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Fine-Scale Patterns of Soil and Plant Surface Temperatures in an Alpine Fellfield Habitat, White Mountains, California

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Abstract

Within alpine environments the interactions of air temperature, solar irradiance, wind, surface albedo, microtopography, and biotic traits all influence patterns of soil and plant canopy temperatures. The resulting mosaic of surface temperatures has a profound impact on ecosystem processes, plant survival, and ecophysiological performance. Previous studies have documented large and persistent variations in microhabitat temperatures over mesoscale alpine terrains. We have used a novel mobile system to examine changes in soil and plant canopy surface temperatures at spatial scales of centimeters and temporal scales of minutes in an alpine fellfield habitat in the White Mountains of California. In the middle of a summer day, the mean surface temperature differences between points 2, 5, and 10 cm apart were 2.9, 5.4, and 9.0 °C, respectively, and extreme differences of 18 °C or more were found over distances of a few centimeters. These thermal patterns are due not only to substrate material but also to biotic conditions of plant canopy architecture and ecophysiological traits of individual species. The magnitude of temperature variation at these fine scales is greater than the range of warming scenarios in Intergovernmental Panel on Climate Change (IPCC) projections, suggesting that these habitats offer the capacity of significant thermal heterogeneity for plant survival.

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Introduction

Local scale patterns in soil topography, substrate structure, plant cover, and soil moisture content have strong impacts on soil and plant microclimate in rugged alpine habitats. Local topography in particular has been shown to have a strong influence on the extremes and dynamics of alpine soil temperatures (Wundram et al., 2010). Such soil temperatures have a direct impact on plant ecophysiological performance, as well as indirect effects on soil microbial processes and even pollination success (Molau, 1997; Germino and Smith, 2001; Körner, 2003; Taschler and Neuner, 2004; Molau et al., 2005; Jordan and Smith, 2005; Kudo and Hirao, 2006; Torres-Diaz et al., 2007). Moreover, soil surface temperature in alpine microclimates may deviate significantly from air temperatures, adding complexity to patterns of surface temperatures (Scherrer and Körner, 2010, 2011). For this reason, conventional weather station data provide only a crude and relatively poor approach to understanding climatic niches of plant and animal species. It is not surprising, therefore, that local topography has a significant impact on alpine species distributions (Körner, 2003; Löffler and Pape, 2008; Jakalaniemi, 2011).

Beyond the microclimate effect of soil temperature, alpine plant canopies can experience significantly warmer or colder temperatures than those of the surrounding air. During the day, high rates of transpiration may cool leaf temperatures below air temperature while high solar input may raise canopy temperature well above air temperature (Salisbury and Spomer, 1964; Grace, 1987; Sage and Sage, 2002). Plant canopies can also insulate soils and at night, radiative heat loss to a cold sky may cool plants below air temperature.

High resolution models of soil and surface temperatures are critical for extrapolating ecosystem processes over a range of spatial and temporal scales in both arctic and alpine ecosystems (Klene et al., 2001a, 2001b). For alpine environments, the complex interaction of air temperature, solar irradiance, wind speed, surface albedo, microtopography, and evapotranspiration influence soil and plant canopy temperatures. Moreover, these factors show variable patterns depending on the temporal and spatial scale of analysis (Wundram et al., 2010). At a broad landscape level, Landsat Thermal Mapper and digital terrain data have been combined with radiative transfer models to map the spatial pattern of radiation balance for alpine ecosystems at Niwot Ridge in Colorado (Duguay and LeDrew, 1991; Duguay, 1994). These studies have limitations, however, in that they provide instantaneous flux estimates rather than hourly or 24-hour totals that are more relevant to ecological, climatological, and hydrological models. Moreover, they offer a relatively crude spatial scale because of the limitations of satellite imagery.

Recent advances in technologies of infra-red thermometry and cyberinfrastructure for data management and analysis now provide the means to collect and analyze large data sets on plant and soil surface temperatures at multiple spatial and temporal scales. These approaches have been used with success in detailed assessments of thermal environments across landscapes in subarctic and alpine regions (Scherrer and Körner, 2010), and soil thermal regimes in arctic tundra under a variety of land covers (Taylor, 2001; Klene et al., 2001b). In this paper, we use such approaches to examine microscale patterns of spatial and temporal changes in soil and plant canopy surface temperatures in an alpine fellfield habitat in the White Mountains of California. The novel aspect of our experimental deployment is the use of a mobile, or actuated, “ther-

mal mapper'' to collect 24-hour patterns of surface temperatures at spatial scales of centimeters and temporal scales of minutes. We use these to data to demonstrate the potential significance of microscale patterns of soil and plant surface temperatures with data relevant to understanding and modeling ecological and ecosystem processes at these fine scales.

Study Area

Our field studies were carried out in the White Mountains of eastern California. The range rises sharply from the Owens Valley at 1250 m elevation to a high point of 4343 m elevation at White Mountain Peak. Lying to the east and in the rain shadow of the Sierra Nevada, the White Mountains receive only about one-third of the rainfall of the Sierra Nevada at the same elevations. The Barcroft Laboratory of the White Mountains Research Station (latitude 37.538443°N, longitude -118.208084°W) at 3801 m has a mean annual precipitation of 478 mm, with the great majority of this falling as winter snow (Fig. 1). Monthly average air temperatures vary from a maximum of about 12 °C in July to -5 °C in January, with minimum average monthly temperatures remaining consistently about 10 °C lower. Despite a relatively small area of 106 km² of alpine habitat above 3500 m elevation, the White Mountains have a moderately rich alpine flora of 163 vascular plant species (Rundel et al., 2008).

We carried out our research at an alpine fellfield site (Fig. 2, part A) located on granitic parent material at 3750 m elevation, 1 km south of the Barcroft Laboratory. This site has plant cover of about 70%, dominated by *Eriogonum ovalifolium* Nutt. var. *nivale* (Canby) M.E. Jones (Polygonaceae), *Poa glauca* M. Vahl. subsp. *rupicola* (Nash) W.A. Weber (Poaceae), *Trifolium andersonii* A. Gray var. *beatleyae* (J.M. Gillett) Isley (Fabaceae), and *Penstemon heterodoxus* A. Gray var. *heterodoxus* (Plantaginaceae). Small boulders 15–40 cm in diameter were scattered across the landscape, as were exposed areas of sandy granitic soil. Measurements were carried out from 1 to 3 August 2005.

