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Catena 49 (2002) 203–215

CATENA

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Variability in an edaphic indicator in alpine tundra

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Received 24 October 2001; received in revised form 12 March 2002; accepted 28 March 2002

Abstract

Spatial patterns of soil in alpine tundra just above timberline may determine patterns of advance by woody species. Patterns of advance since the Little Ice Age show spatial aggregation. If soil resources have similar patterns of aggregation, they might determine the pattern of vegetation change. Effective soil depth (ESD), which takes into account stoniness, was measured in tundra just above present timberline on regular grids at two scales and across solifluction treads and risers. No non-random spatial pattern was found, nor was there any difference related to relict solifluction patterns. Current patterns of woody vegetation could not have developed in direct response to the pattern of effective soil depth found in tundra. These patterns may develop in response to other soil factors, but may also include positive feedback. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Treeline; Rock fragments; Solifluction; Spatial pattern

1. Introduction

The patterns of vegetation at timberlines may indicate the processes that produced them and so may help in developing prediction of future ecotone dynamics (Malanson, 1999). Ecotone change has been identified as a potential early indicator of climatic change because species are at some limit to their distribution. If the limit is climatic, then the gross pattern of species presence or absence should react sensitively to climatic change in this environment.

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If vegetation pattern is a direct reflection of the pattern of the abiotic environmental controls on plant establishment and growth, then we might expect responses to changes in those factors without critical thresholds; if, conversely, pattern reflects positive feedbacks, wherein plants modify the environment to improve their own reproduction and growth and lessen that for others, we might expect critical points. The determination of the quantitative form of the relations between pattern and process are necessary to assess timberlines as useful indicators of climatic change; the range of variation among interacting variables will complicate this effort (Kupfer and Cairns, 1996).

Most studies have addressed the response of timberline in terms of the tree species. If we consider the advance of tree species from the perspective of the invasibility of tundra, we need to examine why some areas of tundra are invaded and others not (Malanson and Butler, 1994). Increasingly, attention is being paid to the spatial pattern of tree species advances since the Little Ice Age (Malanson, 1997). Tree species patterns at timberline vary depending on their topographic setting (Allen and Walsh, 1996). The observed patterns are distinctly aggregated (Fig. 1). Our objective is to examine spatial patterns in tundra that might determine the spatial pattern of their invasibility and thus the development of tree species patterns. We assess the variability in soil resources that might affect the advance of tree species into tundra at alpine timberline.

The pattern of soil resources could be the basis for the pattern of tree species. The resource averaging hypothesis of treelines (Stevens and Fox, 1991) identifies soil resources as a basis for a boundary between trees and vegetation of smaller stature, and



Fig. 1. Patches of krummholz at timberline are a component of aggregated patterns.

the processes are such that the pattern of vegetation would closely reproduce the pattern of resources (Malanson et al., 2001). The effects of geomorphic soil resources on specific patterns of vegetation, or the reverse, have been shown repeatedly (e.g., Valentin et al., 1999; Zonneveld, 1999); effects at ecotones have been elucidated (e.g., Bednorz et al., 2000); and effects specifically at alpine timberline have been identified (Bamberg and Major, 1968; Holtmeier and Broll, 1992; Malanson and Butler, 1994; Seastedt and Vaccaro, 2001; Shiels and Sanford, 2001). Thus, we expect that soil conditions should affect the invasibility of tundra. Higher levels of soil fertility could support greater plant growth, and thus trees (cf. Stevens and Fox, 1991) but high soil fertility could support denser tundra that could inhibit tree species seedlings in their initial stages of development (Malanson and Butler, 1994).

We expect pattern in tundra soils. A basic catena on slopes, which could be affected by slope shape and by local geomorphology such as landforms of patterned ground, is likely (e.g., Klimowicz and Uziak, 1996; Bockheim et al., 2000, cf. Macdonald et al., 1999). Burns and Tonkin (1982) proposed a Synthetic Alpine Slope model in which catena development can lead to geomorphic thresholds—and thus pattern. Pedogenesis along environmental gradients has been described for several sites near timberline (e.g., Stanton et al., 1994). Patterned ground could also affect the catena, but it too is correlated with slope position and shape (Butler and Malanson, 1989; Butler and Malanson, 1999; Walsh et al., 2002). All of these factors would create pattern either at larger or smaller scales than that observed in recent tree species advances. Vegetation itself also creates pattern in soils near timberline (e.g., Holtmeier and Broll, 1992; Pauker and Seastedt, 1996; Seastedt and Adams, 2001). Allen et al. (2002) reported some spatial patterning in soil nutrients, but these were for data that included tundra and krummholz in the sampling grid. Some patterns in tundra soils may be relict from periods with higher timberline.

