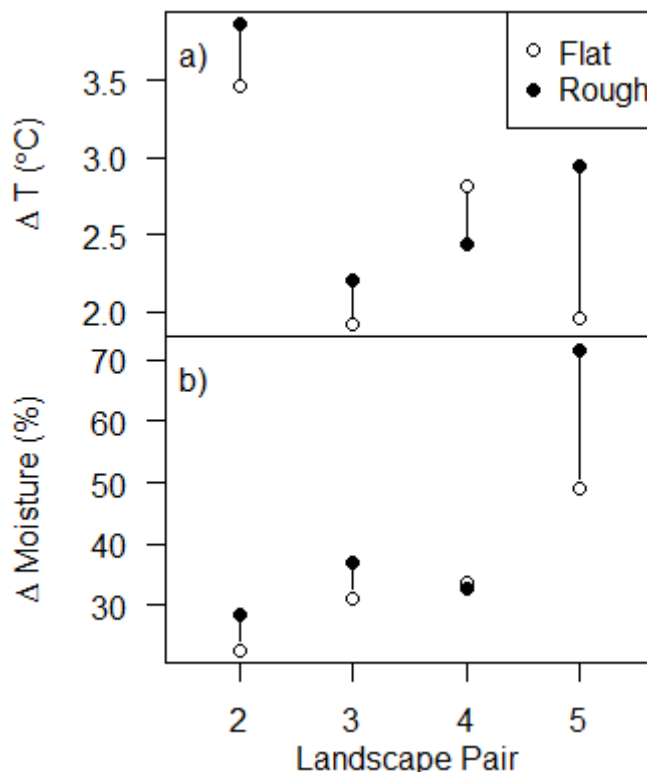

Fig. 2. Spatial range of (a) mean temperature and (b) soil moisture within four flat and four rough landscapes. Spatial range is defined as the difference between the on average highest and on average lowest sample mean of the microclimatic parameters within each landscape.

Table 2. Microclimatic data from four flat (F) and four rough (R) 40x40 m landscape plots at Finse. Sample size (n) is the number of undisturbed temperature loggers in each landscape. The bottom row contains p-values from paired t-tests between flat and rough landscapes.

Landscape	n	Temperature					Soil moisture	
		Mean (°C)	Min (°C)	Max (°C)	Var (mean)	Var (max)	Mean (%)	Var
2F	13	9.25	0.50	37.50	0.48	18.35	28.67	29.64
2R	16	8.95	0.50	44.50	1.53	64.07	29.33	40.57
3F	13	8.33	-0.50	36.00	0.42	23.32	32.99	72.65
3R	16	9.27	0.50	40.00	0.43	24.63	28.65	121.34
4F	15	9.58	-1.50	43.50	0.71	30.67	32.45	42.65
4R	13	9.64	0.50	41.50	0.56	38.90	29.96	62.21
5F	11	10.40	0.00	43.00	0.36	22.70	35.79	119.80
5R	15	9.65	-2.00	48.50	0.83	50.78	37.36	238.72
F vs R		0.97	0.79	0.16	0.29	0.13	0.46	0.14

Species diversity

A total of 85 species of vascular plants were found in the landscapes (see Appendix A for a full species list). The different landscape pairs differed in general richness and species composition. Overall, the expected higher landscape richness of the rough landscapes compared to the flat ones was confirmed in all pairs (Fig. 3a), with the rough landscapes containing 15-55% more species than the paired flat landscape. This difference was also statistically significant (*Paired T-test, P=0.04*).

