

Geomorphic Determinants of Species Composition of Alpine Tundra, Glacier National Park, U.S.A.

Authors: Malanson, George P., Bengtson, Lindsey E., and Fagre, Daniel B.

Source: Arctic, Antarctic, and Alpine Research, 44(2): 197-209

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1938-4246-44.2.197

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Geomorphic Determinants of Species Composition of Alpine Tundra, Glacier National Park, U.S.A.

George P. Malanson* Lindsey E. Bengtson† and Daniel B. Fagre†

*Corresponding author: Department of Geography, University of Iowa, Iowa City, Iowa 52242, U.S.A. george-malanson@uiowa.edu †U.S. Geological Survey, Northern Rocky Mountain Science Center, Glacier National Park, West Glacier, Montana 59936, U.S.A.

Abstract

Because the distribution of alpine tundra is associated with spatially limited cold climates, global warming may threaten its local extent or existence. This notion has been challenged, however, based on observations of the diversity of alpine tundra in small areas primarily due to topographic variation. The importance of diversity in temperature or moisture conditions caused by topographic variation is an open question, and we extend this to geomorphology more generally. The extent to which geomorphic variation per se, based on relatively easily assessed indicators, can account for the variation in alpine tundra community composition is analyzed versus the inclusion of broad indicators of regional climate variation. Visual assessments of topography are quantified and reduced using principal components analysis (PCA). Observations of species cover are reduced using detrended correspondence analysis (DCA). A "best subsets" regression approach using the Akaike Information Criterion for selection of variables is compared to a simple stepwise regression with DCA scores as the dependent variable and scores on significant PCA axes plus more direct measures of topography as independent variables. Models with geographic coordinates (representing regional climate gradients) excluded explain almost as much variation in community composition as models with them included, although they are important contributors to the latter. The geomorphic variables in the model are those associated with local moisture differences such as snowbeds. The potential local variability of alpine tundra can be a buffer against climate change, but change in precipitation may be as important as change in temperature.

DOI: http://dx.doi.org/10.1657/1938-4246-44.2.197

Introduction

The association of alpine tundra with colder climates, and of variation within tundra with various climatic variables, is well established (e.g., Billings, 1988; Walker et al., 1994; Parisod et al., 2010). Many studies have indicated that a warming climate could threaten some alpine tundra (cf. Klanderud and Totland, 2005; Walther et al., 2005; Walker et al., 2006; Lenoir et al., 2008). More specific results on characteristics such as phenology support these concerns (Inouye, 2008; Wipf et al., 2009; Smith et al., 2012). Further, it has long been supposed that forest response to climate warming could figuratively push alpine tundra off the top of mountains (Peters and Darling, 1985), and Diaz and Eischeid (2007) calculated that the climate type associated with alpine tundra will no longer exist in the continental U.S.A. with continued climate change.

The notion of a general loss of alpine tundra has been challenged (Randin et al., 2009a) or at least locally contradicted (Cannone et al., 2008). The geomorphological conditions that create the general variability in microhabitats in alpine tundra are at multiple scales (Lonegran and Del Moral, 1984; Fisk et al., 1998; Liptzin and Seastedt, 2010) and affect the assemblages of alpine tundra in cross-scale interaction. Malanson et al. (2011) reported that the degree of difference in alpine tundra across >1000 km of the Rocky Mountains could be found within a 4 \times 109 m² area in Glacier National Park, Montana (GNP). Mountains have heterogeneous microclimates due to topographic complexity which could limit the

impact of regional climate changes (Scherrer and Körner, 2011). The response of alpine tundra to climate change is also variable at other scales (Engler et al., 2011). Our purpose is to examine the impact of geomorphic heterogeneity on variability of alpine tundra plant communities, which is a major context for plant response to climate change. In doing so we assess the ability of simple geomorphic indicators to be proxies for processes of microclimatic modification.

While we agree with Scherrer and Körner's (2011) general conclusions based on their measurement of a wide range of thermal microhabitats within meter-scale distances, we believe that moisture may be as important as temperature generally and more so for many species in alpine tundra. They concluded that "all but the species depending on the very coldest microhabitats will find thermally suitable 'escape' habitats within short distances," but we are concerned that the range of moisture microhabitats may be more spatially variable and that species will not so easily escape drying. Moisture conditions are likely to be an important source of variation in alpine tundra because of the direct need for water (e.g., Harte et al., 1995) and their indirect effect on microbial activity and nutrient dynamics (e.g., Lipson and Monson, 1998). Moisture conditions are likely to be affected by geomorphology at multiple scales (e.g., Litaor et al., 2008). In the Swiss Alps, Vonlanthen et al. (2006) found that the variation in community structure in alpine tundra was best correlated with a gradient of temperature but secondarily with one related to soils, particularly soil tension. In a discussion of topographically-maintained microrefugia,

Dobrowski (2011) cited water availability as being as important a limit on species as temperature. Other studies have found effects of topography on diversity (Bruun et al., 2006).

Contributing to moisture variation, snow patterns, especially the timing of snowmelt, have long been known to differentiate alpine tundra (Billings and Bliss, 1959; Walker et al., 1994; Arft et al., 1999; Sandvik et al., 2004; Choler, 2005; Huelber et al., 2006; Bjork and Molau, 2007; Kudo et al., 2010). For example, snow manipulation experiments at Niwot Ridge (Colorado Front Range) changed the nitrogen cycle significantly (Williams et al., 1998). These results have been extended to wider observations where topographically induced variation in snow cover had consequences for species richness (Litaor et al., 2008). Notably, the pattern of snow is affected by topography through its effects on redistribution and melting, and snowbeds are often found in specific relation to topography: on concave leeward slopes and just below leeward ridges (i.e., at cornices) (e.g., Dobrowski, 2011). Geomorphology also channels snowmelt (e.g., Baron et al., 2000; Hood et al., 2003; Choler, 2005), and has a direct effect on tundra where it is associated with a disturbance such as solifluction (Johnson and Billings, 1962; Haugland and Beatty, 2005; Vonlanthen et al., 2008; Randin et al., 2009b).

Here we examine what aspects of environmental variability might allow the development of different kinds of tundra within small areas. We focus on geomorphic variables that modify broader climate factors to produce the microenvironments experienced by plants (which are thus decoupled from regional climates in alpine environments; cf. Pape et al., 2009; Wundram et al., 2010) and thus may serve as a proxy for the more difficult and expensive to measure microclimate and microhydrology variables. Our intent is to provide a context for interpreting change in alpine tundra and a framework for focusing monitoring and mitigation strategies in an era of changing climate. This context is needed because the usefulness of the Global Observation Research Initiative in Alpine Environments (GLORIA; Grabherr et al., 2000) network will depend on observational and theoretical context because prior and ongoing studies have produced variable results (e.g., Harte and Shaw, 1995; Walker et al., 2006; Pauli et al., 2007; Randin et al., 2009a; Abadneh and Woolfenden, 2010). Context is also needed for local understanding and mitigation (Malanson et al., 2006). Alpine tundra is an important amenity resource globally (e.g., Gret-Regamey et al., 2008) as well as a contributor to global biodiversity (Körner, 2003). If we can elucidate the relationship between alpine tundra and local environmental variables that interact with and modify broader climate forcing we will have established a better basis for further monitoring, experiment, and interpretation (cf. Nagy and Grabherr, 2009).