Among soil resources, a variety of factors could be important to the advance of tree species. Cairns and Malanson (1998) found that soil depth could be a limitation for tree growth because it would limit the amount of water available; this factor may be generally important in montane landscapes (e.g., Urban et al., 2000). At least for the establishment phase, ongoing research indicates that tundra soils are deep enough that soil depth would not be limiting (G. Schmid, personal communication). Surface stoniness and penetrability could be a factor, but where this factor is controlled by solifluction treads and risers, the overall pattern of advancing tree species does not correspond (Walsh et al., 2002). Nutrients do not seem to vary at this scale either. Here, we investigate a measure that may summarize aspects of all of these: the effective soil depth (ESD). By ESD, we mean the soil that is available to plant roots; i.e., soil that is below large clasts is not effective from the perspective of providing water or nutrients to roots.

Our approach to ESD is derived from studies of the edaphic effects of rock fragments, or stoniness. Poesen and Lavee (1994) noted that rock fragments could affect hydrological, thermal, and productivity aspects of soils. The effects on plant growth are not straightforward: they may be positive, negative, or ambivalent (cf. Ingelmo et al., 1994). Kosmas et al. (1994) noted that rock fragments would decrease plant productivity under wet conditions but could increase it under dry conditions (also see van Wesemael et al., 2000). Rock fragments

can also potentially limit root development in the early post-germination stage (e.g., Funes et al., 1999). Whatever the particular effects, it is clear that soil depth and rock fragments can affect patterns of vegetation.

We address these questions about the variability of ESD in alpine tundra soils: How variable is this soil resource in the tundra just upslope of timberline? How stationary is the variability from site to site? Is there a spatial structure in the variation?

2. Study area

We examined tundra just above timberline in Glacier National Park (GNP), Montana (Fig. 2). Alpine soils in GNP have been described as Lithic Cryochrepts in the Ptarmigan Series (Dutton and Marrett, 1997), which are thin, but have a well developed