For sample richness, the pattern was less clear (Fig. 3b). In pair 2 and 3 the species richness was clearly higher in the rough landscapes, while there were small differences in pair 4 and 5, leading to a non-significant overall difference (*Paired T-test, P=0.22*).
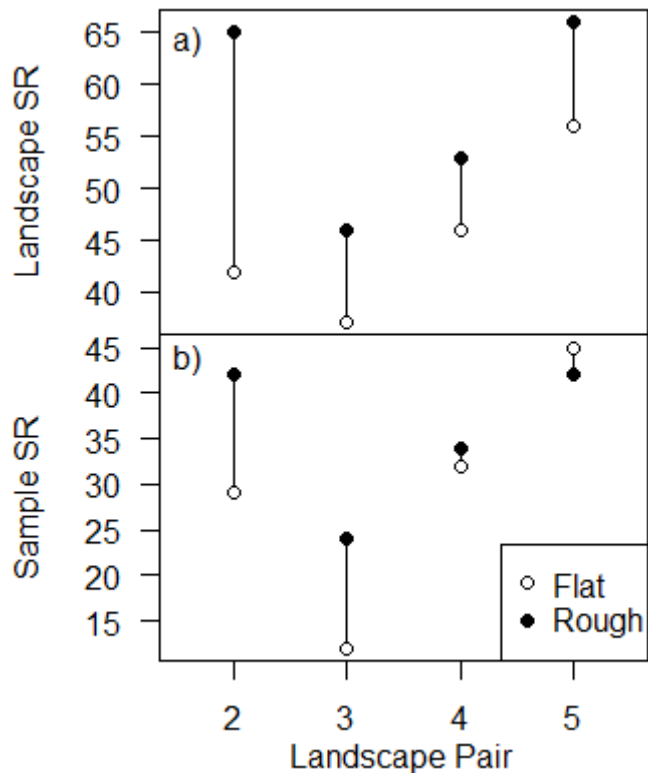

Fig. 3. Vascular-plant species richness at (a) total landscape scale and (b) cumulative sample richness for four rough and four flat 40x40 m landscape plots.
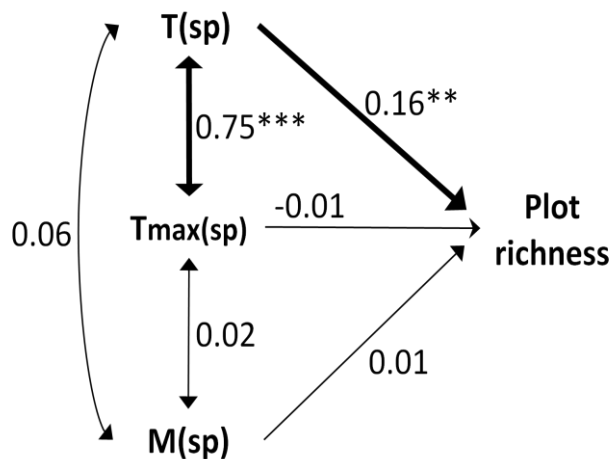
Fig. 4. Path diagram showing estimated direct (single-headed arrows) and indirect effects of microclimatic variables on vascular-plant species richness of 0.25 m² sample plots (n=122) within nine landscapes. Correlations between variables are shown as double-headed arrows. Microclimatic variables are standardized to SD=1. Path coefficients are estimated from a GLMM with Poisson-distributed errors and with landscape and landscape pair entered as random effects. ***P<0.001, **P<0.01

Within landscapes, there was a significant positive direct effect of logger mean temperature on the corresponding sample plot richness (*GLMM, P<0.01,* Fig. 4). Maximum temperature had a strong indirect effect, through its correlation with mean temperature.

At the between-landscape level, for sample richness, the minimum adequate model (*GLM, Pseudo r²=0.95, AICc=56.77*) included mean temperature (*P<0.001*) and spatial temperature range (*P<0.001*). Alternative models considered had AICc values more than 2 units higher than the highest ranked model (Appendix B; Table B1). Path analysis (Fig. 5a) indicated an indirect effect of maximum temperature, through positive correlations with mean temperature and temperature range.