Materials and Methods

FIELD INSTRUMENTATION

The Networked Infomechanical Systems (NIMS) Rapidly Deployable (RD) unit consists of a fixed cableway infrastructure,

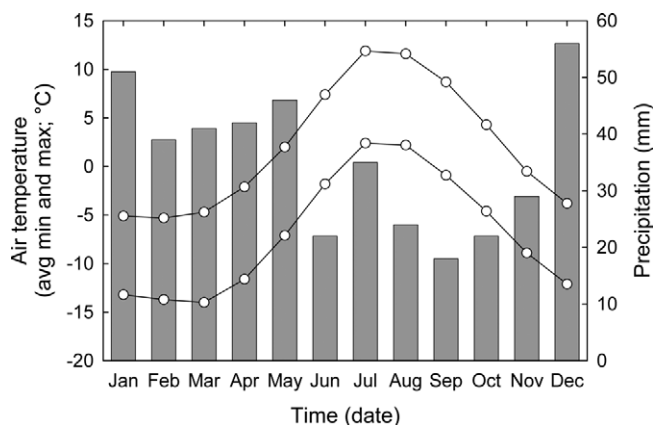


FIGURE 1. Long-term monthly maximum and minimum air temperature means (\pm S.D.) and precipitation from 1955 to 1980 for the Barcroft weather station (3801 m elevation).

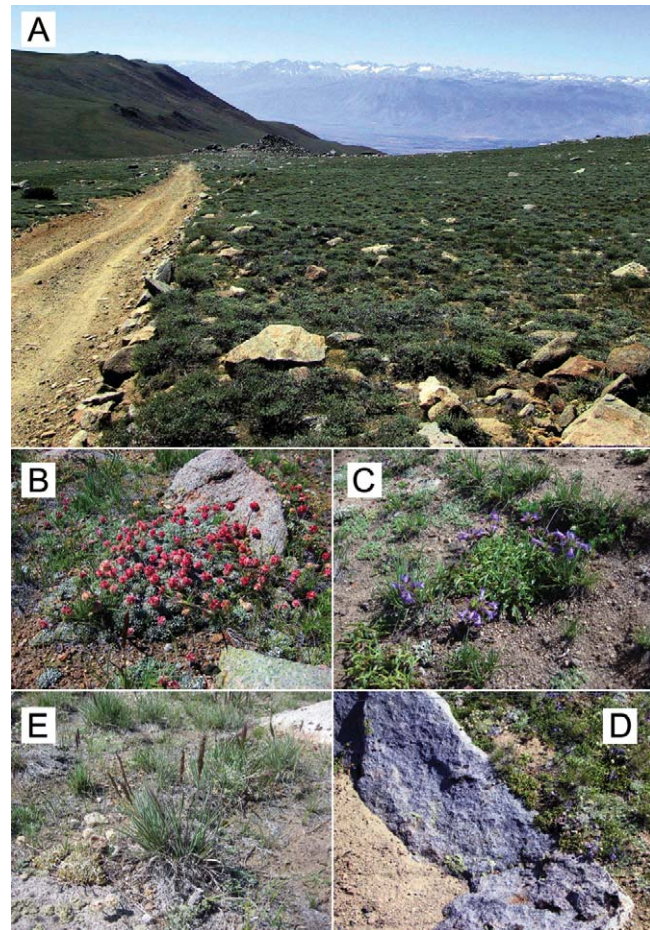


FIGURE 2. Alpine fellfield community on granite substrate at 3750 m elevation in the White Mountains, looking to the east across the Owens Valley to the snow-capped Sierra Nevada in the distance. (A) community surface characteristics; (B) cushions of *Eriogonum ovalifolium*; (C) mats of *Penstemon heterodoxus*; (D) upright leaves of *Poa glauca*; (E) small boulder with surrounding bare soil.

mounting hardware that supports this fixed cable, an auxiliary cable system which moves a shuttle on the fixed cableway, and a computer-controlled actuation module that contains and controls the drive motors for the auxiliary cables (Fig. 3, part A; Brett et al., 2007). The actuation module also acts as a data-collecting interface for the sensors that can be attached to the shuttle. NIMS was developed for and has been applied to a range of environmental sensing applications including terrestrial (Graham et al., 2010), aquatic (Caron et al., 2008), and contaminant observation and management (Harmon et al., 2007). NIMS addresses the new set of requirements for high spatial resolution sampling that have emerged in ecosystem investigations. NIMS, while scalable to deployments in large volumes of over 100-m span and 50-m depth, is applied here in a compact environment directed specifically to the investigation of alpine plant thermal properties. The NIMS RD system deployed for this investigation was a modified version without the fixed cable for moving the sensor platform (Stealey, 2007). Power was supplied by 12V batteries put through an inverter to convert to 110V AC to drive the motors. Actuation of the cable network occurred at high resolution, offering a horizontal position resolution of around 1 mm. An additional cable system was employed to reduce the

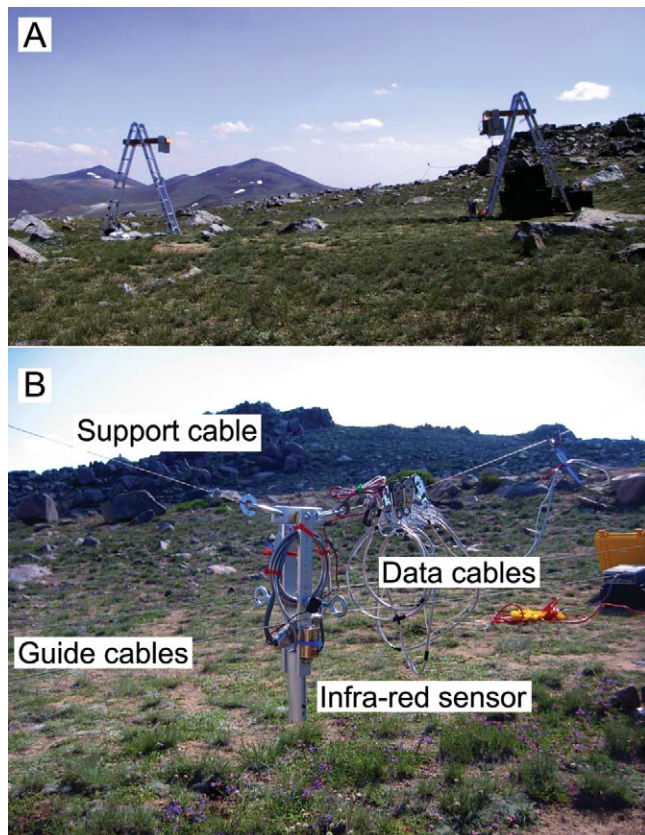


FIGURE 3. Cable-mounted mobile networked infomechanical systems (NIMS) rapidly deployable (RD) deployment with (A) support structures spanning the transect and (B) the infra-red sensor, showing support and guide cables and the festooned data cable.

influence of wind drag force that may otherwise create an undesired deflection of the shuttle.