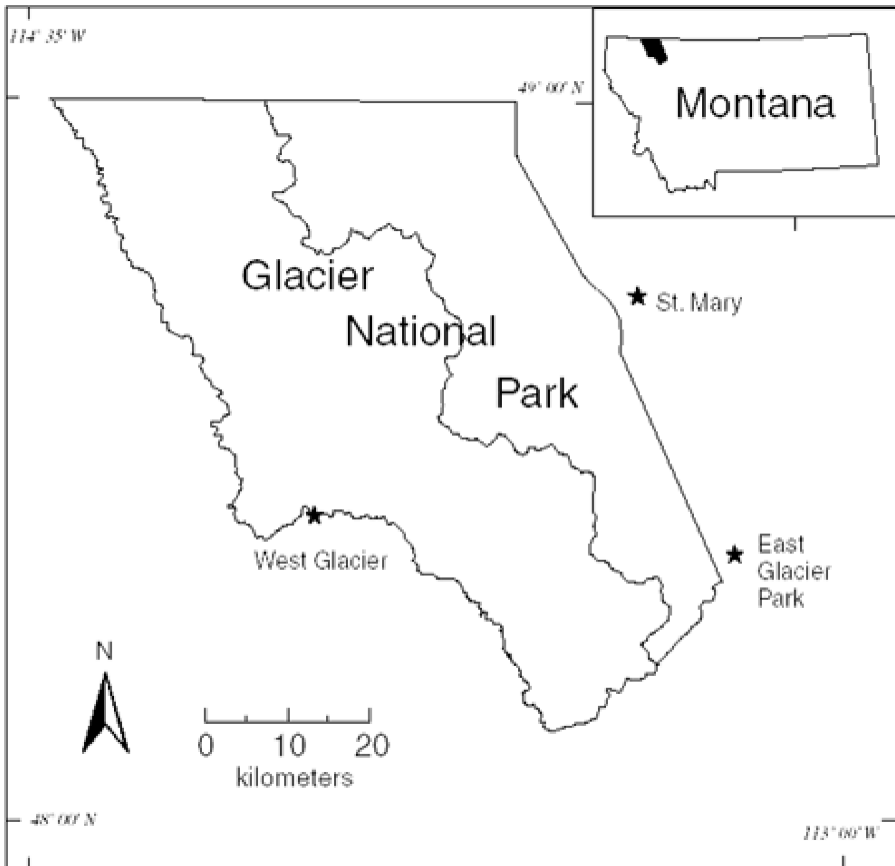


Fig. 2. Location of Glacier National Park, MT, USA showing the continental divide.



Fig. 3. Geomorphic pattern of solifluction terraces at timberline.



Fig. 4. Effective soil depth was sampled with a steel rod.

O2 horizon and stony to very stony sandy loam to sand A, B and C horizons (Nimlos and McConnell, 1962). Cairns (1999) found that differences between krummholz and tundra soils varied with spatial aggregation; they differed regionally in nitrogen and carbon, but locally in these plus phosphorous and potassium, especially on more xeric sites. Tree species at timberline are usually *Abies lasiocarpa* and/or *Picea engelmannii*; *Pseudotsuga menziesii*, *Pinus albicaulis*, and even *Pinus flexilis* are occasionally present.

Becwar and Burke (1982) estimated that 80% of the transition from forest to tundra in GNP occurs over a 550-m range; in contrast, in Rocky Mountain National Park, 80% of the transition occurs over 200 m. Most research on timberline in GNP has focused on its elevation (e.g., Habeck, 1969; Walsh and Kelly, 1990; Brown, 1994). The variability in alpine timberline ecotone elevation in GNP may be due to combinations of variability in macroclimate, microclimate, topography, and snow and debris avalanches, and competition with tundra (Walsh et al., 1992, 1994; Butler and Walsh, 1994; Malanson and Butler, 1994; Cairns and Malanson, 1997; Cairns, 2001).

Major patterns include patches of krummholz above continuous forest, fingers of trees and krummholz extending above continuous forest into tundra, and abrupt upright tree-to-tundra boundaries (Allen and Walsh, 1996; Malanson, 1997). It appears that the present extent of tree species is as high as it has been in ca. 600 years. Many timberline sites, including those examined here, are found on relict solifluction terraces (Fig. 3). Butler and Malanson (1989) described some basic relations on and among these terraces, and Walsh et al. (2002) expanded this description.

3. Methods and materials

On 12 tundra sites just above timberline, we randomly located and laid out a 40 × 40 m plot with a 10 × 10 m grid, giving 25 intersections. Within the lower left corner of 11 of these plots, we established a 4 × 4 m subplot with a 1 × 1 m grid for another 25 points. The baseline corner point, designated as 0/0, was the same for both plots. At each intersection, we randomly chose one of four points 50 cm from the intersection point and at 45° to the grid layout. To sample ESD we pushed a steel rod into the ground three times within 5 cm of this point and recorded the deepest measure (Fig. 4). While penetration is a poor measure of total soil depth, it can be a good indicator of stoniness or ESD. Eriksson and Holmgren (1996) found what appears to be a very close, if nonlinear, relation between penetration and stoniness.

To differentiate treads and risers, we ran five 50 m line transects along the slope in places where solifluction was evident. We sampled ESD for each intercepted tread and riser as above.

4. Analyses and results

A *t*-test found no significant differences between means of treads and risers (15.91 and 15.27, respectively). The CVs (0.49 and 0.46) were similar to those measured on the grids.