For total landscape richness, the minimum adequate model (*GLM, Pseudo r²=0.93, AICc=61.12*), included positive effects of both mean temperature of the landscape (*P=0.044*) and variance in logger maxima within the landscape (*P<0.001*). Another candidate model, containing only absolute maximum temperature within landscapes (*GLM, Pseudo r²=0.76, P<0.001, AICc=60.37*), however, had a slightly lower AICc value (ΔAICc=0.75). Alternative models had more than 2 units higher AICc than the highest ranked model (Appendix B; Table B2). Hence, neither of these two models could be excluded. Path analysis (Fig. 5b) revealed that spatial variance in maximum temperature had the strongest positive direct effect on landscape richness. Again, the effect of maximum temperature appeared to be indirect, through its strong correlation with its variance.
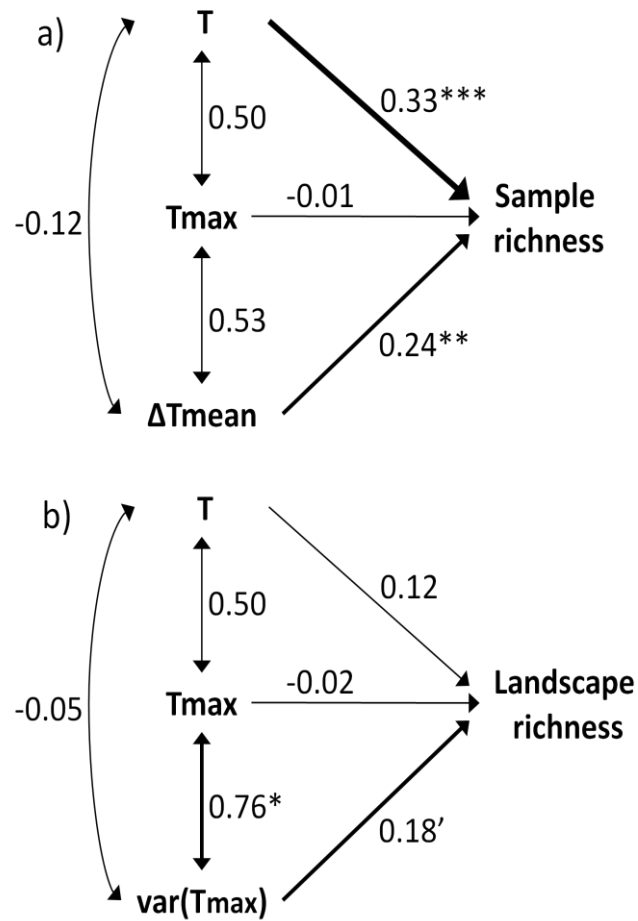
Fig. 5. Path diagrams showing estimated direct (single-headed arrows) and indirect effects of microclimatic variables on (a) cumulative sample richness and (b) total landscape richness of 40x40 m landscape plots (n=9). Correlations between variables are shown as double-headed arrows. Microclimatic variables are standardized to SD=1. Path coefficients are estimated from a GLM with Poisson-distributed errors. ***P<0.001, **P<0.01, *P<0.05, 'P<0.1

Intraspecific trait variation

Results from linear mixed-effects models of trait responses to microclimatic variables within landscapes are reported in table 3. While all three traits measured on *Bistorta* responded significantly to microclimatic variation, only plant height did so for *Luzula*.

Coefficients of variation for *Bistorta* and *Luzula* are presented in tables 4 and 5, respectively. For *Bistorta* there was higher relative variation in plant height in the rough landscape in three out of four landscape pairs, while relative variation in leaf area and bulbil number was higher in the rough landscapes in all four pairs. The differences were statistically significant only for plant height and leaf area in the third pair (Table 4). Relative variation in *Luzula* plant height and leaf area was highest in the rough landscape in three out of four pairs, and significantly so for height in the second pair. For propagule number there did not seem to be any consistent difference between the landscape types (Table 5).

A meta-analysis across traits and landscape pairs revealed that relative variation was overall higher in the rough landscapes for *Bistorta* (*Mann-Whitney U-Test, P=0.009*), but not for *Luzula* (*Mann-Whitney U-Test, P=0.31*).

Table 3. Results from linear mixed-effects models of trait responses to microclimatic variables. All models are fitted with landscape nested within landscape pair as random factors. The minimum adequate model is presented for each species/trait.