The NIMS RD shuttle supported a thermal infra-red temperature sensor (Fig. 3, part B), image sensor, and laser rangefinder positioned approximately 30 cm above the ground surface. The combination of these instruments provided data for identification of each plant under the transect along with measurements of topography and plant and surface soil temperature. Experiments were performed by continuous scanning of the instrument package over a selected measurement transect on 1–2 August 2005. Each scan required an average of 9.8 ± 0.1 min (mean \pm S.D.) to complete. This transect allowed microscale measurements to 1 cm precision over a transect 3.7 m in length, covering a mix of open granite sand, a small boulder, and plant canopy cover of dominant species. The NIMS RD system performed the three sensor measurements in sequence with a dwell at each measurement location to accommodate the measurement rate for each device.

The system operated unattended during both day and night periods. To ensure that position sensor drift did not contribute an error in measurements, a calibration system was placed along the measurement transect. This consisted of a small aluminum plate coated with a high emissivity black paint and placed in the transect. Because the plate temperature differed significantly from that of the underlying soil, its presence displayed a distinctive thermal and topographic signal as well as a feature appearing in camera images.

These signals permitted verification of the position of the instrument package and calibration of location.

STATISTICAL DATA ANALYSES

We used the recursive partitioning and regression tree analysis (rpart version 3.1-50; Therneau and Atkinson, 2002) method in the freely available statistical analysis program R (version 2.13.1; R Development Core Team, 2011) to identify distinct periods in the 24-h temperature time series of different vegetation and substrates along the transect. Specific locations were selected for analysis using images captured of the transect by placing a digital camera on the NIMS RD shuttle platform. Chosen locations for classification contained nearly 100% cover of five different classes: boulder ($n = 11$), bare soil ($n = 10$), *Eriogonum ovalifolium* ($n = 17$), *Poa glauca* ($n = 8$), and *Penstemon heterodoxus* ($n = 14$).

Results

The diurnal spatial and temporal variation in surface temperatures ranged from as high as 50 °C during the afternoon in areas of bare soil to as low as 0 °C at night (Fig. 4). Distinctive “banded” patterns of temperatures present during the daylight hours represent the fine-scale distribution of surface cover, ranging from granite sandy soils which form much of the ground surface (labeled as “S” on the figure) to individual plant canopies. Plant cover included cushions of *Eriogonum ovalifolium* (E), prostrate mats of *Penstemon heterodoxus* (P), and upright tufts of the grass *Poa glauca*

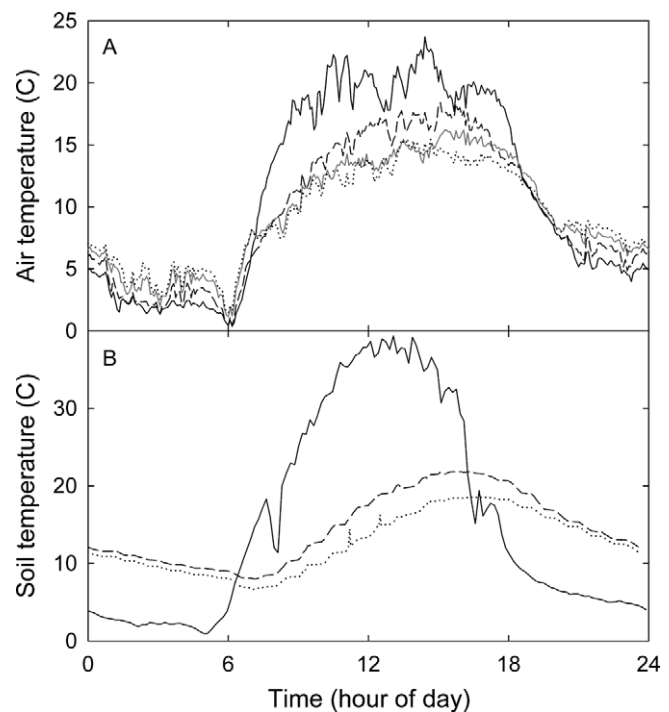


FIGURE 4. Hourly (A) air temperatures at 1 (solid black line), 10 (dashed black line), 30 (solid gray line), and 100 cm (dotted black line) above bare soil and (B) soil temperatures at the soil surface for a bare soil (solid black line) and at 10 cm depth in the soil below bare soil (dashed black line) and below *Eriogonum ovalifolium* (dotted black line) at the study site on 1–2 August 2005.

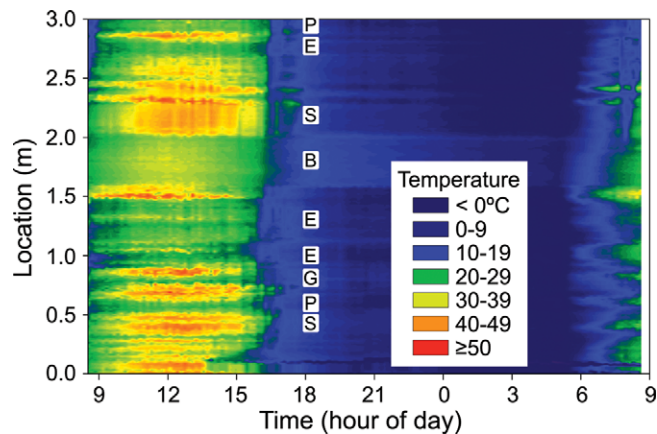


FIGURE 5. A 24-hour cycle of surface temperatures at a spatial resolution of 100 mm across a 3700 mm transect at the fellfield study site. Letters indicate locations where 100% cover of substrate or vegetation type was identified by digital images taken of the transect and include (B) boulder, (S) bare soil, (E) *Eriogonum ovalifolium*, (P) *Penstemon heterodoxus*, and (G) *Poa glauca*.