To examine the effects of geomorphology in addition to or in place of climatic variables, and given spatially extensive climate data is lacking in most mountain areas and interpolations are suspect (e.g., Grafius and Malanson, 2009), we will examine the variability of alpine tundra plant community structure in relation to a range of geomorphic indicators with and without broad geographical gradients that may capture coarse scale climatic variability. In this study we make use of existing data that can be an example for other studies. These data include ordinal scale values of species cover on sites for which there are ratio scale transformations, and

ordinal scale indicators of abiotic environmental variables. These observations of plant species and their environment are common from older studies (especially in Europe), and potentially can be reused. Such studies can then extend the generality of the ongoing experiments and monitoring that are spatially restricted. In particular, these older studies do not have data on microclimates or the details of water availability. We contend that geomorphic variables mediate macroclimate patterns to produce microclimates, and that within a macroclimate region geomorphic variables can capture much of the variation needed to explain the range of alpine vegetation types.

Study Area and Data Source

Glacier National Park (GNP), Montana, has extensive tundra in geomorphically complex situations (Malanson et al., 2007). Here the tundra is typically floristically diverse. Bamberg and Major (1968) identified 185 species in the area of Siyeh Pass, including the broad expanse of East Flattop Mountain, of which 62 occurred in their sixteen 50×20 cm quadrats. Choate (1963) reported 136 species at Logan Pass. She noted that many of the alpine species of GNP are near the southern limits of fairly extensive arctic-alpine ranges. Lesica and McCune (2004) reported that these species were threatened by climate change, while Malanson et al. (2011) found such a broad array of tundra types and habitats to potentially lessen impacts. Lesica (2002) summarized all alpine tundra in GNP into four geomorphic types. One, talus, supports little vegetation due to its instability. What he described as fell fields include relatively rare fell and the broad uplands east of the Continental Divide where solifluction processes often create a stair-step appearance with stony treads alternating with vegetated risers (slightly steeper than the treads but not vertical). Lesica (2002) noted that this vegetation grades into what he called turf (he described these as areas of deeper soil). At the more extreme portion of the gradient is wet meadow. Along this gradient, relatively dry sites are dominated by grasses while sedges dominate the wetter sites. Lastly, Lesica (2002) noted that some types of alpine vegetation are associated with permanent or persistent snow.

Some aspects of the alpine microgeomorphology of GNP have been studied in their own right. At a few isolated convex upland sites in eastern GNP, glaciation did not directly affect mountaintops during the late Pleistocene. Instead, intense periglacial conditions existed that led to the development of turf-banked treads and risers in response to solifluction processes. These treads and risers, described elsewhere (Butler and Malanson, 1989, 1999; Malanson et al., 2002; Walsh et al., 2003; Butler et al., 2004), are the primary environment where alpine tundra is found in GNP. The risers are primarily vegetated by *Dryas octopetala* and/or *Arctostaphylos uva-ursi*.

Damm (2001) did the most extensive classification and description of alpine vegetation in GNP. He classified over 500 detailed samples into over 40 associations (a vegetation classification unit based on species composition), some with further divisions, using the European phytosociological system of Braun-Blanquet (1932). He endeavored to use a 16 m² quadrat for his sites, but in places where the tundra was spatially confined he used smaller quadrats. We use these data as representative of the variation of tundra and assume that error would most likely be for rare species

that would affect the analyses less than others. Second, we excluded lichens and analyze the patterns with vascular plants and mosses because the two groups respond to environmental gradients in opposite ways (e.g., Hudson and Henry, 2010). In a number of cases, even with good effort, it was not possible to identify all mosses to species, and so only the genus was reported. The rarest species, i.e. those listed in footnotes to the tables, were not included.

Damm (2001) collected basic descriptive information about his sites. These observations include elevation, aspect, and slope—and we use these variables directly, except changing aspect to degrees difference from southwest. His *previously unreported* field

sheets (example included as Appendix 1) include information on topography, geology, soils, surface rocks, and topographic exposure, which we reduce (below). Based on his marking of his field sheets we derived a score of 1-5 for each nominal variable in the category; 1 = no mark; 2 = dotted slash; 3 = solid slash; 4 = solid slash and dotted x; 5 = solid x. Where we had percentage values (e.g., rock cover in size classes) we used them. Recording was sparse for some variables such as soil profile depth and we did not use those. The list of variables for PCA reduction from Damm (2001) is shown in Table 1.

Damm (2001) originally surveyed his sites with a low-resolu-

 $TABLE\ 1$ Variables recorded by Damm (2001) that were reduced using principal components analysis (PCA).

PCA Axes	General factor	Character/Element	PCA Axes	General factor	Character/Element
Slope:			Rock substrate		
	Location			Rock sizes (cm)	
		Summit			< 0.5
		Ridgetop			0.5-2
		Valley-bottom			2-5
		Slope			5-10
	Slope position				10-25
		Foot			25-50
		Low			>50
		Middle		Rock type	
		Upper		••	Platy
	Slope relief				Isodiametric
		Smooth			Sharp-edged
		Rolling			Abrased-edged
		Outcrops			Weathered
		Terraced			Sorted
		Irregular			Irregular
		Concave			Cliff
		Convex			Frost rubble
	Valley location				Talus
	•	Cirque			Glacial, alluvial debris
		End	Soils		,
		Middle		Organic matter	
		Entrance		C	Pure
		Talus cone			High
		Talus/scree			Medium
		Ravine			Low
		Depression			Absent
		Snowbed		Moisture	
		Boulders			Dry
		Outcrops			Fresh
		Cliff			Moist
		Spring			Wet, seep
		Bench			Seasonal
		Moraine	Exposure:		
		Streambank	1	Wind	
		Seep			Extreme
					High
					Middle
					Slight
					Protected
				Snow duration	
					Long
					Reasonable
					Moderate
					Exposed
					Exposed

tion GPS, but many sites were resurveyed later with better precision (he had left micro-cairns at his sites and was able to relocate them quite accurately). If Damm (2001) had sampled some types of vegetation all in one area, any test of the importance of site location would be biased. We plotted the UTM coordinates for all sites as a representation of the geographic spread of sampling, and then plotted the coordinates of the plots that Damm (2001) identified as associations and grouped as such in separate tables. In most cases the plots for single associations were scattered across the geographic range of GNP and so it seems clear that site selection was not biased greatly. Given missing data for many cases, however, we finally reduced the number of plots to 396.

For comparison we examined general climate gradients across GNP derived from Daymet data (http://www.daymet.org). Daymet is a spatial interpolation procedure specifically designed for irregularly spaced stations and complex topography (Hungerford et al., 1989). The available data are from 1980 to 2003 and are at 1 km spatial resolution. We entered the coordinates for alpine locations across the range of GNP to derive the descriptive results (Fig. 1 and Table 2).

TABLE 2
Climate indicators interpolated in DAYMET for points representing the gradients of latitude and longitude across GNP; data are from 1980 to 2003.