Table 1
Statistics on effective soil depth (ESD) ($N=25$ per grid)

	40 m grids			4 m grids		
	Mean	S.D.	CV	Mean	S.D.	CV
Site 1	15.54	6.69	0.43			
Site 2	16.72	12.30	0.74	22.44	10.95	0.49
Site 3	10.64	7.88	0.74	11.16	4.97	0.45
Site 4	39.70	27.91	0.70	21.72	15.80	0.73
Site 5	10.84	5.01	0.46	11.20	6.05	0.54
Site 6	12.36	7.58	0.61	8.08	5.24	0.65
Site 7	11.18	9.25	0.83	9.62	7.18	0.75
Site 8	21.61	7.61	0.35	22.52	13.35	0.59
Site 9	18.16	10.02	0.55	10.84	8.21	0.76
Site 10	6.52	4.45	0.68	5.54	5.64	1.00
Site 11	26.64	12.00	0.45	22.44	11.12	0.50
Site 12	18.32	11.49	0.63	45.36	25.33	0.56
All Data	17.36	14.41	0.83	17.36	15.92	0.92

We analyzed the ESD by computing the means and the coefficient of variation (CV) for the 12 coarse scale and 11 fine scale grids. We analyzed the spatial pattern in ESD by computing Moran's I and semivariograms for the 12 coarse scale and 11 fine scale grids. Moran's I indicates correlation among measures as a function of location; the semivariogram can also test for spatial autocorrelation, and can quantify pattern intensity and scale (Fortin, 1999).

Mean ESD ranged from 6.52 to 39.7 cm on the coarser grid and from 5.54 to 45.36 cm on the finer grid (Table 1). The mean depth for all 10 m and all 1 m grid samples was identical: 17.36 cm. Individual CVs ranged from 35% to 53% on the coarse grid and from

Table 2
Moran's I -statistics

Plot	40 m grids			4 m grids		
	Corr	z -Stat	p value	Corr	z -stat	p value
1	-0.2037	-0.7906	0.4292	NA	NA	NA
2	-0.4187	-2.0223	0.0431	-0.0686	-0.2906	0.7713
3	-0.0711	-0.0698	0.9444	-0.0642	-0.2488	0.8036
4	-0.0769	-0.097	0.9227	-0.2103	-1.7036	0.0885
5	-0.3748	-1.7133	0.0867	0.0417	0.8233	0.4104
6	0.0362	0.5627	0.5736	-0.0394	0.006	0.9952
7	0.0298	0.4746	0.6351	-0.1355	-1.0042	0.3153
8	-0.2566	-0.8428	0.3993	0.0201	0.6289	0.5294
9	0.2509	1.6709	0.0947	-0.0776	-0.376	0.7069
10	-0.0462	0.0858	0.9316	-0.0312	0.0913	0.9272
11	-0.1587	-0.551	0.5817	0.0655	1.0864	0.2773
12	0.0861	0.8713	0.3836	-0.1301	-0.9046	0.3657

All points within 11 and 1.5 m of each other are considered connected for the 40- and 4-m grids, respectively.

45% to 100% on the fine grid. The range and the CV were greater for the combined 1 m samples even though they were within the coarser scale grids.

No non-random pattern emerged in the spatial analyses (Table 2; Fig. 5). Moran's *I* detected no significant spatial autocorrelation. Any lag spatial autocorrelation that a semivariogram might show must be at a lag of less than 1 m if it exists at all.