(G). The fine vertical stripes of high temperatures during the day show that soil typically experienced surface temperatures of 45–50 °C during the afternoon, often immediately adjacent to areas with plant cover with surface temperatures 20–25 °C cooler. A small flat boulder (B), positioned from 1.6 to 2.0 m on the transect, maintained moderate surface temperatures of 25–30 °C through most of the day and then a moderated night temperature a few degrees warmer than surrounding surfaces. In contrast to the sharp differences in surface temperature at fine spatial scales during the day, a relatively small temperature variation was observed across the full transect at night, reaching a minimum of 11.0 °C difference at 05:06 h.

The broad range of spatial and temporal variation in surface temperatures contrasts with the comparatively smaller gradients in air and soil subsurface temperatures at the study site. Solar noon during measurements occurred just after 12:00 h and air temperatures at 100 cm above the soil surface peaked about two hours later at 15 °C, a pattern also reflected in the meteorological data from the nearby Barcroft weather station at 3600 m elevation. Air temperatures at 10 and 1 cm above the soil surface reached maxima of 18 °C and 23 °C, respectively, with broad and noisy peaks due to wind across the early afternoon (Fig. 4, part A). These air temperatures strongly converged at night, with the lowest temperatures reached at about 06:00 h, just before dawn. Freezing air temperatures were never present during our period of measurement but may occur at any time during the summer at this site.

Diurnal soil temperatures at 10 cm depth differed between sites under open soil and under an *E. ovalifolium* (Fig. 4, part B). Temperature under bare soil was warmer throughout the diurnal cycle, but became close to that below the cushion plant at night when temperatures reached about 7 °C. The maximum difference in temperature between 10 cm below bare soil and below the cushion was 4.2 °C, which occurred at 13:15 h. The 24-h, mean bare soil surface temperature was 15.5 °C along the transect; at 10 cm below the bare soil it was 14.5 °C, and below the cushion was 12.7 °C. Temperatures peaked for the bare soil surface at 39.3 °C at 13:04 h; for 10 cm below the bare soil surface, temperature peaked

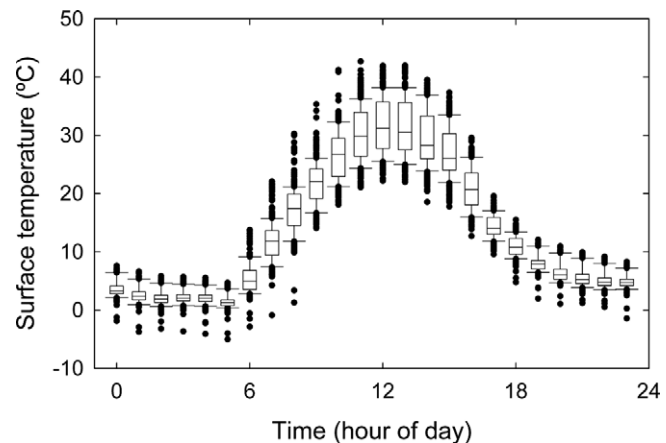


FIGURE 6. Hourly surface temperature across the entire transect. Depicted are the median (as the horizontal line between boxes), the 10th and 25th (as boxes) and the 75th and 95th (as error bars) percentile distributions, and all outliers (as points) of surface temperature. Data are from 308 locations along the transect with six time periods centered on the hour, approximately 10 min apart, averaged for each hour of measurement.

at 21.9 °C at 16:21 h; and for below the cushion at 18.6 °C at 16:30 h.

Median, hourly temperatures across the study transect indicate that temperature variation of the fellfield surface was relatively small over the night hours, with 50% of measured values falling within a few degrees of each other (Fig. 6). The lowest hourly median transect temperature of 2 °C was reached just before dawn between 04:00 and 05:00 h. After sunrise (at 04:57 h), median transect temperatures quickly rose to 10 °C at 06:00–07:00 h and to 30 °C from 11:00 to 12:00 h. The variability of surface temperatures across the transect increased sharply from 06:00 to 07:00 h, peaking at midday from 11:00 to 14:00 h (Fig. 6).

Contemporaneous temperature differences measured between adjacent locations on the transect 2, 5, and 10 cm apart indicate large temperature differences occur over small spatial scales (Fig. 7). The maximum temperature difference between adjacent locations 2 cm apart was 18.3 °C at 13:52 h, when the standard deviation of temperature measured for the entire transect was at a maximum; the mean temperature difference between locations 2 cm apart at this time was 2.9 °C. When the maximum temperature on the transect was observed (50.1 °C at 12:05 h), the maximum temperature difference at 5 cm separation was 19.0 °C (mean difference between 5 cm locations was 5.4 °C), and that at 10 cm was 25.2 °C (mean difference was 9.0 °C). The maximum instantaneous temperature difference between any two points on the transect occurred at 13:43 h with a 39.4 °C difference occurring at a distance of about 2 m; at the same time, a slightly lower 37.2 °C difference occurred at a distance of 3 cm (Fig. 7).

The temperature difference between air measured at 1 cm above bare soil and surface locations along the transect corresponding to 100% cover of plants or substrate ($n = 5$ for each category) showed different patterns of heating and cooling (Fig. 8). For example, all three plant species (Fig. 8, parts A, B, and C) had measured temperatures below air temperature between 07:35 and 08:40 h, whereas soil or boulder (Fig. 8, parts D and E) did not fall below