Species	Trait	Best model					
		Variable	Estimate ± SE	DF	t-value	P-value	
Bistorta vivipara	Height (mm)	Intercept	107.33 ± 25.72	110	4.17	<0.001	***
		T(sp)	-9.93 ± 3.92	110	-2.54	0.013	*
		Tmin(sp)	6.07 ± 2.65	110	2.29	0.023	*
		Tmax(sp)	1.92 ± 0.57	110	3.37	0.001	**
	Leaf area (mm^2)	Intercept	586.53 ± 135.76	107	4.28	<0.001	***
		T(sp)	-34.78 ± 13.92	107	-2.50	0.014	*
		Tmin(sp)	24.61 ± 12.99	107	1.89	0.061	'
	# Bulbils	Intercept	23.09 ± 3.00	132	7.70	<0.001	***
		M(sp)	0.15 ± 0.09	132	1.78	0.077	'
Luzula spicata	Height (mm)	Intercept	88.22 ± 17.76	112	4.97	<0.001	***
		Tmax(sp)	1.26 ± 0.51	112	2.48	0.014	*
	Leaf area (mm$^{2)}$)	Intercept	65.99 ± 3.31	135	19.96	<0.001	***
	# Capsules	Intercept	22.72 ± 1.16	135	19.56	<0.001	***

***P<0.001, **P<0.01, *P<0.05, 'P<0.1

Table 4. Coefficient of variation (CV) values for traits of *Bistorta vivipara* from eight landscapes. F-Tests were performed on variances of log-transformed data.

Pair	Trait	Flat		Rough	$F_{15,15}$	F-test P
	Height	0.19	<	0.27	0.56	0.27
2	Leaf area	0.37	<	0.45	0.56	0.27
	# Bulbils	0.36	<	0.38	0.77	0.63
	Height	0.20	<	0.49	0.19	0.002**
3	Leaf area	0.33	<	0.66	0.35	0.052'
	# Bulbils	0.27	<	0.51	0.48	0.17
	Height	0.32	<	0.33	1.93	0.21
4	Leaf area	0.43	<	0.45	1.09	0.87
	# Bulbils	0.30	<	0.36	0.56	0.27
	Height	0.23	>	0.20	1.56	0.40
5	Leaf area	0.45	<	0.50	0.67	0.44
	# Bulbils	0.25	<	0.26	0.85	0.76

Table 5. Coefficient of variation (CV) values for traits of *Luzula spicata* from eight landscapes. F-Tests were performed on variances of log-transformed data.

Pair	Trait	Flat		Rough	$F_{15,15}$	F-test P
	Height	0.21	<	0.39	0.22	0.006**
2	Leaf area	0.46	<	0.53	0.76	0.61
	# Capsules	0.41	<	0.45	0.83	0.72
	Height	0.23	<	0.35	0.44	0.12
3	Leaf area	0.54	>	0.36	2.10	0.16
	# Capsules	0.54	>	0.39	1.24	0.68
	Height	0.24	>	0.20	1.54	0.41
4	Leaf area	0.36	<	0.44	1.13	0.82
	# Capsules	0.30	>	0.26	1.21	0.71
	Height	0.19	<	0.23	0.75	0.58
5	Leaf area	0.32	<	0.54	0.54	0.24
	# Capsules	0.27	=	0.27	0.93	0.89

DISCUSSION

As expected, spatial variation in microclimatic variables (temperature and moisture) were higher in topographically complex landscapes than in flatter ones. This variation was associated with, and may have contributed to, higher species richness in rough landscapes, although the differences were most pronounced at the larger scale ($1600m^2$) of investigation. Patterns of intra-specific trait variation in the two landscape types were less clear; there was a trend towards higher variation in rough landscapes for one species but not for the other.

