

Infra-red thermometry in alpine terrain

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DANIEL SCHERRER

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Prof. Dr. Christian Körner
Prof. Dr. Antoine Guisan

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Prof. Dr. Eberhard Parlow
Dekan



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Chapter 1

General Introduction

General introduction

The alpine life zone

In this thesis I refer to the term "alpine" in a biogeographic sense, describing a well-defined life zone. Alpine landscapes in this sense can be found all around the globe from 60° South to 70° North (Figure 1). The lower boundary of the alpine belt is defined by the natural, climatic tree line, which is associated with a seasonal mean temperature of c. 6.5 °C (Körner, 1998; Körner & Paulsen, 2004, and newer data by these authors). The upper boundary is more difficult to define. Vascular plants can be found up to 6000 m in some regions, but closed vegetation commonly ends at lower elevations (Körner, 2003). The life zone above, where plants grow in isolation from highly fragmented communities, is often called "nival", while "alpine" stands for mostly closed vegetation. Due to scree, rock terrain and avalanche tracks the nival and alpine belt strongly overlap. At high latitudes we often find a transition from "arctic-alpine" to "lowland-arctic" (sensu 'tundra'), both characterized by the absence of trees. The main difference between lowland-arctic and alpine landscapes is topography. While lowland-arctic landscapes are mostly flat areas, the arctic-alpine belt and the alpine belt in general, are dominated by a highly variable macro- (slopes) and micro-topography. In the main study area of this thesis (Swiss Alps) the alpine belt ranges from c. 2200 m to 2800 m (Körner *et al.*, 2003).

The most striking difference between alpine sites of different latitude is the seasonality. While the growing season lasts 12 months near the equator it may be as short as 1.5 months in sub-arctic regions. If one compares the yearly average conditions of the alpine regions around the world, they might seem very different, but during the growing season the climatic conditions and productivity are similar as was shown for the European alpine belts (Körner *et al.*, 2003). During the unfavourable climatic conditions outside the growing season ('winter'), plants persist in a frost hardy state and/or are well protected from severe freezing under snow cover. Snow cover follows topography and thus adds to the geo-diversity effects on life in alpine terrain. Alpine life conditions are often considered as harsh, with strong winds, high solar radiation and cold temperatures. This anthropocentric view is influenced by our own experience as hikers or skiers and by weather station data, but does not account for the actual life conditions for alpine biota

which may be substantially warmer due to aerodynamic decoupling, as will be shown here. Alpine life is also not necessarily constrained by a short growing season. In the tropic-alpine life zone there is little seasonality and almost no wind. Also, in the Alps, the inner parts are not as wind-beaten as weather stations might be when placed at the highest and most exposed ridges or summits as is often the case (e.g., Jungfrauoch, Säntis, Zugspitze). Hence, there is a great discrepancy between human experience and weather station data on one side and the climate experienced by alpine biota on the other side. This discrepancy had been evidenced by numerous point data in the past, but was never quantified over space and time, the task of this project.

Plant adaptation to cold climate

As mentioned before, alpine landscapes are found above the high elevation tree line (the 6.5 °C isotherm of seasonal mean temperature). At temperatures below 5 °C plant growth (tissue formation) is extremely slow (Körner & Woodward, 1987). Therefore plants living in such cold environments must be able to increase their tissue temperature above air temperature. Since plants are poikilothermic organisms, the only way to escape the cold is some sort of 'air conditioning' by aerodynamic decoupling from the free atmospheric circulation, micro-habitat selection and restricting life activity to warmest periods.