Elevation temp. temp. precip						
Location (m) (°C) (°C) (cm) Divide Mt. east 2577 4.8 -5.6 171 Rogers Pk. west 2232 6.4 -5.5 164 Summit Mt. south 2676 5.1 -5.0 173 Mt. Custer north 2656 4.2 -7.6 193				daily	daily	Annual
Rogers Pk. west 2232 6.4 -5.5 164 Summit Mt. south 2676 5.1 -5.0 173 Mt. Custer north 2656 4.2 -7.6 193		Location				precip. (cm)
Summit Mt. south 2676 5.1 -5.0 173 Mt. Custer north 2656 4.2 -7.6 193	Divide Mt.	east	2577	4.8	-5.6	171
Mt. Custer north 2656 4.2 -7.6 193	Rogers Pk.	west	2232	6.4	-5.5	164
	Summit Mt.	south	2676	5.1	-5.0	173
Logan Pass center 2031 6.6 -4.9 159	Mt. Custer	north	2656	4.2	-7.6	193
	Logan Pass	center	2031	6.6	-4.9	159



FIGURE 1. The locations of the sites for which Daymet climate data was derived for descriptive context. The latitude and longitude of Logan Pass are 48.6952°N, 113.7180°W.

Methods

Because we had indicators for so many independent variables that relied on Damm's (2001) rankings, we reduced his data on topography, geology, soils, and exposure using principal components analyses (PCA) to derive axes to represent combinations and interactions of these variables for each site. We used PCA separately for the variables in these categories: slope conditions; soils (organic matter and moisture); rock type; exposure; and the cover percentages in the classes of rock size. We used the PCA axes for which the broken-stick eigenvalue exceeded the observed eigenvalue (cf. Frontier, 1976; Jackson, 1993). These PCAs produced two or three axes meeting this criterion that we used subsequently and which we refer to as Slope1-3; Soils1-2; RockT1-2; Expo1-2; and RockS1-3.

We retained Damm's (2001) more direct measures for slope, aspect (which we corrected to difference from 270°), and elevation. We used his geographic coordinates (UTMN, UTME) as variables and derived three additional location-based variables: east or west of the Continental Divide (Eastness: binary, 1,2); Eastness \times UTME (EastEast); and Eastness \times Aspect (EastAspect). These direct geographic indictors are the factors different from geomorphology and may be related to broader climatic gradients (Table 2 and Fig. 1). The list of independent variables derived by PCA and other direct variables is given in Table 3.

We ordinated the site \times species from Damm (2001) using detrended correspondence analysis (DCA) in PC-ORD (McCune and Mefford, 1999); we rescaled the axes to 26 segments and did not downweight rare species. We transformed the Braun-Blanquet cover classes to percent cover using the midpoints of the classes. We also used non-metric multidimensional scaling (NMDS) in pre-

liminary analyses. Ordination provides a mapping of sites in statistical space based on the similarity of their plant community composition. NMDS is a preferred method for many types of exploratory ordination because it makes few assumptions about the form and relations of the data; DCA does make such assumptions and manipulates the data to conform to them, but it often produces results that are more interpretable in terms of relations with environmental gradients. Because NMDS produced a roughly spherical cloud of points, we analyzed the DCA results (with trial rotations we found that a Pearson correlation of an NMDS axis with the primary DCA axis was > .9; we took this result as an indication that the DCA results were not simply an artifact of the method). A combination of ordination methods is a useful quality control approach (e.g., Robbins and Matthews, 2010).

We next regressed the DCA1 ordination scores on the environmental variables, including the axis scores determined in PCA. We used the ''best subset'' algorithm in SPSS-19 to select a model, with minimizing the Akaike Information Criterion as the criterion. This linear regression algorithm compares all combinations of independent variables. Because this algorithm does not produce the more widely recognized accumulated R², we also ran a common stepwise multiple regression. Because the direct geographic variables that we assumed correspond to climate gradients are at a different scale (UTMN, UTME, Eastness, EastEast, EastAspect), we ran and interpreted analyses with and without them.

Results

The DCA ordinations produced a spread of points of over 600 and 500 units (100 units is equivalent to one standard deviation

TABLE 3
List of all independent variables.

Source	Name	Comments:
PCA	Slope1	ridge, smooth, not irregular, not convex
Slope2	slope, middle, smooth, not outcrops, not irregular, convex	-
Slope3	not slope, not upper, convex	
Soils1	high organic, fresh	
Soils2	medium organic, not seasonal or fresh	
RockT1	not abraded, not talus	
RockT2	abraded, weathered frost rubble	
Expo1	not extreme wind, reasonable snow duration	
Expo2	not high wind, not moderate snow duration	
RockS1	not mid-sized	
RockS2	biggest	
RockS3	smaller	
Damm (2001), direct		
	Elevation	meters
	Inclination	degrees
	Aspect	degrees; difference from 225°
	UTME	geographic coordinates of longitude
	UTMN	geographic coordinates of latitude
	Elevation × Inclination	
	Elevation \times Aspect	
	Aspect × Inclination	
	East	binary; 1 if west, 2 if east of Continental Divide
	East \times UTME	
	East \times Aspect	

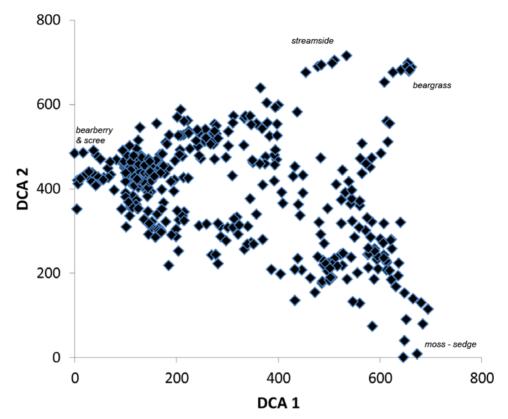


FIGURE 2. The pattern of sites on the first two axes of the detrended correspondence analysis (DCA) of the site X species cover data. The plant community types identified are the extremes referred to in the text.

of species turnover; Gauch, 1982) on the first two axes (Fig. 2; eigenvalues 0.83 and 0.62, but the latter is not indicative of variance due to rescaling; the coefficients of determination for the correlations between ordination and original n-dimensional distances have cumulative R² of .291 and .385; the overall inertia is 25.59). Given the predominance and better reliability of the first axis (DCA 1), we examined it alone in relation to the environmental variables. The arrangement of plant community types along DCA1 seems to reflect differences in available soil moisture. At one end of the axis are plots classified by Damm (2001) as bearberry communities (northern goldenrod-bearberry association with its bearberryrough fescue subassociation; based on Solidago multiraiata, Arctostaphylos uva-ursi, and Festuca scabrella) and scree slope communities of Stellaria americana or Saxifraga bronchialis; at the other end are streamside communities of the Saxifraga lyallii variation of the Senecio triangularis-Mimulus lewisii association, drier but deeper soils of beargrass (Xenophyllum tenax) or of Tofieldia glutinosa-Carex lenticularis moss and sedge-dominated plots (Fig. 3).

Basic Pearson correlations among all variables indicate a high degree of collinearity in a few cases (only the most relevant are shown here [Table 4]; others are available in Appendix 2). Most notably, given the orientation of GNP and the mountain ranges it encompasses, UTMN and UTME are highly correlated (0.89). Additionally, among the highest correlations are UTME with Rock-Type1 and Exposure1. Due to overall weak support for DCA 2, we do not analyze it further, but our conjecture that the array of community types on Figure 2 could be related to soil moisture is

strengthened by the high correlation (0.68) between DCA 2 and Soil1, our best proxy for soil moisture, with the beargrass and moss-sedge communities being at opposite ends of our Soils1 gradient with the bearberry communities in the middle.