Topographic complexity and microclimatic variation

While mean temperatures were quite similar across landscapes of contrasting complexity, spatial variation in mean and maximum temperatures were comparatively higher in the 40x40 m landscape plots chosen so as to be micro-climatically heterogeneous than in the more homogeneous ones. Moisture variation was also highest in the rough landscape in all four pairs, while mean moisture stayed more or less constant. Soil moisture has been suggested to respond more strongly to topographic variation than temperature, and to have buffering effects on both minimum and maximum temperatures (Fridley 2009, Dobrowski 2011). There was, however, no correlation between moisture and any temperature variable in the present data, indicating that soil moisture plays a more limited role in controlling the heat balance in this system. Alternatively soil surface temperature, as measured in this study, might be less buffered by moisture than soil temperature below the surface.

The spatial range of mean temperatures within landscapes were generally highest in the rough landscapes, and was in the range of 2-4°C, comparing well to IPCC global warming scenarios for the next century (IPCC 2007), as well as results from other field- and modelling studies (Scherrer & Körner 2011, Graae et al. 2012, Lenoir et al. 2013). This means that there are life conditions within landscape plots similar to what is expected over an elevational range of approximately 350-700m (using a standard lapse rate of 5.5 K per kilometer [Körner 2007]), and a latitudinal range of approximately 2.7-5.5 degrees or 308-616 km (using a lapse rate of 0.73°C per degree latitude [de Frenne et al. 2013]).

These results confirm the importance of landscape-scale studies assessing local variation in microclimatic conditions, and calls for caution when interpreting models based

on mean values (Armbruster et al. 2007, Lenoir et al. 2013). It is also important to note that even the least variable landscape plots in this area contained substantial microclimatic variation. Furthermore, the Finse study site is located at moderately high latitude (60°N), where microclimatic variation is expected to be especially high due to low solar angles (Armbruster et al. 2007). This implies that, at least at intermediate to high latitudes, even subjectively flat mountain terrain might provide some spatial buffering effect against future warming, with the effect increasing with increasing topographic heterogeneity. This result adds strength to the conclusion reached from studies across larger scales (Graae et al. 2012, Lenoir et al. 2013).

Species diversity and environmental drivers

When considering all species found in the landscape plots, rough landscapes were indeed more species rich than flatter ones in this area. This pattern is common in the literature and consistent across various measures of heterogeneity (Lundholm 2009). On the smaller sample scale, the pattern was less clear. It must be noted that the rough landscapes often contained "rare" species (for instance *Draba ssp., Saxifraga tenuis* and *Arabis alpina)*, typically found growing in small crevices, rocky outcrops or shady north-facing spots, and therefore seldom included in the sample plots. Hence, such species therefore contribute to the higher total species richness observed in all rough landscapes, while seldom contributing to the richness of the sample plots.

There is various evidence pointing towards the importance of sampling scale in studies of species richness in heterogeneous environments. In his review of heterogeneity-diversity studies, Lundholm (2009) found that the spatial scale of investigation influenced the strength of heterogeneity effects, with the effect being strongest (most positive) on intermediate sampling scales. The importance of sampling scale has also been emphasized in studies utilizing hierarchical sampling design (Dufour et al. 2006), and it has been shown that species-area curves have higher slopes on intermediate sampling scales such as the 40x40m landscape plots surveyed here (Crawley & Herral 2001). In summary, it seems that heterogeneity effects on species richness increases with sampling scale, as within-plot heterogeneity increases, at least until a certain plot size is reached.

Mean temperature of the sample plots emerges as a good predictor of sample plot species richness in this system, with a linear increase in species richness with increasing mean temperature. This probably reflect an increase in available energy as a result of an increased radiation load, as species richness has been shown to increase with available energy in low-productive tundra vegetation (Virtanen et al. 2012). Path analysis revealed that, not surprisingly, mean and maximum temperatures are strongly correlated. The analysis also suggested that the effect of maximum temperature was indirect, while mean temperature had a positive direct effect on species richness.