Unlike trees, the low stature of alpine vegetation allows such aerodynamic decoupling from atmospheric conditions by close interaction with topography. The interplay of (micro-) topography (exposure and wind shelter), plant stature and solar radiation leads to micro-habitat conditions not represented by weather station data. Micro-meteorological measurements show that leaf temperatures of alpine plants can be up to 20 K warmer than air temperature (Salisbury & Spomer, 1964; Larcher & Vogel, 1980; Larcher *et al.*, 2010). On clear sky days these effects of exposure and plant morphology are known to exert greater influence on plant temperature than several hundred meters of elevation (Körner, 2003; Löffler *et al.*, 2006). Of course there are also cloudy days without sunshine when leaf temperatures are close to air temperature, but under these conditions there is minimal plant growth. Tissue formation is mostly limited to pe-

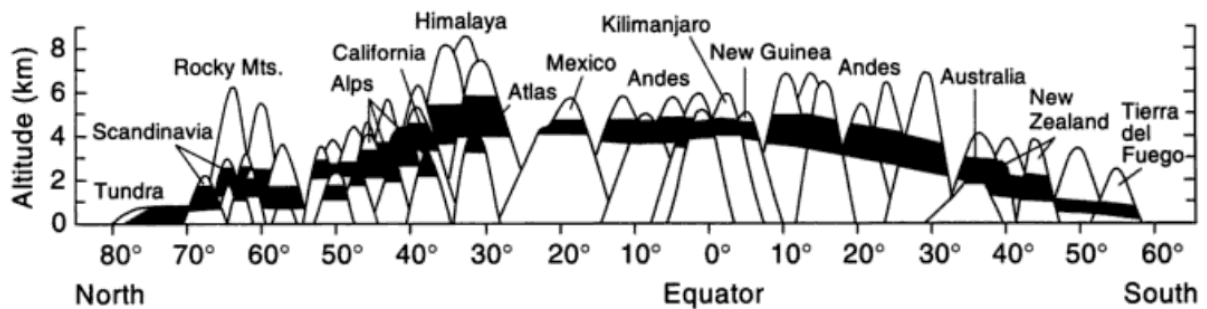


Figure 1: A schematic presentation of the altitudinal position of the alpine life zone from the arctic to antarctic latitudes (from Körner, 2003)

riods of favourable conditions in the alpine life zone, while photosynthesis is able to utilize colder periods as well. Yet, temperature adaptation of photosynthesis clearly reflects the importance of warm periods, with the temperature optimum of net photosynthesis of alpine plants not differing from that in congeneric lowland species (c. 22 °C; Körner & Diemer, 1987). Hence, alpine plants are small ‘by design’ (genotypic dwarfs) rather than restricted in their size expansion by actual climatic conditions (Körner, 2003). The structural adaptation in combination with developmental flexibility (timing) permits alpine plants to perform basic metabolism including tissue formation under conditions not much different from those at lower elevation. Yet, it remained unknown how these life conditions at plant level vary in time and space in rough alpine terrain at scales of various km².

Climatic warming and alpine biota

Since the mid-20th century an increase in the average temperature of Earth’s near surface air and oceans has been recorded and it is projected that this global warming will continue. The warming is largely caused by increasing concentrations of greenhouse gases resulting from human activity and to a minor extent by astronomical forcing (IPCC, 2007). Global surface temperature increased by 0.74 K during the last century and projections suggest a further rise of 1.1 to 6.4 K during the 21st century (Meehl *et al.*, 2007, Figure 2). Global warming is not expected to be similar across all regions. For most alpine areas, especially the Alps, climate warming is expected to be more pronounced than the global average (Meehl *et al.*, 2007). In fact, during the last century the Alps warmed by +1.5 K which is double the global average.

A rich literature debates the consequences of past and future warming for plants and animals in high elevation ecosystems (see below). Among the most common assumptions is that the steep environmental gradients and the reduction in area with increasing