The regression analyses produced significant models with good explanatory power (Best Subsets algorithm AIC 3708.7 and Accuracy 70.0%; Stepwise algorithm AIC 3718.8, Accuracy 68.7%, and Adjusted R² .684). The geographic variables UTME and UTMN can account for much of the variance in the models (Table 5), but exposure variables, which are from Damm's estimates of wind and snow duration, are also important.

When we ran these same analyses without the geographic coordinates (noting the collinearity with UTME and UTMN; Table 6), the models are weaker but still significant (Best Subsets algorithm AIC 3822.3 and Accuracy 59.7%; Stepwise algorithm AIC 3826.3, Accuracy 58.9%, and Adjusted R² .575). The exposure variable that captures the degree of protection from wind and the duration of snow now accounts for most of the variance.

Discussion

The reasonable approximation of the models without the geographic variables indicates that the geomorphic indicators used in this analysis are highly related to the variation in alpine tundra plant community composition at the scale of GNP. Without considering the climate gradients within the park, and given that we are not including variables that we expect could be important but for which we have no data (i.e., soil texture and chemistry: e.g., see





FIGURE 3. Examples of the plant associations found at opposite ends of the primary DCA axis, with characteristic (A) *Arctostaphylos uva-ursi* (bearberry) and (B) *Tofieldia glutinosa-Carex lenticularis* (false asphodel-Kellogg sedge).

Bowman and Seastedt, 2001; Loffler and Pape, 2008; or isolation and dispersal: e.g., Marchand et al., 1980; Molau and Larsson, 2000; Vittoz et al., 2009), simple geomorphic indicators account for much of the variation in composition and thus in regional diversity. To the extent to which we do capture soil conditions such as soil moisture, other geomorphic variables explain more variance. Overall, the use of geomorphic variables that are relatively easy to determine in the field proved to be a useful approach in an effort to understand how climate is modified at the plant scale.

The topographic variables that are important in the models are those that are associated with available moisture. The PCA axes of exposure represent variation in what Damm (2001) estimated were variations in winds, which affect snow redistribution, and snow cover directly, which includes shade (it is possible that these exposure gradients are related to temperature, since greater surface wind speed should allow greater convectional transfer of heat). The second group of variables includes those of soil characteristics, primarily moisture in Damm's (2001) terms, and rock sizes, that affect drainage and water holding capacity. The third group in-

cludes slope and the interaction of slope and elevation, which are key factors in overall soil moisture models for alpine areas (Burns and Tonkin, 1982).

The considerable multicollinearity among the independent variables makes specific attributions of probable cause and effect difficult. For example, the prominence of the geographic variables, especially noting the correlation of UTME and UTMN due to the orientation of the mountains, could be due to their collinearity with other variables (note that the relative importance and R^2 of the first variable in the models without them is similar to that of UTME alone) but the overall additional explanation could be due to an environmental pattern or artifact (e.g., perhaps the most easterly or westerly areas have unique conditions—but our analysis of the distribution of Damm's (2001) associations would argue against this conclusion), or it could reflect historical processes.

However, topographic variables alone can account for the same amount of variance in the plant community floristic structure as can the addition of geographic coordinates assumed to coincide with major climatic gradients. In the context of Scherrer and

TABLE 4

Pearson correlation coefficients for selected variables (N=396; for 2-tailed test: *p<.01; **p<.001).

	DCA1	DCA2	UTME	UTMN
Elevation	0.046	-0.123	0.166*	0.25**
Inclination	-0.3**	0.239**	0.209**	-0.202**
AspectCor	0.148*	-0.062	0.153*	-0.246**
Slope1	0.113	-0.117	-0.025	0.006
Slope2	-0.138*	0.168*	0.33**	-0.241**
Slope3	0.346**	-0.213**	-0.304**	0.191**
RockS1	0.428**	-0.205**	-0.337**	0.25**
RockS2	0.008	0.086	-0.147*	0.079
RockS3	-0.127	0.083	0.063	0.012
RockT1	-0.271**	-0.049	0.402**	-0.334**
RockT2	0.02	-0.072	-0.055	0.131*
RockT3	-0.221**	0.239**	0.13*	-0.03
Soils1	-0.302**	0.683**	0.229**	-0.159*
Soils2	0.356**	-0.02	-0.357**	0.256**
Soils3	-0.152*	-0.084	0.154*	-0.148*
Expo1	0.643**	-0.137*	-0.464**	0.31**
Expo2	0.176**	-0.019	-0.087	0.08
Expo3	0.038	-0.052	-0.165*	0.193**
UTME	-0.659**	0.284**	1	-0.889**
UTMN	0.457**	-0.262**	-0.889**	1

Körner's (2011) results, it is notable that the topographic variables that are important either with or without the inclusion of location coordinates are those related to exposure, and defined by Damm (2001) as "wind exposure" and "estimated snow duration." These are normally the inverse of each other and the PCA axes are both related to the combination of lower winds and longer snow duration in terms of which variables loaded on them. In general, water is considered to be a direct resource for plant growth, while temperature has indirect effects by regulating rates (cf. Austin, 1987).

Topographic factors are often related to snow cover, which may be the proximate cause of resource variation to which plant species are constrained and which differentiates communities. Snow cover may be an environmental factor quite sensitive to climate change. Snow cover would be reduced by warmer temperatures in which a larger proportion of precipitation fell as rain; snow cover would be reduced by higher warm-season temperatures causing faster snowmelt and shorter duration of cover, leading to local drought conditions in late summer; and snow cover can be affected by a change in the temperature and water content of snow as it falls, with warmer, wetter snowfalls being less susceptible to redistribution by wind and so resulting in fewer and/or smaller snow patches, again leading to late summer drought. Those species depend on late summer snowmelt that could be most threatened, complementing those species of the coldest microclimates as identified by Scherrer and Körner (2011). Among those that might be threatened are the plant communities that have the showiest flowers with high appeal to the public, such as the streamside communities of Mimulus lewisii (Fig. 3). Many of these are found at rivulets draining late-lasting snowfields or glaciers that are already waning (Hall and Fagre, 2003; Pederson et al., 2011).

The importance of topography at multiple scales, and perhaps especially at spatial scales close to the sizes of individual plants, should be of interest in alpine regions more generally, while the particular interaction with snow may be more climate-specific. Glacier National Park experiences snowfall that is often redistributed by wind. Drier snowfalls (e.g., Rocky Mountain National Park, Colorado) may experience redistribution with less local storage, while wetter locales (e.g., Olympic National Park, Washington) may have more stable snowpacks. A focus on the extremes as noted in this study should be considered for monitoring impacts in any case.

Acknowledgments

This research was supported by a seed grant from the University of Iowa Center for Global and Regional Environmental Research to Malanson, by a U.S. Geological Survey Park-Oriented Biological Support grant to Fagre, and by NSF award BCS-1121305. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government. This is a contribution from the Mountain GeoDynamics Research Group.

TABLE 5

Linear models developed with the primary DCA axis as the dependent or target variable; direct geographic variables are included.