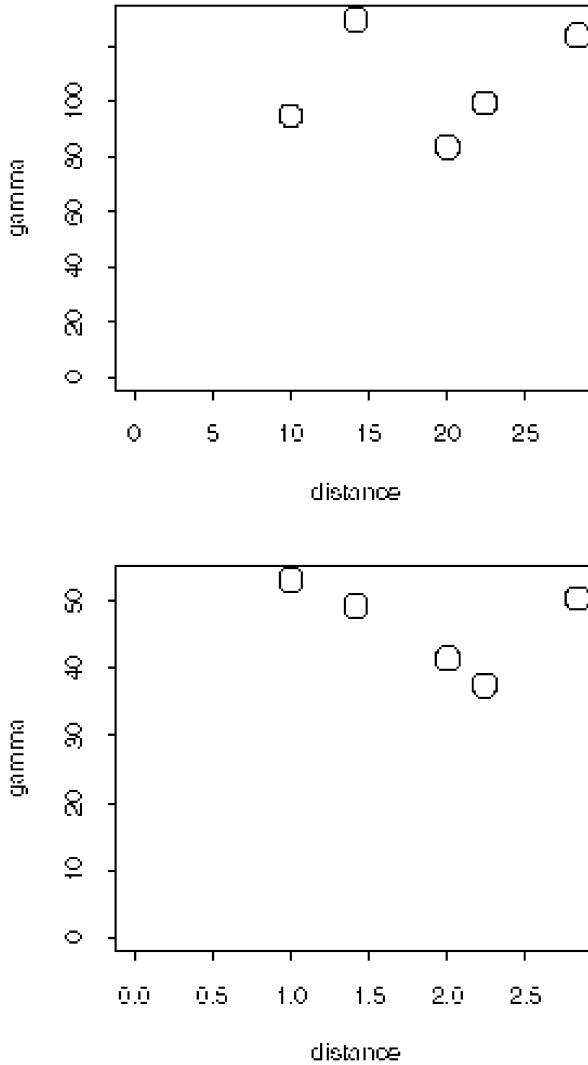


Fig. 5. Examples of semivariograms of the coarse grids (40 × 40 m extent and 10 m resolution) and fine grids (4 × 4 m extent and 1 m resolution).

5. Discussion

The variance in ESD is consistent across scale from a 4×4 m at 1 m resolution to 40×40 m at 10 m resolution. The variability at the fine scale is simply repeated up to and possibly exceeding the coarse scale. At greater scale, features such as breaks in slope, avalanche paths, debris flows, and lithologic and stratigraphic differences would create spatial patterning in ESD. The finer scale geomorphic features, such as the treads and risers of solifluction terraces, also do not create non-random spatial pattern in ESD at the 4×4 m scale in our sampling design. The similarity in ESD below both treads and risers indicates that the process produces potentially ecologically relevant pattern only at the surface.

The spatial pattern of the advance of trees and krummholz into tundra is not controlled by ESD. The patterns that are seen, primarily fingers and patches, are of extent greater than 1 m and less than 20 m. Non-random patterns of ESD do not exist at this scale. Even with resource averaging, the patterns of the vegetation would still match the patterns of the resource. The pattern of tree species could be related in some way to solifluction patterns in terms of the surface characteristics experienced by a seed beginning to germinate, but these are at a scale of about 1 m. Other forms of potential geomorphic control that may be relevant elsewhere are not relevant at this site. No incised channels exist across the study area such as might concentrate (or preclude) moisture to aid in seedling establishment. Although minor amounts of animal pedoturbation exist in the area (sensu [Butler, 1995](#)) in the form of burrowing ground squirrels, it is spatially limited to a few protected sites behind boulders, or within or adjacent to already existing treeline patches where soil is deeper. Fine-scale frost sorting, as evidenced by unvegetated frost boils such as occur throughout tundra sites in eastern Glacier Park ([Butler and Malanson, 1999](#)) has been observed on the higher parts of Lee Ridge, but at a scale of less than 20 cm, certainly not at a scale sufficient to explain patterns of fingers at scales in excess of 1 m. The role of underlying lithology and past glaciation (cf. [Butler et al., 2002](#)) seem equally unlikely as possible explanations, particularly since the ridge is of uniform lithology and lies well above the elevation of the highest adjacent Pleistocene terminal/lateral moraine complex. One possibility, which we are in the process of examining, is soil penetrability. Neither treads nor risers vary notably in the ease with which they may be penetrated by a soil penetrometer, but turf exfoliation (Rasenabschälung) (sensu [Perez, 1992](#)) exists at several locations on Lee Ridge, and those sites possess soils that are significantly easier to penetrate ([Butler et al., manuscript in preparation](#)). To the degree it is represented by ESD, geomorphology alone cannot determine the vegetative pattern because there is a mismatch in scale. Even if recent advances were into areas with relict soils from earlier high timberlines, the initial process would still be unrelated to ESD.

We hypothesize that the pattern of vegetation is a result of patterns of resources other than ESD, such as good sites for seedling establishment, that are extended in space by positive feedbacks ([Wilson and Agnew, 1992](#); [Timoney et al., 1993](#); [Malanson, 1997](#)) wherein the growing woody plants modify the environment to improve the conditions for woody plant establishment and growth. Good sites for seedling establishment could involve soil surface characteristics, such as faunal pedoturbation by mammals ([Butler,](#)

1995) not studied here. Positive feedback could produce both the larger patches and the fingers observed in addition to a straighter switch.