elevation make alpine landscapes particularly sensitive to global warming (Diaz *et al.*, 2003; Beniston, 2006). Accordingly, most plants and animals are expected to respond to this warming by migration to higher elevations and/or latitudes following their current climate envelope (niche). ‘Nival’ summits had been shown to become richer in species during the last hundred years (for references see Walther *et al.*, 2002; Bahn & Körner, 2003; Walther *et al.*, 2005), although these trends may also reflect a lag of returning of plants after the ‘little ice age’. The tree line, a highly temperature dependent bioclimatic boundary given the aerodynamically coupled tree stature, has shown very little change in position (Gehrig-Fasel *et al.*, 2007). However, tree growth at the tree line has become dramatically enhanced in the last 60 years (Paulsen *et al.*, 2000). Plant species in the montane belt shifted their abundance peak 29 m upslope in the last decades (Lenoir *et al.*, 2008). However, there is also evidence for substantial resistance to climatic forcing in clones which inhabit the same location over thousands of years (Steinger *et al.*, 1996). It seems that the speed of migration differs between pioneer taxa and late successional taxa.

The evidence for actual migration of plants due to climate warming is still very scarce and confounding effects are hard to exclude. Most publications on migration of species in a climate warming context are thus, based on model predictions.

Predicting the future of alpine biodiversity

In the last decade a number of modelling studies have been published, offering spatially discrete projections of the likely impacts of climate warming on species distribution and biodiversity. The most popular approach are species distribution models (SDMs; Guisan & Zimmermann, 2000; Guisan & Thuiller, 2005). SDMs statistically fit the environmental niche (Hutchinson, 1957) by relating abiotic habitat conditions with occurrences of a species. Most SDM-

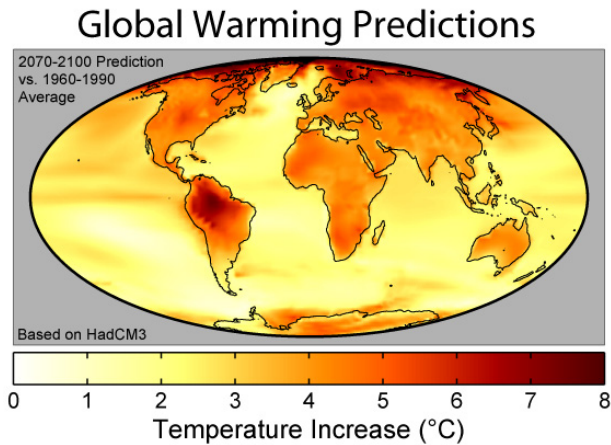


Figure 2: This figure shows the predicted distribution of temperature change due to global warming from the Hadley Centre HadCM3 climate model. The plotted colours show predicted surface temperature changes expressed as the average prediction for 2070-2100 relative to the model's baseline temperatures in 1960-1990. The average change is 3.0 °C, placing this model on the lower half of the Intergovernmental Panel on Climate Change's 1.4-5.8 °C predicted climate change from 1990 to 2100. Image created by Robert A. Rohde / Global Warming Art

studies for the Alps expect strong impacts of climate warming on biodiversity through habitat loss and thus, regional species extinctions. However, the predictions of SDMs may vary significantly depending on the type of model (Araujo & New, 2007) and the spatial resolution (Trivedi *et al.*, 2008; Randin *et al.*, 2009). There is an ongoing debate on model validation (Araujo & Guisan, 2006), transferability in space (Randin *et al.*, 2006) and uncertainty (Pearson *et al.*, 2006). Spatial scale (resolution) is expected to exert a severe impact on the model output in alpine areas dominated by a high variability in macro and micro-topography. Since models rely on available meteorological records it remains to be resolved to what extent the application of climate station data to alpine plant life is justified.

Aim of this work

In this thesis, I aimed at

- (1) A documentation of the thermal characteristics of alpine landscapes at high spatial resolution, using thermal imagery (vegetation surface temperature) and networks of buried temperature loggers (root zone temperature) of alpine mountain slopes of contrasting exposures in the Alps and Arctic. (*Chapter 2*)
- (2) A quantification of mosaics of thermal habitats and associated plant species diversity patterns. By correlating vegetation surveys with micro-habitat temperatures species/community prefer-

Table 1: The spatial ground resolution and spatial area covered by the thermal camera ($f' = 35$ mm) dependent on the camera-object distance.