	Best Subse	ts Algorithm		Stepwise Algorithm Information criterion: 3718.786; Accuracy 68.7%				
Infor	mation criterion: 37	708.738; Accuracy: 7	70.0%					
Variable	Coefficient	Significance	Importance	Variable	Coefficient	Adj R ²	Significance	
Intercept	23324	.000v		Constant	25404		.000	
UTME	009	.000	.086	UTME	01	.434	.000	
Expo1	26.3	.000	.081	Expo1	26.51	.590	.000	
Expo2	15.7	.000	.073	UTMN	004	.625	.000	
UTMN	004	.000	.072	Incl	-2.09	.648	.000	
Incl	-20.4	.000	.069	Expo2	14.06	.662	.000	
ElevAspect	.166	.003	.069	RockS1	1.13	.673	.000	
RockS1	1.277	.005	.069	Aspect	.33	.679	.004	
ElevInc	.003	.006	.069	Soils1	-6.09	.684	.011	
Soils1	-6.488	.011	.069					
Elev	050	.014	.069					

TABLE 6

Linear models developed with the primary DCA axis as the dependent or target variable; direct geographic variables are excluded.

	Best Subse	ets Algorithm		Stepwise Algorithm					
Info	rmation criterion: 3	822.259; Accuracy:	59.7%	Info	Information criterion: 3826.27; Accuracy 58.9%				
Variablev	Coefficient	Significance	Importance	Variable	Coefficient	Adj R ²	Significance		
Intercept	760.48	.000		Constant	353.85		.000		
Expo1	38.815	.000	.115	Expo1	39.81	.430	.000		
Expo2	16.947	.000	.091	Incl	-11.68	.473	.000		
RockS1	2.184	.000	.090	Soils2	18.01	.501	.000		
Soils1	-10.896	.000	.089	Expo2	17.80	.526	.000		
RockS2	5.920	.000	.089	Soils1	-11.00	.552	.000		
Soils2	12.782	.001	.089	RockS1	1.85	.564	.001		
Incl	-26.178	.001	.089	RockS2	.001	.570	.013		
Elevinc	.003	.005	.088	RockT1	-7.056	.575	.014		
Elev	051	.025	.087						
RockT1	-6.218	.031	.087						

References Cited

- Abadneh, L., and Woolfenden, W., 2010: Monitoring for potential effects of climate change on the vegetation of two alpine meadows in the White Mountains of California, USA. *Quaternary International*, 215: 3–14.
- Arft, A. M., Walker, M. D., Gurevitch, J., Alatalo, J. M., Bret-Harte, M. S., Dale, M., Gugerli, F., Henry, G. H. R., Jones, M. H., Hollister, R. D., Jonsdottir, I. S., Laine, K., Levesque, E., Marion, G. M., Molau, U., Molgaard, P., Nordenhall, U., Raszhivin, V., Robinson, C. H., Starr, G., Stenstrom, A., Stenstrom, M., Totland, O., Turner, P. L., Walker, L. J., Webber, P. J., Welker, J. M., Wookey, P. A., 1999: Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, 69: 491–511.
- Austin, M. P., 1987: Models for the analysis of species response to environmental gradients. Vegetatio, 69: 229–232.
- Bamberg, S. A., and Major, J., 1968: Ecology of the vegetation and soils associated with calcareous parent material in three alpine regions of Montana. *Ecological Monographs*, 127–167.
- Baron, J. S., Hartman, M. D., Band, L. E., and Lammers, R. B., 2000. Sensitivity of a high-elevation Rocky Mountain watershed to altered climate and CO₂. Water Resources Research, 36: 89–99.
- Billings, W. D., 1988: Alpine vegetation. In Barbour, M. G., and Billings, W. D. (eds.), North American Terrestrial Vegetation. Cambridge: Cambridge University Press, 391–420.
- Billings, W. D., and Bliss, L. C., 1959: An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology*, 40: 388–397.
- Bjork, R. G., and Molau, U., 2007: Ecology of alpine snowbeds and the impact of climate change. Arctic, Antarctic, and Alpine Research, 39: 34–43.
- Bowman, W. D., and Seastedt, T. R. (eds.), 2001: Structure and Function of an Alpine Ecosystem: Niwot Ridge, Colorado. Oxford: Oxford University Press, 352 pp.
- Braun-Blanquet, J., 1932: *Plant Sociology*. New York: McGraw-Hill, 439 pp.
- Bruun, H. H., Moen, J., Virtanen, R., Grytnes, J.-A., Oksanen, L., and Angerbjorn, A., 2006: Effects of altitude and topography on species richness of vascular plants, bryophytes and lichens in alpine communities. *Journal of Vegetation Science*, 17: 37–46.
- Burns, S. F., and Tonkin, P. J., 1982: Soil-geomorphic models and the spatial distribution and development of alpine soils. *In Thorn*, C. E. (ed.), *Space and Time in Geomorphology*. London: Allen and Unwin, 25–43.
- Butler, D. R., and Malanson, G. P., 1989: Periglacial patterned ground,

- Waterton-Glacier International Peace Park, Canada and USA. Zeitschrift für Geomorphologie, 33: 43–57.
- Butler, D. R., and Malanson, G. P., 1999: Site locations and characteristics of miniature patterned ground, eastern Glacier National Park, Montana, USA. *Landform Analysis*, 2: 45–49.
- Butler, D. R., Malanson, G. P., and Resler, L. M., 2004: Turf-banked terrace treads and risers, turf exfoliation, and possible relationships with advancing treeline. *Catena*, 58: 259–274.
- Cannone, N., Diolaiuti, G., Guglielmin, M., and Smiraglia, C., 2008: Accelerating climate change impacts on alpine glacier forefield ecosystems in the European Alps. *Ecological Applications*, 18: 637–648.
- Choate, C. M., 1963: Ordination of the alpine plant communities at Logan Pass, Glacier National Park, Montana. M.A. thesis, University of Montana, Missoula, 221 pp.
- Choler, P., 2005: Consistent shifts in alpine plant traits along a mesotopographical gradient. Arctic, Antarctic, and Alpine Research, 37: 444–453.
- Damm, C., 2001: A phytosociological study of Glacier National Park, Montana, U.S.A., with notes on the syntaxonomy of alpine vegetation in western North America. Ph.D. thesis, Georg-August Universitaet, Goettingen, Germany.
- Diaz, H. F., and Eischeid, J. K., 2007: Disappearing alpine tundra Koppen climatic type in the western United States. *Geophysical Research Letters*, 34: L18707, http://dx.doi.org/10.1029/2007GL031253.
- Dobrowski, S. Z., 2011: A climatic basis for microrefugia: the influence of terrain on climate. *Global Change Biology*, 17: 1022–1035.
- Engler, R., Randin, C. F., Thuiller, W., Dullinger, S., Zimmermann, N. E., Araujo, M. B., Pearman, P. B., Le Lay, G., Piedallu, C., Albert, C. H., Choler, P., Coldea, G., De Lamo, X., Dirnbock, T., Gegout, J. C., Gomez-Garcia, D., Grytnes, J. A., Heegaard, E., Hoistad, F., Nogues-Bravo, D., Normand, S. Puscas, M. Sebastia, M. T., Stanisci, A., Theurillat, J. P., Trivedi, M. R., Vittoz, P., Guisan, A., 2011: 21st century climate change threatens mountain flora unequally across Europe. *Global Change Biology*, 17: 2330–2341.
- Fisk, M. C., Schmidt, S. K., and Seastedt, T. R., 1998: Topographic patterns of above- and belowground production and nitrogen cycling in alpine tundra. *Ecology*, 79: 2253–2266.
- Frontier, S., 1976: Étude de la décroissance des valeurs propres dans une analyse en composantes principales: comparaison avec le modèle du bâton brisé. *Journal of Experimental Marine Biology and Ecology*, 25: 67–75.
- Gauch, H. G., Jr., 1982: *Multivariate Analysis in Community Ecology*. Cambridge: Cambridge University Press, 298 pp.
- Grabherr, G., Gottfried, M., and Pauli, H., 2000: GLORIA: A GLobal