Across landscape plots within the study area, both mean temperature of the landscapes and spatial temperature range explained significant amounts of variation in cumulative sample richness. There might therefore be both an energy effect, with higher temperatures being an effect of higher radiation load, and a heterogeneity effect caused by variation in radiation load. Again, path analysis suggested that the effect of maximum temperature was indirect. At the largest scale, total landscape richness responded to both mean temperature of the landscape and variation in maximum temperature, again indicating an effect of heterogeneity. In fact, at this scale, variation in maximum temperature had the strongest direct effect in the path analysis. However, the relationship between landscape richness and microclimatic variables was generally weaker than for cumulative sample richness. This might reflect the fact that for sample richness microclimatic variables were measured in the sample plots, where species were sampled. In the case of landscape richness, the same microclimatic measurements were assumed to be a random sample of all microclimates within the landscape. Therefore the measurements may be more tightly coupled in the former case, leading to stronger relationships.

The relative roles of available energy (mean supply of limiting resources) and heterogeneity (variation in limiting resources) as drivers of species richness has been extensively debated (Grace 1999; Stevens & Carson 2002; Lundholm 2009). Since maximum temperature and its variation are tightly coupled, it is hard to separate the effect of the two. Both variables explained significant amounts of variance in species richness, so both are probably contributing to species richness in this system.

While moisture variance was consistently higher in the rough landscapes, there was no detectable effect of moisture or moisture variation on species richness in this study. This is in contrast to other studies, which have suggested a strong effect of moisture on species diversity (Moeslund et al. 2013). It has, however, been suggested that moisture shortage is less of a limitation to alpine plants than in lowland systems (Körner 2003), consistent with the lack of moisture effects observed in this study.

Intraspecific trait variation

While all traits of *Bistorta* responded significantly to one or more microclimatic variables, only height did so for *Luzula*. This also appeared to influence the patterns of relative variation between rough and flat landscapes, since relative variation in traits of *Bistorta* were higher in the rough landscapes compared to the paired flat ones in nearly all cases. However, with a few exceptions, there was a general lack of statistically significant differences in relative variation between landscape types for both species. This might have several possible explanations. First, observed phenotypic variation might be low even though potential phenotypic plasticity is high, due to for example passive responses to environmental stress or resource limitation (van Kleunen & Fischer 2005; Valladares et al. 2007). Second, it might be that gene flow between landscapes (i.e. subpopulations) has weakened the pattern of higher variation in the rough landscapes, and that plasticity is actually favoured over the whole study site (Sultan & Spencer 2002). Third, the number of plants sampled (i.e. the sample size) were simply too low to detect a statistical difference for individual pairs.

Under the (maybe overly) simple assumption of independence across traits and pairs, a meta-analysis showed a significant trend towards higher phenotypic variation within rough landscapes for *Bistorta*. This species reproduces mostly asexually by bulbils, suggesting that dispersal distances, and hence gene flow between subpopulations, should be lower than for *Luzula*, which reproduces sexually and is wind-pollinated. This suggests that in rough landscapes, where typical dispersal distances might still be larger than the grain of heterogeneity, the observed pattern might indicate selection for plasticity (Alpert & Simms 2002; Baythavong 2011). Even though genetic variation has been demonstrated repeatedly in populations of *Bistorta* (Bauert 2006; Vik et al. 2012), heterogeneous habitats such as rough landscapes should select for plasticity over local differentiation. Indeed, a common

garden experiment on *Bistorta* from the same landscapes found that plasticity tended to be higher in plants originating from rough landscapes (Gardiner 2013). Still, data on more different species with contrasting dispersal and reproductive ecologies (e.g. "mostly clonal" vs. obligate out-crossing species) would be needed to conclusively answer such questions.

Conclusions: Species replacement, plasticity or adaptive evolution?