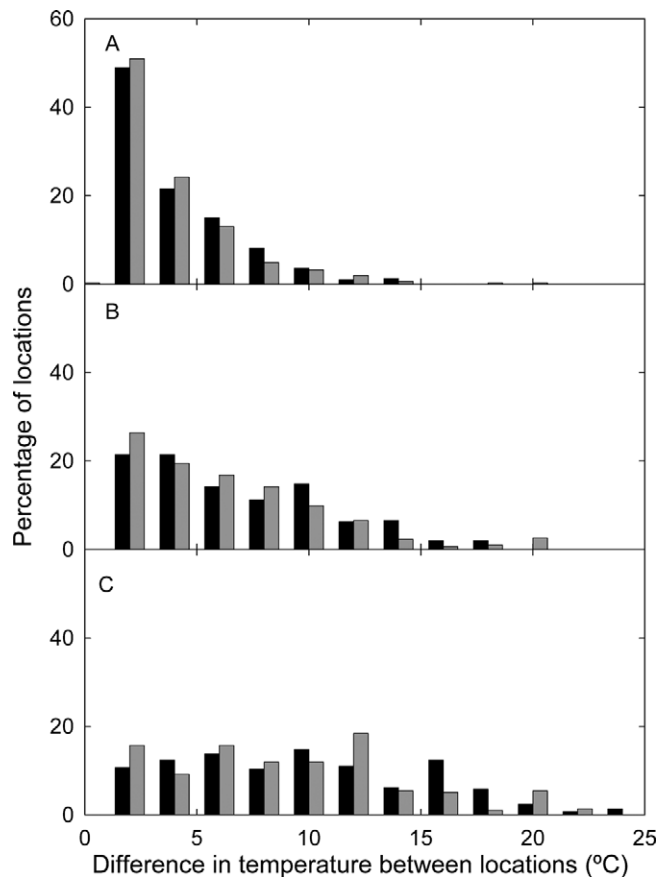


FIGURE 7. Frequency of temperature differences recorded between adjacent locations (A) 2 cm, (B) 5 cm, and (C) 10 cm distance apart along the transect during the time period when the maximum temperature was recorded (black bars; 12:05 h), and the time when the maximum standard deviation of temperature was recorded (gray bars; 13:52 h).

air temperature at this time. Plants tended to have lower maximum temperature differences near noon than bare soil but had similar maxima as areas categorized as boulder. Immediately after sunrise, temperatures for all substrates increased quickly above air temperature; however, well before sunset (which occurred at 19:00 h), surface temperatures for all substrate classes decreased rapidly to below air temperature (starting at about 16:00 h; Fig. 8).

Recursive partitioning (rpart) analysis of the temperature difference data (Fig. 8) resulted in a decision tree (Fig. 9) that was capable of separating the substrate categories of boulder, bare soil, and the three plant species. The first split in the rpart decision tree occurred at 08:35 h and separated the boulder and bare soil surfaces from the plants with the temperature threshold of 3.3 °C (Fig. 9). The separation of these two general classes of substrate was 98.3% accurate and misclassified one *P. heterodoxus* as a boulder. This split is at the start of the time period where the plants' temperatures drop below that of the air temperature while the boulder and bare soil remain above air temperature. Separating the boulder from the bare soil in the next rpart split was based on the rapid heating of the soil surface compared to the much slower heating of the larger thermal mass of the boulder; the time of the split occurred when the temperature of the bare soil rose above that of the boulder at 09:30 h. The splits between the compact, prostrate cushions of

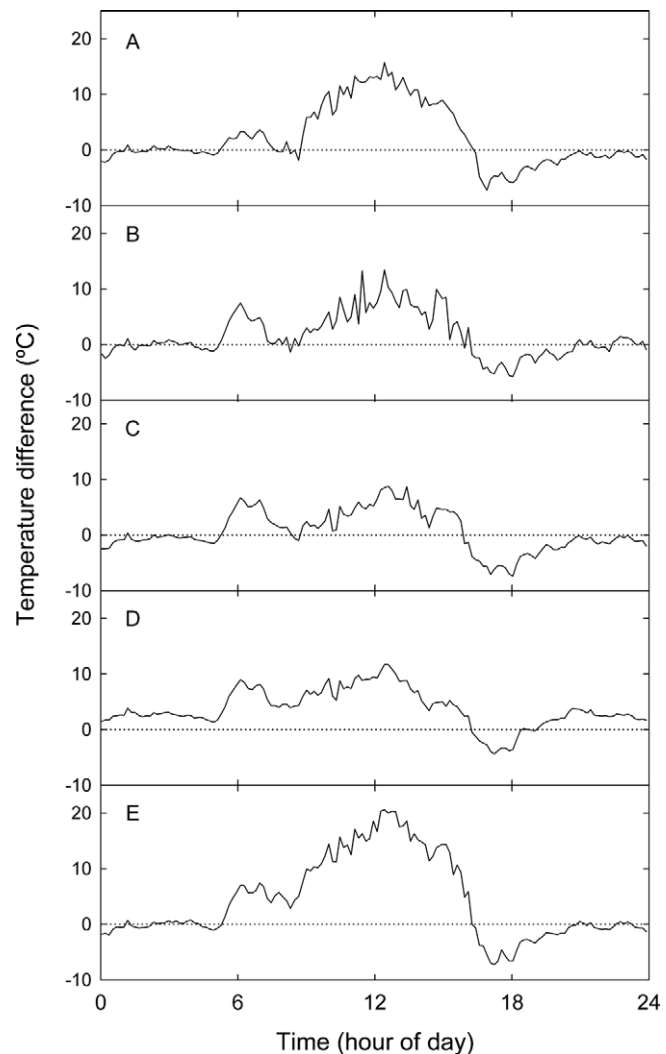


FIGURE 8. Mean temperature difference between air measured at 1 cm above bare soil and surface temperature at locations on the transect corresponding to (A) *Penstemon heterodoxus*, (B) *Poa glauca*, (C) *Eriogonum ovalifolium*, (D) boulder, and (E) bare soil. Data are means of 5 locations at the study site on 1–2 August 2005.

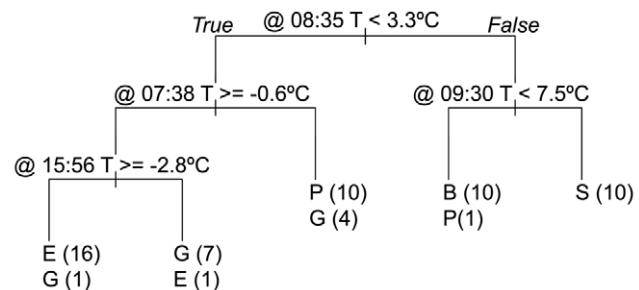


FIGURE 9. The classification results from the recursive partition decision tree analysis indicating the splits for separating the surface categories based on the difference between surface temperature and the air temperature at 1 cm height above bare soil (Fig. 8). Classifications are (B) boulder, (S) bare soil, (E) *Eriogonum ovalifolium*, (P) *Penstemon heterodoxus*, and (G) *Poa glauca*. Numbers in parentheses after each class indicate the number of instances of a location being classified into each category.