- Observation Research Initiative in alpine environments. *Mountain Research and Development*, 20: 190–191.
- Grafius, D. R., and Malanson, G. P., 2009: Precipitation and temperature estimation error at alpine treeline ecotones using the Mountain Climate Simulator model (MT-CLIM). *Physical Geography*, 30: 285–307.
- Gret-Regamey, A., Walz, A., and Bebi, P., 2008: Valuing ecosystem services for sustainable landscape planning in alpine regions. *Mountain Research and Development*, 28: 156–165.
- Hall, M. H. P., and Fagre, D. B., 2003: Modeled climate-induced glacier change in Glacier National Park, 1850–2100. *BioScience*, 53: 131–140.
- Harte, J., and Shaw, R., 1995: Shifting dominance within a montane vegetation community: results of a climate warming experiment. *Science*, 267: 876–880.
- Harte, J., Torn, M. S., Chang, F. R., Feifarek, B., Kinzig, A. P., Shaw, R., and Shen, K., 1995: Global warming and soil microclimate: results from a meadow-warming experiment. *Ecological Applications*, 5: 132–150.
- Haugland, J. E., and Beatty, S. W., 2005: Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography*, 32: 145–153.
- Hood, E. W., Williams, M. W., and Caine, N., 2003: Landscape controls on organic and inorganic nitrogen leaching across and alpine/subalpine ecotone, Green Lakes Valley, Colorado Front Range. *Ecosystems*, 6: 31–45.
- Hudson, J. M. G., and Henry, G. H. R., 2010: High Arctic plant community resists 15 years of experimental warming. *Journal of Ecology*, 98: 1035–1041.
- Huelber, K., Gottfried, M., Pauli, H., Reiter, K., Winkler, M., and Grabherr, G., 2006: Phenological responses of snowbed species to snow removal dates in the Central Alps: implications for climate warming. Arctic, Antarctic, and Alpine Research, 38: 99–103.
- Hungerford, R. D., Nemani, R. R., Running, S. W., and Coughlan, J. C., 1989: MTCLIM: a mountain microclimate simulation model. U.S. Forest Service Research Paper INT-414.
- Inouye, D. W., 2008: Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, 89: 353–362.
- Jackson, D. A., 1993: Stopping rules in Principal Components Analysis: a comparison of heuristical and statistical approaches. *Ecology*, 74: 2204–2214.
- Johnson, P. L., and Billings, W. D., 1962: The alpine vegetation of the Beartooth Plateau in relation to cryopedogenic processes and patterns. *Ecological Monographs*, 32: 105–135.
- Klanderud, K., and Totland, O., 2005: Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. *Ecology*, 86: 2047–2054.
- Körner, C., 2003: Alpine Plant Life. Berlin: Springer, 344 pp.
- Kudo, G., Kimura, M., Kasagi, T., Kawai, Y., Hirai, A. S., 2010. Habitat specific responses of alpine plants to climatic amelioration: comparison of fellfield to snowbed communities. *Arctic, Antarctic, and Alpine Research*, 42: 438–448.
- Lesica, P., 2002: A Flora of Glacier National Park. Corvallis: Oregon State University Press, 520 pp.
- Lesica, P., and McCune, B., 2004: Decline of arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *Journal of Vegetation Science*, 15: 679–690.
- Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P., and Brisse, H., 2008: A significant upward shift in plant species optimum elevation during the 20th century. *Science*, 320: 1768–1771.
- Lipson, D. A., and Monson, R. K., 1998: Plant-microbe competition for soil amino acids in the alpine tundra: effects of freeze-thaw and dry-rewet events. *Oecologia*, 113: 406–414.
- Liptzin, D., and Seastedt, T. R., 2010: Regional and local patterns of soil nutrients at Rocky Mountain treelines. *Geoderma*, 160: 208–217.
- Litaor, M. I., Williams, M., and Seastedt, T. R., 2008: Topographic

- controls on snow distribution, soil moisture, and species diversity of herbaceous alpine vegetation, Niwot Ridge, Colorado. *Journal of Geophysical Research–Biogeosciences*, 113(G2): G02008, http://dx.doi.org/10.1029/2007JG000419.
- Loffler, J., and Pape, R., 2008: Diversity patterns in relation to the environment in alpine tundra ecosystems of northern Norway. *Arctic, Antarctic, and Alpine Research*, 40: 373–381.
- Lonegran, W. A., and Del Moral, R., 1984: The influence of microrelief on community structure of subalpine meadows. *Bulletin of the Torrey Botanical Club*, 111: 209–216.
- Malanson, G. P., Butler, D. R., Cairns, D. M., Welsh, T. E., and Resler, L. M., 2002: Variability in a soil depth indicator in alpine tundra. *Catena*, 49: 203–215.
- Malanson, G. P., Scott, K., Fagre, D., and Holzer, K., 2006: Ordination context of GLORIA sites in Glacier National Park, USA. *In Price*, M. F. (ed.), *Global Change in Mountain Regions*. Duncow, U.K.: Sapiens Publishing, 154–155.
- Malanson, G. P., Butler, D. R., and Fagre, D. B., 2007: Alpine ecosystem dynamics and change: a view from the heights. *In* Prato, T., and Fagre, D. (eds.), *Sustaining Rocky Mountain Landscapes: Science, Policy and Management of the Crown of the Continent Ecosystem.* Washington, DC: Resources for the Future Press, 85–101.
- Malanson, G. P., Rose, J. P., Schroeder, P. J., and Fagre, D. B., 2011: Contexts for change in alpine tundra. *Physical Geography*, 32: 97–113
- Marchand, P. J., and Roach, D. A., 1980: Reproductive strategies of pioneering alpine species: seed production, dispersal, and germination. Arctic and Alpine Research, 12: 137–146.
- McCune, B., and Mefford, M. J., 1999: PC-ORD Multivariate Analysis of Community Data. Gleneden Beach, Oregon: MjM Software, 237 pp.
- Molau, U., and Larsson, E. L., 2000: Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal* of *Botany*, 78: 728–747.
- Nagy, L., and Grabherr, G., 2009: *The Biology of Alpine Habitats*. New York: Oxford University Press, 376 pp.
- Pape, R., Wundram, D., and Loeffler, J., 2009: Modelling near-surface temperature conditions in high mountain environments: an appraisal. *Climate Research*, 39: 99–109.
- Parisod, C., Wipf, S., and Guesewell, S., 2010: Plant and vegetation responses to a changing environment: an alpine issue. *Botanica Helyetica*, 120: 83–84.
- Pauli, H., Bottfried, M., Reiter, K., Klettner, C., and Grabherr, G., 2007: Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Global Change Biology*, 13: 147–156.
- Pederson, G. T., Gray, S. T., Woodhouse, C. A., Betancourt, J. L., Fagre, D. B., Littell, J. S., Watson, E., Luckman, B. H., and Graumlich, L. J., 2011: The unusual nature of recent snowpack declines in the North American Cordillera. *Science*, 333: 332–335.
- Peters, R. L., and Darling, J. D. S., 1985: The greenhouse effect and nature reserves. *BioScience*, 35: 707–717.
- Randin, C. F., Engler, R., Normand, S., Zappa, M., Zimmermann, N. E., Pearman, P. B., Vittoz, P., Thuiller, W., and Guisan, A., 2009a: Climate change and plant distribution: local models predict high-elevation persistence. *Global Change Biology*, 15: 1557–1569.
- Randin, C. F., Vuissoz, G., Liston, G. E., Vittoz, P., and Guisan, A., 2009b: Introduction of snow and geomorphic disturbance variables into predictive models of alpine plant distribution in the western Alps. Arctic, Antarctic, and Alpine Research, 41: 347–361.
- Robbins, J. A., and Matthews, J. A., 2010: Regional variation in successional trajectories and rates of vegetation change on glacier forelands in south-central Norway. *Arctic, Antarctic, and Alpine Research*, 42: 351–361.
- Sandvik, S., Heegaard, E., Elven, R., and Vandvik, V., 2004: Responses of alpine snowbed vegetation to long-term experimental warming. *Ecoscience*, 11: 150–159.
- Scherrer, D., and Körner, C., 2011: Topographically controlled thermal-