In summary, small-scale variation in environmental conditions might provide substantial buffering of climate warming in mountain landscapes. Even subjectively "flat" mountain terrain contained microclimatic variation similar to what is expected over large altitudinal or latitudinal ranges, and this variation was associated with variation in species richness. While intra-specific adaptive and/or plastic responses cannot be ruled out based on these results, it appears like the faster process of short distance migration and changes in species abundances will dominate as the biotic response to climate warming in this system. This is similar to the conclusion reached from a study at the arctic archipelago of Svalbard (see Armbruster et al. 2007). Short distance migration should not be limited by dispersal, as it might be over long altitudinal or latitudinal distances. Furthermore, the spatial range of mean temperatures over short distances was equal to or larger than the temperature increases obtained in climate manipulation experiments showing clear effect on plant communities (e.g. Klanderud & Totland 2005; Walker et al. 2006). Local changes in plant communities could also lead to changes in biotic interactions such as competition and facilitation, and have consequences for invertebrate communities (Rae et al. 2006) and ecosystem function (Wookey et al. 2009). By and large, this supports the prediction of local community rearrangement as an important biotic response to climate change. Even under the most extreme warming scenarios, mountain landscapes will still contain suitable habitats for many species predicted to lose all suitable habitat based on large-scale models. It therefore seems like mountains can come to serve as a "safe haven", making them good target areas for biodiversity conservation in the future.

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Table A1. List of vascular plant species found within nine 40x40m landscape plots at Finse. S = species found in sample plots, L = species found within landscape.

	1R		2F		2R		3F		3R		4F		4R		5F		5R	
	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L	S	L
Alchemilla alpina L.					x				x		x					x		x
Alchemilla spp. L.															x	x		x
Antennaria dioica (L.) Gaertn.	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Anthoxanthum odoratum L.	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Arabis alpina L.		x		x		x						x		x				x
Arctostaphylos uva-ursi (L.) Spreng.		x			x	x								x				
Astragalus alpinus L.	x	x													x	x		
Avenella flexuosa (L.) Dreyer		x			x	x	x								x	x	x	x
Bartsia alpina L.	x	x	x	x	x	x					x	x	x	x	x	x	x	x
Bistorta vivipara (L.) Delarbre	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Campanula rotundifolia L.		x			x	x				x					x	x	x	x
Cardamine bellidifolia L.						x	x		x									x
Carex lachenalii Schkuhr								x		x	x	x		x				
Carex saxatilis L.								x									x	x
Carex capillaris L.															x	x	x	x
Carex atrata L.	x	x	x	x		x			x	x	x	x	x	x	x	x	x	x
Carex bigelowii Torr. ex Schwein.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Carex rupestris All.	x	x			x	x									x	x	x	x
Carex vaginata Tausch			x	x		x		x		x	x	x	x	x	x	x	x	x
Cerastium alpinum L.	x	x		x	x	x				x		x		x		x		x
Chamerion angustifolium (L.) Holub		x																
Deschampsia alpina (L.) Roem. & Schult.						x		x		x		x						x
Diphasiastrum alpinum (L.)Holub		x	x	x	x	x		x			x	x	x	x	x	x	x	x
Draba nivalis Lilj.		x				x	x											
Draba norwegica Gunnerus						x								x				x
Dryas octopetala L.	x	x			x	x							x	x	x	x	x	x
Empetrum nigrum L.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Equisetum variegatum Schleich. ex Weber & Mohr		x													x	x		
Erigeron uniflorus L.	x	x	x	x	x	x				x		x	x	x	x	x	x	x
Eriophorum angustifolium Honck.																		x
*Euphrasia spp.*L.	x	x	x	x	x	x				x	x	x	x	x	x	x	x	x
Festuca ovina L.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Festuca rubra L.															x	x		
Festuca vivipara (L.) Sm.							x	x	x	x							x	x
Gentiana nivalis L.	x	x			x	x				x		x	x	x		x	x	x
Gentianella campestris (L.) Börner		x				x								x			x	x
Harrimanella hypnoides (L.) Coville		x	x	x	x	x				x		x	x	x	x	x		x
Hieracium spp. L.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x