E. ovalifolium and the more upright *P. glauca* and mat form of *P. heterodoxus* occurred at different times, when *E. ovalifolium* was warmer than either of the other two species. The absolute cross-validated error rate for this separation is 63%. *P. heterodoxus* was successfully categorized into one group 71% of the time, *P. glauca* 88% of the time, and *E. ovalifolium* 100% of the time (Fig. 9).

Discussion

Local scale patterns in soil topography, substrate structure, plant cover, and soil moisture content all have strong impacts on soil surface temperatures in both arctic and alpine ecosystems. There has been a long history of research into patterns of surface and boundary layer air temperatures in arctic tundra and boreal forest because of the importance of soil surface temperatures to many ecological, hydrological, geomorphological, and climatological investigations relating to permafrost (Henry and Molau, 1997; Goulden et al., 1998; Marchand et al., 2005; Walker et al., 2006). In comparison, there have been fewer studies of the significance of spatial and temporal patterns of surface temperatures in alpine habitats where topography produces much more complex boundary layer conditions.

Alpine ecosystems experience a high energy input in the summer months, producing a strong thermal boundary layer at soil and plant canopies surfaces and relatively low latent heat transfer as water becomes limiting after snowmelt. The result of this complexity is a diversity of fine-scale thermal habitats related to the microtopography of the landscape as high midday soil surface temperatures are reached. Our data showing mean midday surface temperatures at about 30 °C, and reaching as high as 50 °C (Fig. 7) are consistent with previous reports in alpine fellfields (Salisbury and Spomer, 1964; Gates and Janke, 1966; LeDrew and Weller, 1978; Rundel et al., 2005). These results are sharply different from that seen in arctic tundra where midday solar irradiance is relatively low and moist soils allow for high levels of latent heat transfer. As a result, soil surface temperatures in arctic tundra seldom exceed air temperatures by more than 5–10 °C (LeDrew and Weller, 1978), although temperatures up to 14 °C greater than air temperature have been reported (Sullivan et al., 2008).

Microclimate temperatures of alpine fellfield plants strongly affect the uptake of CO₂ by photosynthesis, the loss of CO₂ in canopy respiration, and the loss of CO₂ through belowground respiration in both root and microbial systems, and through these alter ecosystem carbon exchange. These temperatures are a function of not only topographic microclimate but also the architecture of plant growth form and plant height which impact energy balance. Upright plants with foliage away from the ground surface track air temperatures fairly closely, while cushions and mats with their photosynthetic tissues maintained close to the ground surface often have tissue temperatures 10–20 °C above air temperatures at midday. A low prostrate form of mat or cushion growth near the boundary layer of the ground reduces the potential for convective heat exchange (Grace, 1988; Leuning and Cremer, 1988; Germino and Smith, 2001). The ecophysiological significance of relatively high temperatures near the soil surface is well illustrated by the C₄ grass *Muhlenbergia richardsonis*, which grows successfully in select microsites as high as nearly 4000 m in the White Mountains (Sage and Sage, 2002).

Previous ecophysiological studies at our field site have reported shoot temperatures as much as 15–20 °C or more above ambient temperature in late morning in the prostrate cushion and mat-forming species, *Trifolium andersoni* var. *beatleyae*, *Eriogonum ovalifolium* var. *nivale*, and *Penstemon heterodoxus*, which position their photosynthetic tissue very close to ground level. *Poa glauca* subsp. *rupicola*, with upright foliage but with the majority of its actively photosynthesizing tissue in a tight rosette, operated at about 10 °C above ambient temperature (Rundel et al., 2005).

It is noteworthy that *Eriogonum*, *Penstemon*, and *Poa* all have surface temperatures that dropped to at or below air temperature in mid-morning (Fig. 8). This drop in temperature corresponds to the time of day when photosynthetic production peaks and transpiration cools tissues by latent heat of evaporation (Rundel, unpublished data). Indeed, this is the characteristic that statistically separated the areas of our measured transect into those containing plants versus bare soil or rock (Fig. 9). The influence of vegetative surfaces on the surface temperature is significant during the periods of transpiration and also on the subsurface temperatures, most likely due to an insulating effect. The dry surface of soil or sand, because of its poor thermal conductivity, can reach high temperatures when not insulated (Graham et al., 2010). These high temperatures can be conducted to the subsurface soil, which can have a higher thermal conductivity because of increased moisture with depth, with often profound effects on small-scale plant distributions (e.g., Schob et al., 2009). These results suggest the interesting possibility that infra-red images of alpine landscape surfaces at appropriate times of the day can not only serve to map vegetation cover but also separate individual plant species based on surface temperatures that reflect both growth form and individual ecophysiological traits of photosynthetic activity.

From an ecophysiological perspective, elevated surface temperatures may increase leaf temperatures to provide more favorable conditions of microclimate for photosynthetic production, but they may also increase to levels high enough to cause negative impacts. Intense summer irradiance heating soil surfaces and low-growing alpine plants can produce high and potentially damaging or lethal tissue temperatures, providing a potential selective force in some alpine microhabitats. Neuner et al. (1999) documented that temperatures above 45 °C were reached on 11% of summer days in *Saxifraga paniculata*, a rosette species, in the Alps. This species has adapted to these temperatures close to or at lethal levels by folding of old leaves to shade the rosette center and lower its temperature by up to 10 °C. The apical bud of *Argyroxiphium sandwicense* (silversword) in the center of its parabolic rosette heats to 25 °C higher than air temperature at midday in its subalpine and alpine habitats of the Hawaiian Islands. The heating effect on the apical bud has been hypothesized to increase the rates of physiological processes in the developing leaves, but may produce lethal tissue temperatures that exclude the species from lower elevations (Melcher et al., 1994).