- habitat differentiation buffers alpine plant diversity against climate change. *Journal of Biogeography*, 38: 406–416.
- Smith, J. G., Sconiers, W., Spasojevic, M. J., Ashton, I. W., and Suding, K. N., 2012: Phenological changes in alpine plants in response to increased snowpack, temperature, and nitrogen. *Arctic, Antarctic,* and Alpine Research, 44: 135–142.
- Vittoz, P., Dussex, N., Wassef, J., and Guisan, A., 2009: Diaspore traits discriminate good from weak colonisers on high-elevation summits. *Basic and Applied Ecology*, 10: 508–515.
- Vonlanthen, C. M., Buhler, A., Veit, H., and Eugster, W., 2006: Alpine plant communities: as statistical assessment of their relation to microclimatological, pedological, geomorphological, and other factors. *Physical Geography*, 27: 137–154.
- Walker, M. D., Webber, P. J., Arnold, E. H., and Ebertmay, D., 1994: Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology*, 75: 393–408.
- Walker, M. D., Wahren, C. H., Hollister, R. D., Henry, G. H. R., Ahlquist, L. E., Alatalo, J. M., Bret-Harte, M. S., Calef, M. P., Callaghan, T. V., Carroll, A. B., Epstein, H. E., Jonsdottir, I. S., Klein, J. A., Magnusson, B., Molau, U., Oberbauer, S. F., Rewa, S. P., Robinson, C. H., Shaver, G. R., Suding, K. N., Thompson, C. C., Tolvanen,

- A., Totland, O., Turner, P. L., Tweedie, C. E., Webber, P. J., and Wookey, P. A., 2006: Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences USA*, 103: 1342–1346.
- Walsh, S. J., Bian, L., McKnight, S., Brown, D. G., and Hammer, E. S., 2003: Solifluction steps and risers, Lee Ridge, Glacier National Park, Montana, USA: a scale and pattern analysis. *Geomorphology*, 55: 381–298.
- Walther, G. R., Beissner, S., and Burga, C. A., 2005: Trends in the upward shift of alpine plants. *Journal of Vegetation Science*, 16: 541–548.
- Williams, M. W., Brooks, P. D., and Seastedt, T., 1998: Nitrogen and carbon soil dynamics in response to climate change in a high-elevation ecosystem in the Rocky Mountains, USA. *Arctic and Alpine Research*, 30: 26–30.
- Wipf, S., Stoeckli, V., and Bebi, P., 2009: Winter climate change in alpine tundra: responses to changes in snow depth and snowmelt timing. *Climatic Change*, 94: 105–121.
- Wundram, D., Pape, R., and Loeffler, J., 2010: Alpine soil temperature variability at multiple scales. Arctic, Antarctic, and Alpine Research, 42: 117–128.

MS accepted December 2011

APPENDIX 1

Autnahmebogen version 1.4

						time	
coun of windy, In		- Jumpi - 101 (day) (?)	to but	N	ate: 7 - /7 ame: CD		275
Location:	witchi Valley KH; 18m NW of &	, ~ 20 m above ad/alice htt; 10 m s	228; ~ 30 m alo		,5"-Map: '	10.92118D N	75ah 30 I
Elevation:	* 960(A) m (A)	Aspect:	230 ° Ir	nclination	: 25 •	Size: 4	_x <u> </u>
Topography	:						
summit () ridget	op (): di	rection:	- v	alley-bot	tom: ()	
slope (⋈)	Total-Ir	clination:					
Positio	on on slop	e: foot () 10	ow () mi	idle (/	upper	()
Slope-	relief:	smooth () rollir	ig () ou	crops () terra	ced ()
	j	rregular () conve	x () c	oncave ()	
Location :	in valley:	cirque	() end	() m:	iddle (/)	entra	nce (/)
depression	n () spr	ing () s	treambank	() seep	ed wall () mora	ine ()
talus cone	e) (/) be	ench ()					
Geology:	your old h	eles stope wit	I few order	of around	"		
Parent n	naterial:	ale grey. Tury.	Angillik , bregun	the oust-findish	HCl-r	eaction:	()
color:	white quarzite			100	ose ()	compacte	ed (X)
rock cov	ver (incl.	lichenize	d): 2 %	open	soil (<0	,1cm): 1	
layer-ir	nclination	-8	rising to	wards: SSE	- Shree	b. humans	
size class	<0,5cm	0,5-2cm	2-5cm	5-10cm	10-25cm	25-50cm	>50c
coverage	- *	- %	- 8	- 8	0.18	1 %	0.5
rock-textur	ce: sharp	edged (X)		ed () s			gular (
Soils:							
Profile-		_cm Root					
Profile-		_cm Rooteure () h:					
Profile- Organic Moisture	matter: p	ure () h	igh (/) m	edium (/)) wet,se	low ()	absent (() al ()
Profile- Organic Moisture	matter: p	ure () h	igh (/) m	edium (/)) wet,se	low ()	absent (() al ()
Profile- Organic Moisture	matter: p	ure () h	igh (/) m	edium (/)) wet,se	low ()	absent (() al ()
Profile- Organic Moisture	matter: p e: dry (/) cimated wa ction: u.v.	ure () h	igh (/) m	edium (/)) wet,se	low ()	absent (() al ()
Profile- Organic Moisture est Solifluc	matter: p e: dry (/) cimated wa ction: u.v.	ure () h	igh (/) m	edium (/)) wet,se	low ()	absent (() al ()
Profile- Organic Moisture est Solifluc	matter: p e: dry (/) cimated wa ction: u.v.	ure () h	igh (/) m	edium (/)) wet,se	low ()	absent (() al ()
Profile- Organic Moisture est Solifluc Remarks:	matter: p e: dry (/) cimated wa ction: u.v.	tercapacity fresh (tercapacity fresh v fres	igh (/) m) moist (y/supply: ###################################	edium (/)) wet, see ye al lew; sue dry dry from Soil	low () eeped () w blow away d-surmant -pH (root	absent (seasona nu, lly; t-horizor) prote	() al () a):
Profile- Organic Moisture est Solifluc Remarks:	matter: p e: dry (/) cimated wa ction: u.v.	tercapacity fresh (tercapacity fresh v fres	igh (/) m) moist (y/supply: ###################################	edium (/)) wet, see ye al lew; sue dry dry from Soil	low () eeped () w blow away d-survey d-survey sight (root moderate	absent (seasona nu, lly; t-horizor) prote	() al () al :

Appendix 2. Pearson correlations between all pairs of variables. 1 foot = 0.305 m.