Species																	
Huperzia selago (L.) Bernh. ex Schrank & Mart.	x	x	x	x	x	x		x			x	x	x	x		x	x	x
Juncus biglumis L.											x	x					x	x
Juncus trifidus L.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Juniperus communis L.		x		x	x	x			x	x								x
Kobresia myosuroides (Vill.) Fiori					x	x			x	x			x	x				
Leontodon autumnalis var. taraxaci (L.) Hartm.					x	x					x	x			x	x		
Luzula multiflora ssp. frigida (Buch.) V.I.Krecz.			x	x	x	x	x	x		x		x	x	x	x	x		
Luzula spicata (L.) DC.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Omalotheca norvegica (Gunnerus) Sch.Bip. & F.W.Schultz		x						x										
Oxyria digyna (L.) Hill		x						x				x		x				x
Parnassia palustris L.															x	x		x
Phleum alpinum L.						x												
Phyllodoce caerulea (L.) Bab.													x	x		x		x
Pinguicula vulgaris L.																x		
Poa alpina L.	x	x	x	x	x	x		x		x	x	x				x	x	x
Potentilla crantzii (Crantz) Beck ex Fritsch	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Pyrola minor L.						x									x	x		
Ranunculus acris L.		x		x	x	x			x	x	x	x			x	x		x
Ranunculus glacialis L.				x										x				
Rhodiola rosea L.	x	x			x	x		x	x	x		x		x		x	x	x
Rubus chamaemorus L.							x	x										
Rumex acetosella L.						x				x						x		x
Salix herbacea L.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Salix lapponum L.		x										x		x				x
Salix reticulata L.		x			x	x							x	x	x	x	x	x
Saussurea alpina (L.) DC.	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x
Saxifraga cernua L.		x				x				x				x				
Saxifraga cespitosa L.		x	x	x		x				x		x		x			x	x
Saxifraga oppositifolia L.	x	x	x	x	x	x		x		x			x	x		x	x	x
Saxifraga stellaris L.				x			x	x		x			x	x				x
Saxifraga tenuis (Wahlenb.) Harry Sm. ex Lindm.		x		x		x		x		x				x				x
Selaginella selaginoides (L.) P.Beauv.	x	x	x	x	x	x					x	x	x	x	x	x	x	x
Sibbaldia procumbens L.	x	x	x	x	x	x		x	x	x	x	x	x	x		x		
Silene acaulis (L.) Jacq.	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x
Taraxacum spp. F.H.Wigg.		x	x	x	x	x		x	x	x	x	x	x	x	x	x		x
Thalictrum alpinum L.	x	x	x	x	x	x			x	x	x	x	x	x	x	x	x	x
Tofieldia pusilla (Michx.) Pers.															x	x	x	x
Trientalis europaea L.		x				x								x				x
Trisetum spicatum (L.) K.Richt.				x				x				x				x	x	x
Vaccinium myrtillus L.	x	x				x				x				x	x	x		x
Vaccinium uliginosum L.	x	x			x	x											x	x

Species																		
Vaccinium vitis-idaea L.	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x
Veronica alpina L.		x		x	x	x			x	x		x		x	x	x		x
Veronica fruticans Jacq.		x			x									x				x
Viola palustris L.					x													
Viola biflora L.		x																
Viscaria alpina (L.) G.Don	x	x		x		x		x			x	x	x	x	x	x	x	x

APPENDIX B

Table B1. Model comparison for generalized linear models of cumulative sample plot species richness, fitted with Possion distributed errors.

Model parameters	AICc	ΔAICc	AICc weight
Tmean+Trange	56.77	0	0.698
Tmean+var(Tmax)	59.92	3.15	0.144
Tmean+Trange+var(Tmax)	61.45	4.68	0.067
Tmean+Trange+Tmax	61.57	4.8	0.063
Tmean+Tmax	63.88	7.11	0.020
Tmean	65.91	9.14	0.007
Tmax	65.96	9.16	0.007

Table B2. Model comparison for generalized linear models of total landscape species richness, fitted with Possion distributed errors.

Model parameters	AICc	ΔAICc	AICc weight
Tmax	60.37	0	0.473
Tmean+var(Tmax)	61.12	0.75	0.325
Tmean+Tmax	63.78	3.24	0.086
Tmean+Trange	64.36	3.99	0.064
Tmean+Trange+var(Tmax)	65.89	5.52	0.030
Tmean+Trange+Tmax	67.20	6.83	0.016
Tmean	69.22	8.85	0.006