By improving the local environment for trees, trees can produce more spatial autocorrelation than would be determined by the underlying resources. Positive feedbacks could improve the local environment in at least three categories:

- increasing organic matter, soil nutrients, fine soil and correlated water holding capacity (cf. Cairns, 1999);
- decreasing wind and thus trapping snow and increasing soil moisture and reducing desiccation (e.g., Cairns, 2001);
- raising canopy temperatures through lower albedo (but see Korner, 1998 for lower root temperatures).

These positive feedbacks can create patches where only a smaller area of resource sufficient for establishment and growth existed. Fingers can result if there is a directional component to the feedback. Such directional components could include slope and wind (Holtmeier, 1982). Other linear patterns, such as “tiger bush” in southern Africa, result from positive feedback (e.g., Leprun, 1999).

Temporal dynamics that capture intraspecific positive feedbacks (cf. Noble, 1993) as well as positive interactions between species (Callaway, 1997; Brooker and Callaghan, 1998) are needed in order to create a more complete model of the ecotone. Efforts to improve our understanding of the alpine timberline ecotone through computer models have indicated that such feedbacks are important, but none can yet adequately simulate the interaction of pattern and process (Bekker et al., 2001).

Acknowledgements

This research was funded by NSF grant SBR-9714347 to GPM and by a grant from the USGS Biological Resources Division to D.R.B., D.M.C. and G.P.M. We thank Dan Fagre, our USGS PI, for coordinating our field research. Chelsea Kelley assisted in the field. This is a contribution of the Mountain GeoDynamics Research Group.

References

- Allen, T.R., Walsh, S.J., 1996. Spatial composition and pattern of alpine treeline, Glacier National Park, Montana. *Photogrammetric Engineering and Remote Sensing* 62, 1261–1268.
- Allen, T.R., Walsh, S.J., Cairns, D.M., Messina, J., Butler, D.R., Malanson, G.P., 2002. Geostatistics and spatial analysis: characterizing form and pattern at the alpine treeline. In: Bishop, M., Shroder, J. (Eds.), *Geographic Information Science and Mountain Geomorphology*. Springer-Praxis, London, in press.
- Bamberg, S.A., Major, J., 1968. Ecology of the vegetation and soils associated with calcareous parent materials in three alpine regions of Montana. *Ecological Monographs* 38, 127–167.
- Becwar, M.R., Burke, M.J., 1982. Winter hardiness limitations and physiography of woody timberline flora. In: Li, P.H., Sakai, A. (Eds.), *Plant Cold Hardiness and Freezing Stress: Mechanisms and Crop Implications*, vol. 2. Academic Press, New York, pp. 307–323.