Distance (m)	Area covered (m ²)	Spatial resolution (m ² pixel ⁻¹)
2	1.15 x 0.85	1.3^{-5} (0.13 cm ²)
25	14.3 x 10.5	0.002 (20 cm ²)
100	57.4 x 43.1	0.03
500	287 x 215	0.8
1000	574 x 431	3.2

ences should emerge. Applying uniform warming scenarios to those thermal mosaics should enable the shift in habitat abundance to be quantified. (*Chapter 3*)

- (3) A quantitative assessment of habitat abundance as a function of spatial resolution from cm² to km² scales. (*Chapter 4*)

The work was conducted in the Alps (Chapter 2-4) and Northern Europe (N-Norway, N-Sweden, Svalbard; Chapter 2), aiming at a large scale comparison. The technology central to this project was a new infra-red thermometry camera. The thermal camera (Figure 3; VarioCAM; Infa Tec GmbH, Dresden, Germany) records the long-wave infra-red radiation of an object in the spectral range of 7.5 to 14 μ m on a micro-bolometer array with 320x240 pixels at 50Hz. The 76.800 individual radiation intensity measurements are directly transformed into temperature by an auto-calibration routine, using an inbuilt near-ideal black body and software to correct for single image point deviation from black body temperature. Additionally, the micro-bolometer array is connected to a Peltier element stabilizing the internal temperature independent of ambient temperature.



Figure 3: Thermal camera recording an alpine slope in Abisko (N-Sweden) on July 27, 2008.

The accuracy of the absolute temperature is ± 1 K (at 25 °C) and the relative differences between sensor readings have an accuracy of ± 0.1 K. Some examples

of spatial ground resolutions dependent on camera-object distances are given in Table 1.

Most of the work was done in the Swiss Alps at a new alpine field station at the Furka Pass (<http://pages.unibas.ch/botschoen/alpfor/index.html>). The thesis was part of a European project network ECOchange (<http://www.ecochange-project.eu/>).

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Chapter 2

Infra-red thermometry of alpine
landscapes challenges climatic warming
projections

Infra-red thermometry of alpine landscapes challenges climatic warming projections

DANIEL SCHERRER and CHRISTIAN KÖRNER

Institute of Botany, University of Basel, Schönbeinstr. 5, CH-4056 Basel, Switzerland

Abstract

Rough mountain terrain offers climatic conditions (niches) to plants and animals poorly represented by conventional climate station data. However, the extent to which actual temperatures deviate from those of the freely circulating atmosphere had never been assessed at a landscape level. Here, we quantify thermal life conditions across topographically rich mountain terrain by using a combination of thermal (IR) imagery of surface temperature with data from a large number of miniature data loggers buried at 3 cm soil depth. The data obtained from six alpine (Alps) and arctic-alpine slopes (Norway, Sweden, Svalbard) evidence persistent root zone temperatures of 2–4 K above air temperature during summer. Surface temperatures show strong positive (2–9 K) and negative (3–8 K) deviations from air temperature on bright days and clear nights, respectively. As to be expected, south oriented slopes are warmer than west and north slopes but microclimatic variation on clear sky days was strong within all slopes, with 8.4 ± 2.5 K (mean \pm SD) surface temperature differences persisting over several hours per day along horizontal (i.e., equal elevation) transects. Life conditions of alpine organisms are thus strongly decoupled from conditions in the free atmosphere and cannot reliably be inferred from climate station data in both, temperate and arctic latitudes. Microtopography can mimic temperature differences of large elevational (or latitudinal) gradients over very short horizontal distances. This is important in the context of climate change because it shows that species do not necessarily need to climb several hundred meters in elevation to escape the warmth. Quite often, few meters of horizontal shift will do. For plants unable to, or too slow to adapt to a warmer climate, thermal microhabitat mosaics offer both refuge habitats as well as stepping stones as atmospheric temperatures rise.