At the broad scale of environmental modeling and climate change, global change models (GCMs) predict that alpine areas will experience higher levels of temperature increase than global averages (Theurillat and Guisan, 2001; Beniston, 2005). Concerns about the potential impacts of higher temperatures on high elevation communities have led to a variety of studies, including experimen-

tal warming manipulations to look at impacts of increased temperatures on alpine and subalpine plant phenology and community structure (Harte et al., 1995; Price and Waser, 2000; Klein et al., 2005). As useful as GCMs can be, they operate on grid scales of kilometers along horizontal axes and tens of meters along the vertical. Thus, they are most effective at heights well above the soil, excluding the plant canopy levels where alpine microclimate affects biological and local ecosystem processes. For alpine ecosystems, there is thus a range of complicating factors that confounds the straightforward interpolation from macroclimate to microclimate (Wundram et al., 2010). Boundary layer dynamics at the level of the ground surface complicate predictions because of the complexity of interactive factors such as wind shear, pressure gradients, and energy balance cause the environment to become decoupled from free air conditions above the ground surface.

These traits of microclimate for alpine habitats suggest that models predicting upslope movements of species under increasing temperatures may not be entirely realistic and that there may well be sufficient microclimate heterogeneity to slow such migration. Scherrer and Körner (2010, 2011) used infra-red thermometry with an image resolution of about 1 m² to document a large and persistent variation in microhabitat temperatures over mesoscale alpine landscape terrain, mimicking temperature gradients present along elevational gradients of several hundred meters. Their results suggest that alpine plants under global change may well find appropriate thermal niches for establishment and survival over very short distances without elevational shifts. They further suggest that the mesoscale pattern of surface temperature variation over their study scale may be found to be even greater at finer spatial scales of less than 1 m², which is what we report here. Our studies confirm these conclusions in showing that surprisingly large gradients in surface temperatures can occur over distances of even a few centimeters. It is particularly significant to note that these sharp gradients in surface temperatures reflect not only the differing thermal properties of the physical substrates but additionally the growth forms of the plant canopies and the ecophysiological traits of the individual plant species.

All of these points of discussion are based, of course, on an assumption that temperature provides a primary controlling mechanism for species distributions in alpine habitats. However, we know very little about the significance of moisture availability for such distributions, as well as the interactions of temperature and soil moisture. GCM models are able to make temperature predictions with far more confidence than precipitation, leaving open the question of moisture controls.

Conclusions

The topographic variability of alpine fell field habitats creates a fine pattern of thermal microhabitat conditions at a scale of centimeters. The magnitude of these temperature differences is greater than the range of warming scenarios over the next century in IPCC projections. Patterns are due not only to substrate material but to the presence of low-lying plants that alter the temperature locally through transpiration and shading of the soil surface. These patterns suggest that projections of changes in potential elevational range of alpine species distributions with global change should be made with caution. If the assumption is made that short dispersal and

establishment is possible for alpine plants, then fellfield habitats may offer significant buffering from global warming because of the mosaic of thermal microclimates present. However, there remains a poor understanding of the relative significance of limiting factors such as temperature means and extremes and moisture availability in species establishment and survival in alpine habitats. Individual growth forms and ecophysiological traits of individual species have a significant influence in determining their microhabitat temperature.

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References Cited

- Beniston, M., 2005: Climatic change and its possible impacts in the alpine region. *Revue de Géographie Alpine—Journal of Alpine Research*, 93: 25–32.
- Brett, L. J., Batalin, M. A., and Kaiser, W. J. 2007: NIMS RD: a rapidly deployable cable based robot. ICRA'07, 2007 *IEEE International Conference on Robotics and Automation*, 10–14 April 2007, Roma, Italy, 144–150.
- Caron, D. A., Stauffer, B., Moorthi, S., Singh, A., Batalin, M., Graham, E. A., Hansen, M., Kaiser, W. J., Das, J., Pereira, A., Dhariwal, A., Zhang, B., Oberg, C., and Sukhatme, G. S., 2008: Macro- to fine-scale spatial and temporal distributions and dynamics of phytoplankton and their environmental driving forces in a small montane lake in southern California, USA. *Limnology and Oceanography*, 53: 2333–2349.
- Duguay, C. R., 1994: Remote-sensing of the radiation balance during the growing season at the Niwot Ridge long-term ecological research site, Front Range, Colorado, USA. *Arctic and Alpine Research*, 26: 393–402.
- Duguay, C. R., and LeDrew, E. F., 1991: Mapping surface albedo in the east slope of the Colorado Front range, USA, with Landsat thematic mapper. *Arctic and Alpine Research*, 23: 213–223.
- Gates, D. M., and Janke, R., 1966: The energy balance of an alpine tundra. *Oecologia, Plantarum*, 1: 39–62.
- Germino, M. J., and Smith, W. K., 2001: Relative importance of microhabitat, plant form and photosynthetic physiology to carbon gain in two alpine herbs. *Functional Ecology*, 15: 243–251.
- Goulden, M. L., Wofsy, S. C., Harden, J. W., Trumbore, S. E., Crill, P. M., Gower, S. T., Fries, T., Daube, B. C., Fan, S.-M., Sutton, D. J., Bazzaz, A., and Munger, J. W., 1998: Sensitivity of boreal forest carbon balance to soil thaw. *Science*, 279: 214–217.
- Grace, J., 1987: Climatic tolerance and the distribution of plants. *New Phytologist*, 106: 113–130.
- Grace, J., 1988: The functional significance of short stature in montane vegetation. In Werger, M. J. A. (ed.), *Plant Form and Vegetation Structure*. The Hague: SPB Academic, 201–209.
- Graham, E. A., Lam, Y., and Yuen, E. M., 2010: Forest understory soil temperatures and heat flux calculated using a Fourier model and scaled using a digital camera. *Agricultural and Forest Meteorology*, 150: 640–649.
- Harmon, T. C., Ambrose, R. F., Gilbert, R. M., Fisher, J. C., Stealey, M., and Kaiser, W. J., 2007: High resolution river hydraulic and water quality characterization using rapidly deployable Networked Infomechanical Systems (NIMS RD). *Environmental Engineering Science*, 24: 151–159.