- Bednorz, F., Reichstein, M., Broll, G., Holtmeier, F.K., Urfer, W., 2000. Humus forms in the forest–alpine tundra ecotone at Stillberg (Dischmatal, Switzerland): spatial heterogeneity and classification. *Arctic, Antarctic and Alpine Research* 32, 21–29.
- Bekker, M.F., Malanson, G.P., Alftine, K.J., Cairns, D.M., 2001. Feedback and pattern in computer simulations of the alpine treeline ecotone. In: Millington, A.C., Walsh, S.J., Osborne, P.E. (Eds.), *GIS and Remote Sensing Applications in Biogeography and Ecology*. Kluwer Academic Publishing, Dordrecht, pp. 123–138.
- Bockheim, J.G., Munroe, J.S., Douglass, D., Koerner, D., 2000. Soil development along an elevational gradient in the southeastern Uinta Mountains, Utah, USA. *Catena* 39, 169–185.
- Brooker, R.W., Callaghan, T.V., 1998. The balance between positive and negative plant interactions and its relationship to environmental gradients: a model. *Oikos* 81, 196–207.
- Brown, D.G., 1994. Comparison of vegetation–topography relationships at the alpine treeline ecotone. *Physical Geography* 15, 125–145.
- Burns, S.F., 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*. George Allen and Unwin, London, pp. 25–43.
- Butler, D.R., 1995. *Zoogeomorphology: Animals as Geomorphic Agents*. Cambridge Univ. Press, Cambridge.
- Butler, D.R., Malanson, G.P., 1989. Periglacial patterned ground, Waterton-Glacier International Peace Park, Canada and USA. *Zeitschrift für Geomorphologie* 33, 43–57.
- Butler, D.R., 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., Walsh, S.J., 1994. Site characteristics of debris flows and their relationship to alpine treeline. *Physical Geography* 15, 181–199.
- Butler, D.R., Malanson, G.P., Bekker, M.F., Reseler, L., 2002. Lithologic, structural, and geomorphic controls on ribbon forest patterns. *Geomorphology*, in review.
- Cairns, D.M., 1999. Multi-scale analysis of soil nutrients at alpine treeline in Glacier National Park, Montana. *Physical Geography* 20, 256–271.
- Cairns, D.M., 2001. Patterns of winter desiccation in krummholz forms of *Abies lasiocarpa* at treeline sites in Glacier National Park, Montana, USA. *Geografiska Annaler* 83A, 157–168.
- Cairns, D.M., Malanson, G.P., 1997. Examination of the carbon balance hypothesis of alpine treeline location, Glacier National Park, Montana. *Physical Geography* 18, 125–145.
- Cairns, D.M., Malanson, G.P., 1998. Environmental variables influencing carbon balance at the alpine treeline ecotone: a modeling approach. *Journal of Vegetation Science* 9, 679–692.
- Callaway, R.M., 1997. Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112, 143–149.
- Dutton, B.L., Marrett, D.J., 1997. *Soils of Glacier National Park East of the Continental Divide*. Land and Water Consulting, Missoula, MT.
- Eriksson, C.P., Holmgren, P., 1996. Estimating stone and boulder content in forest soils—evaluating the potential of surface penetration methods. *Catena* 28, 121–134.
- Fortin, M.-J., 1999. Spatial statistics in landscape ecology. In: Klopatek, J.M., Gardner, R.H. (Eds.), *Landscape Ecological Analysis*. Springer, New York, pp. 253–279.
- Funes, G., Basconcelo, S., Diaz, S., Cabido, M., 1999. Seed bank dynamics of *Lachemilla pinnata* (Rosaceae) in different plant communities of mountain grasslands in central Argentina. *Annales Botanici Fennici* 36, 109–114.
- Habeck, J.R., 1969. A gradient analysis of a timberline zone at Logan Pass, Glacier National Park, Montana. *Northwest Science* 43, 65–73.
- Holtmeier, F.-K., 1982. “Ribbon-forest” and “hedges.” Strip-like distribution patterns of trees at the upper timberline in the Rocky Mountains. *Erdkunde* 36, 142–153.
- Holtmeier, F.-K., Broll, G., 1992. The influence of tree islands and microtopography on pedoecological conditions in the forest–alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arctic and Alpine Research* 24, 216–228.
- Ingelmo, F., Cuadrado, S., Ibanez, A., Hernandez, J., 1994. Hydric properties of some Spanish soils in relation to their rock fragment content: implications for runoff and vegetation. *Catena* 23, 73–85.