			_						
	DCA1	DCA2	DCA3	Elevation(ft)		DCA1	DCA2	DCA3	Elevation(ft)
DCA2	-0.404				Soils1	-0.247	-0.287	0.016	0.094
DCA3	0.078	-0.204			Soils2	0.112	0.256	0.092	-0.122
Elevation(ft)	0.029	-0.096	-0.121		Soils3	-0.027	-0.195	0.123	-0.038
Inclination	-0.289	0.364	0.268	-0.254	Climate1	0.323	0.450	-0.055	-0.008
AspectCor	0.149	-0.072	-0.204	0.116	Climate2	0.008	-0.089	0.203	0.044
Slope1	0.108	-0.150	-0.239	0.239	Climate3	-0.069	-0.112	0.052	-0.046
Slope2	-0.141	0.051	-0.241	-0.165	UTME	-0.304	-0.337	-0.147	0.063
Slope3	0.357	-0.245	0.086	-0.129	UTMN	0.191	0.250	0.079	0.012
RockS1	0.447	-0.256	0.000	-0.189	Elev.Incl	-0.384	-0.155	0.359	0.078
RockS2	0.033	0.262	0.330	0.017	Elev.Aspect	-0.012	0.066	-0.091	0.055
RockS3	-0.124	0.202	-0.056	0.123	Incl.Aspect	-0.303	-0.090	0.075	0.060
RockT1	-0.124	-0.017	0.020	0.123	Eastness	0.018	-0.039	-0.132	0.010
					Eastless				
RockT2	0.017	-0.139	-0.064	0.259		-0.047	-0.106	-0.153	0.024
RockT3	-0.233	0.251	-0.164	0.120	EastAspect	0.019	0.072	-0.121	0.055
Soils1	-0.310	0.449	-0.384	-0.015		RockT1	RockT2	RockT3	Soils1
Soils2	0.354	-0.152	0.033	-0.027	D 1.552				
Soils3	-0.154	0.027	0.241	-0.073	RockT2	0.007			
Climate1	0.657	-0.208	-0.022	-0.106	RockT3	-0.003	0.004		
Climate2	0.170	0.068	0.092	0.174	Soils1	-0.099	0.060	0.315	
Climate3	0.023	-0.099	-0.027	0.375	Soils2	-0.403	-0.103	-0.088	0.008
UTME	-0.660	0.339	-0.118	-0.166	Soils3	0.186	-0.005	-0.071	0.004
UTMN	0.457	-0.303	0.100	0.250	Climate1	-0.378	-0.099	-0.218	-0.221
Elev.Incl	-0.272	0.354	0.258	-0.112	Climate2	0.108	0.083	-0.013	0.000
Elev.Aspect	0.141	-0.077	-0.215	0.209	Climate3	0.160	0.124	0.005	0.005
Incl.Aspect	-0.118	0.232	-0.032	-0.039	UTME	0.402	-0.055	0.13	0.229
Eastness	-0.139	-0.039	-0.161	0.106	UTMN	-0.334	0.131	-0.03	-0.159
EastEast	-0.262	0.037	-0.171	0.068	Elev.Incl	-0.190	-0.307	0.074	0.123
EastAspect	0.086	-0.069	-0.231	0.089	Elev.Aspect	0.098	0.126	-0.011	0.012
					Incl.Aspect	-0.036	-0.163	0.095	0.145
	Inclination	AspectCor	Slope1	Slope2	Eastness	0.257	0.066	-0.043	0.036
AspectCor	-0.188				EastEast	0.320	0.050	-0.009	0.077
Slope1	-0.374	0.211			EastAspect	0.165	0.050	-0.027	0.016
Slope2	-0.084	0.150	0.003		LastAspect	0.103	0.050	-0.027	0.010
Slope3	-0.359	0.130	-0.010	0.008		Soils2	Soils3	Climate1	Climate2
RockS1	-0.126	0.009	0.016	-0.014	Soils3	-0.009			
RockS2	0.346	-0.093	-0.166	-0.383	Climate1	0.312	-0.288		
					l			-0.004	
RockS3	0.062	0.048	0.022 0.179	0.079	Climate2	-0.017	0.004	-0.004	0.020
RockT1	-0.170	0.098		0.212	Climate3	-0.080	0.053		0.020
RockT2	-0.330	0.091	0.114	0.068	UTME	-0.357	0.154	-0.464	-0.087
RockT3	0.051	-0.016	-0.071	-0.018	UTMN	0.256	-0.148	0.31	0.080
Soils1	0.128	0.006	-0.032	0.154	Elev.Incl	0.028	0.068	-0.122	-0.045
Soils2	0.020	0.025	-0.072	-0.135	Elev.Aspect	0.019	-0.174	0.116	0.051
Soils3	0.086	-0.173	0.052	-0.041	Incl.Aspect	0.025	-0.056	-0.009	-0.005
Climate1	-0.121	0.133	-0.038	-0.039	Eastness	-0.168	0.060	-0.132	-0.037
Climate2	-0.064	0.042	0.144	-0.152	EastEast	-0.234	0.087	-0.218	-0.053
Climate3	-0.213	-0.024	0.161	-0.115	EastAspect	-0.034	-0.129	0.086	0.012
UTME	0.209	0.153	-0.025	0.330		CI:2	LITALE	LITEMANI	F1 I 1
UTMN	-0.202	-0.246	0.006	-0.241		Climate3	UTME	UTMN	Elev.Incl
Elev.Incl	0.986	-0.167	-0.344	-0.112	UTME	-0.165			
Elev.Aspect	-0.206	0.992	0.224	0.139	UTMN	0.193	-0.889		
Incl.Aspect	0.527	0.591	-0.057	0.077	Elev.Incl	-0.168	0.179	-0.166	
Eastness	-0.122	0.045	0.138	0.087	Elev.Aspect	0.008	0.139	-0.221	-0.172
EastEast	-0.073	0.079	0.122	0.153	Incl.Aspect	-0.084	0.288	-0.335	0.540
EastAspect	-0.188	0.940	0.214	0.174	Eastness	0.034	0.229	-0.111	-0.112
- Eustrispeet	0.100	0.510	0.211	0.171	EastEast	0.002	0.415	-0.283	-0.069
	Slope3	RockS1	RockS2	RockS3	EastAspect	-0.039	0.223	-0.277	-0.171
	F								
RockS1	0.372					Flow Aspect	Incl Acrost	Factnoss	FootFoot
RockS2	0.372	0.005				Elev.Aspect	Incl.Aspect	Eastness	EastEast
	0.372	0.005 -0.015	0.002		Incl.Aspect	Elev.Aspect 0.566	Incl.Aspect	Eastness	EastEast
RockS2	0.372		0.002 -0.056	-0.053	Incl.Aspect Eastness		Incl.Aspect 0.003	Eastness	EastEast
RockS2 RockS3	0.372 -0.008 -0.030	-0.015		-0.053 -0.017		0.566	•	Eastness 0.979	EastEast