- Harte, J., Torn, M. S., Chang, F. R., Feifarek, B., Kinzig, A., Shaw, R., and Shen, K., 1995: Global warming and soil microclimate—Results from a meadow-warming experiment. *Ecological Applications*, 5: 132–150.
- Henry, G. H. R., and Molau, U., 1997: Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology*, 3: S1–S9.
- Jakalanieniemi, A., 2011: Narrow climate and habitat envelope affect the survival of relict populations of a northern *Arnica angustifolia*. *Environmental and Experimental Botany*, 72: 415–421.
- Jordan, D. N., and Smith, W. K., 2005: Microclimate factors influencing the frequency and duration of growth season frost for sub-alpine plants. *Agricultural and Forest Meteorology*, 77: 17–30.
- Klein, J. A., Harte, J., and Zhao, X. Q., 2005: Dynamic and complex microclimate responses to warming and grazing manipulations. *Global Change Biology*, 11: 1440–1451.
- Klene, A. E., Nelson, F. E., and Shiklomanov, N. I., 2001a: The N-factor in natural landscapes: variability of air and soil-surface temperatures, Kuparuk River Basin, Alaska, U.S.A. *Arctic, Antarctic, and Alpine Research*, 33: 140–148.
- Klene, A. E., Nelson, F. E., and Shiklomanov, N. I., 2001b: The n-factor as a tool in geocryological mapping: seasonal thaw in the Kuparuk River basin, Alaska. *Physical Geography*, 22: 449–466.
- Körner, C., 2003: *Alpine Plant Life*. Berlin, Springer Verlag.
- Kudo, G., and Hirao, A. S., 2006: Habitat-specific responses in the flowering phenology and seed set of alpine plants to climate variation: implications for global change impacts. *Population Ecology*, 48: 49–58.
- LeDrew, E. F., and Weller, G., 1978: A comparison of the radiation balance during the growing season for an arctic and alpine tundra. *Arctic and Alpine Research*, 10: 665–678.
- Leuning, R., and Cremer, K. W., 1988: Leaf temperatures during radiation frost. Part I. Observations. *Agricultural and Forest Meteorology*, 42: 121–133.
- Löffler, 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.
- Marchand, F. L., Mertens, S., Kockelbergh, F. K., Beyens, L., and Nijs, I., 2005: Performance of high arctic tundra plants improved during but deteriorated after exposure to a simulated extreme temperature event. *Global Change Biology*, 11: 2078–2089.
- Melcher, P. J., Goldstein, G., Meinzer, F. C., Minyard, B., Giambelluca, T. W., and Loope, L. L., 1994: Determinants of thermal balance in the Hawaiian giant rosette plant, *Argyroxiphium sandwicense*. *Oecologia*, 98: 412–418.
- Molau, U., 1997: Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. *Global Change Biology*, 3(Suppl. 1): 97–107.
- Molau, U., Nordenhall, U., and Eriksen, B., 2005: Onset of flowering and climate variability in an alpine landscape: a 10-year study from Swedish Lapland. *American Journal of Botany*, 92: 422–431.
- Neuner, G., Braun, V., Buchner, O., and Taschler, D., 1999: Leaf rosette closure in the alpine rock species *Saxifraga paniculata* Mill. *Plant, Cell & Environment*, 22: 1539–1548.
- Price, M. V., and Waser, N. M., 2000: Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications*, 10: 811–824.
- R Development Core Team, 2011: *R: a Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, ISBN 3-900051-07-0, <http://www.R-project.org>.
- Rundel, P. W., Gibson, A. C., and Sharifi, M. R., 2005: Plant functional groups in alpine fellfield habitats of the White Mountains, California. *Arctic, Antarctic, and Alpine Research*, 37: 358–365.
- Rundel, P. W., Gibson, A. C., and Sharifi, M. R., 2008: The alpine flora of the White Mountains. *Madroño*, 55: 202–215.
- Sage, R. F., and Sage, T. L., 2002: Microsite characteristics of *Muhlenbergia richardsonis* (Trin.) Rydb., an alpine C₄ grass from the White Mountains, California. *Oecologia*, 132: 501–508.
- Salisbury, F. B., and Spomer, G. G., 1964: Leaf temperatures of plants in the field. *Planta*, 60: 497–505.
- Scherrer, D., and Körner, C., 2010: Infra-red thermometry of alpine landscapes challenges climatic, warming projections. *Global Change Biology*, 16: 2602–2613.
- Scherrer, D., and Körner, C., 2011: Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, 38: 406–416.
- Schob, C., Kammer, P. M., Choler, P., and Veit, H., 2009: Small-scale plant species distribution in snowbeds and its sensitivity to climate change. *Plant Ecology*, 200: 91–104.
- Stealey, M. J., 2007: *The Networked Infomechanical Systems Rapidly Deployable (NIMS-RD) Platform*. Ph.D. dissertation, Department of Electrical Engineering, University of California, Los Angeles.
- Sullivan, P. F., Welker, J. M., Steltzer, H., Sletten, R. S., Hagedorn, B., Arens, S. J. T., and Horwath, J. L., 2008: Energy and water additions give rise to simple responses in plant canopy and soil microclimates of a high arctic ecosystem. *Journal of Geophysical Research–Biogeosciences*, 113: G03S08, <http://dx.doi.org/10.1029/2007JG000477>.
- Taschler, D., and Neuner, G., 2004: Summer frost resistance and freezing patterns measured in situ in leaves of major alpine plant growth forms in relation to their upper distribution boundary. *Plant Cell and Environment*, 27: 737–746.
- Taylor, A. G., 2001: Relationship of ground temperatures to air temperatures in forests. In Dyke, L. D., and Brooks, G. R. (eds.), *The Physical Environment of Mackenzie Valley: a Baseline for Assessment of Environmental Change*. Geological Survey of Canada Bulletin, 547: 111–117.
- Therneau, T., and Atkinson, B., 2002: rpart. Rochester, Minnesota: Mayo Foundation for Medical Education and Research.
- Theurillat, J. P., and Guisan, A., 2001: Potential impact of climate change on vegetation in the European Alps: a review. *Climatic Change*, 50: 77–109.
- Torres-Diaz, C., Cavieres, L. A., Munoz-Ramirez, C., and Arroyo, M. T. K., 2007: Consecuencias de las variaciones microclimáticas sobre la visita de insectos polinizadores en dos especies de *Chaetanthera* (Asteraceae) en los Andes de Chile central. *Revista Chilena de Historia Natural*, 80: 455–468.
- Walker, M. D., Wahren, C. H., Hollister, R. D., et al., 2006: Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, 103: 1342–1346.
- Wundram, D., Pape, R., and Löffler, J., 2010: Alpine soil temperature variability at multiple scales. *Arctic, Antarctic, and Alpine Research*, 42: 117–128.

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