- Klimowicz, Z., Uziak, S., 1996. Arctic soil properties associated with micro-relief forms in the Bellsund region (Spitsbergen). *Catena* 28, 135–149.
- Korner, C., 1998. A reassessment of high-elevation treeline positions and their explanation. *Oecologia* 115, 445–459.
- Kosmas, C., Moustakas, N., Danalatos, N.G., Yassoglou, N., 1994. The effect of rock fragments on wheat biomass production under highly variable moisture conditions in Mediterranean environments. *Catena* 23, 191–198.
- Kupfer, J.A., Cairns, D.M., 1996. The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography* 20, 253–272.
- Leprun, J.C., 1999. The influence of ecological factors on tiger bush and dotted bush patterns along a gradient from Mali to northern Burkina Faso. *Catena* 37, 25–44.
- Macdonald, B.C.T., Melville, M.D., White, I., 1999. The distribution of soluble cations within chenopod-patterned ground, arid western New South Wales, Australia. *Catena* 37, 89–105.
- Malanson, G.P., 1997. Effects of feedbacks and seed rain on ecotone patterns. *Landscape Ecology* 12, 27–38.
- Malanson, G.P., 1999. Considering complexity. *Annals, Association of American Geographers* 89, 746–753.
- Malanson, G.P., Butler, D.R., 1994. Competitive hierarchies, soil fertility gradients, and the elevation of treeline in Glacier National Park, Montana. *Physical Geography* 15, 166–180.
- Malanson, G.P., Xiao, N., Alftine, K.J., 2001. A simulation test of the resource averaging hypothesis of ecotone formation. *Journal of Vegetation Science* 12, 743–748.
- Nimlos, T.J., McConnell, R.C., 1962. The morphology of alpine soils in Montana. *Northwest Science* 36, 99–112.
- Noble, I.R., 1993. A model of the responses of ecotones to climate change. *Ecological Applications* 3, 396–403.
- Pauker, S.J., Seastedt, T.R., 1996. Effects of mobile tree islands on soil carbon storage in tundra ecosystems. *Ecology* 77, 2563–2567.
- Perez, F.L., 1992. Processes of turf exfoliation (Rasenabschälung) in the high Venezuelan Andes. *Zeitschrift für Geomorphologie* 36, 81–106.
- Poesen, J., Lavee, H., 1994. Rock fragments in top soils—significance and processes. *Catena* 23, 1–28.
- Seastedt, T.R., Adams, G.A., 2001. Effects of mobile tree islands on alpine tundra soils. *Ecology* 82, 8–17.
- Seastedt, T.R., Vaccaro, L., 2001. Plant species richness, productivity, and nitrogen and phosphorus limitations across a snowpack gradient in alpine tundra, Colorado, USA. *Arctic, Antarctic and Alpine Research* 33, 100–106.
- Shiels, A.B., Sanford, R.L., 2001. Soil nutrient differences between two krummholz-form tree species and adjacent alpine tundra. *Geoderma* 102, 205–217.
- Stanton, M.L., Rejmanek, M., Galen, C., 1994. Changes in vegetation and soil fertility along a predictable snowmelt gradient in the Mosquito Range, Colorado, USA. *Arctic and Alpine Research* 26, 364–374.
- Stevens, G.C., Fox, J.F., 1991. The causes of treeline. *Annual Review of Ecology and Systematics* 22, 177–191.
- Timoney, K.P., La Roi, G.H., Dale, M.R.T., 1993. Subarctic forest-tundra vegetation gradients: the sigmoid wave hypothesis. *Journal of Vegetation Science* 4, 387–394.
- Urban, D.L., Miller, C., Halpin, P.N., Stephenson, N.L., 2000. Forest gradient response in Sierran landscapes: the physical template. *Landscape Ecology* 15, 603–620.
- Valentin, C., d'Herbes, J.M., Poesen, J., 1999. Soil and water components of banded vegetation patterns. *Catena* 37, 1–24.
- van Wesemael, B., Mulligan, M., Poesen, J., 2000. Spatial patterns of soil water balance on intensively cultivated hillslopes in a semi-arid environment: the impact of rock fragments and soil thickness. *Hydrological Processes* 14, 1811–1828.
- Walsh, S.J., Kelly, N.M., 1990. Treeline migration and terrain variability: integration of remote sensing digital enhancements and digital elevation models. *Proceedings, Applied Geography Conference* 13, 24–32.
- Walsh, S.J., Malanson, G.P., Butler, D.R., 1992. Alpine treeline in Glacier National Park, Montana. In: Janelle, D.G. (Ed.), *Geographical Snapshots of North America*. Guilford Press, New York, pp. 167–171.
- Walsh, S.J., Butler, D.R., Allen, T.R., Malanson, G.P., 1994. Influence of snow patterns and snow avalanches on the alpine treeline ecotone. *Journal of Vegetation*, 657–672.

- Walsh, S.J., Butler, D.R., Malanson, G.P., Crews-Meyer, K.A., Messina, J.P., Xiao, N., 2002. Mapping, modeling, and visualization of the influences of geomorphic processes on the alpine treeline ecotone, Glacier National Park, Montana, USA. *Geomorphology*, (in press).
- Wilson, J.B., Agnew, A.D.Q., 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* 23, 263–336.
- Zonneveld, I.S., 1999. A geomorphological based banded ('tiger') vegetation pattern related to former dune fields in Sokoto (Northern Nigeria). *Catena* 37, 45–56.