Keywords: Alps, Arctic, leaf temperature, microclimate, soil temperature, thermal niche, topography

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Introduction

The alpine life zone is often considered a harsh environment, dominated by extreme climatic conditions and rough terrain, forcing plants and animals to a high degree of specialization and adaptation (Billings & Mooney, 1968; Körner & Larcher, 1988; Körner, 2003). Low stature is among the most typical characteristics of alpine plants and allows the vegetation to aerodynamically decouple from the free atmosphere, depending on topography (Körner, 2003). On steep slopes, ridges and depressions, the interplay between exposure and vegetation is leading to mosaics of life conditions (Geiger, 1965; Barry, 1981; Körner, 2003). The temperature experienced by an alpine plant can be totally different from the conditions experienced by a mountaineer or measured by a conventional weather station

(e.g., Takasu, 1953; Salisbury & Spomer, 1964; Cernusca, 1976; Larcher & Wagner, 1976; Körner & Cochrane, 1983; Gauslaa, 1984). Numerous studies, in alpine regions all over the world, have shown that leaves of plants can easily become warmer by 15 K during sunny weather and colder by 5 K during clear nights than the 2 m aboveground air temperature (Takasu, 1953; Salisbury & Spomer, 1964; Larcher & Vogel, 1980; Grace, 1987). Above the climatic tree line, exposure and plant morphology are known to exert greater influence on plant temperature than several hundred meters of elevation (Körner, 2003; Löffler *et al.*, 2006).

Climate warming scenarios predict higher than average warming in most alpine areas (Meehl *et al.*, 2007) and therefore alpine regions are often considered as particularly threatened (Beniston *et al.*, 1997; Theurillat & Guisan, 2001; Schröter *et al.*, 2005). In fact, the Alps warmed by +1.5 K compared with the global average of +0.7 K during the last century. There is evidence of upslope migration of plant species both in the montane

belt (Lenoir *et al.*, 2008) and in the alpine/nival belt (Walther *et al.*, 2002, 2005). However, there is also evidence for substantial resistance to centennial climatic forcing in clones of alpine plants which have been identified to inhabit the very same location over thousands of years (Steinger *et al.*, 1996; Bahn & Körner, 2003). It is an open question, whether and which species will be forced upslope in a warmer climate. More ruderal (pioneer) taxa on open ground may migrate fast (Grabherr *et al.*, 1994; Pauli *et al.*, 2007), whereas other, late successional taxa may not. Currently all such projections rest upon the application of available meteorological data (Randin *et al.*, 2009). Here, we question the appropriateness of such space for time scenarios, given that meteorological data are unlikely to reflect actual life conditions in mountainous terrain.

Earlier studies that examined microhabitat and plant tissue temperatures, for technical reasons, were mostly confined to point measurements on individual plants or leaves. Recent technological developments made new methods available that permit a much broader spatial coverage. Modern thermal (IR) imagery screens surface temperatures of full mountain slopes at very high precision and micro loggers allow dense networks for ground temperature measurements. In this study, we assessed by thermal imagery and microloggers, both surface and root zone temperatures at landscape scale with the following aims: (1) to quantify the deviation of surface and root zone temperatures from the 2 m aboveground air temperature under different weather conditions, (2) to assess the spatial variation of surface and root zone temperature on alpine slopes, (3) to estimate and compare the impact of micro and macrotopography (exposure) on surface and root zone temperature, and (4) to separate the influence of vegetation type, from topography effects. The results will assist more realistic migration scenarios on mountain slopes in a climatic warming context.

Materials and methods

Test regions and study sites

In total, we had three different temperate-alpine and subarctic-alpine test regions, namely: At the Furka Pass in the Swiss Alps (centre: 46°34'35"N, 08°25'17"E) three sites with NNW (2500 m), W (2480 m) and SSE (2430 m) exposure, at Abisko in North Sweden (68°21'20"N, 18°50'50"E, 1000 m) one site with SE exposure, at Kåfjorddalen in North Norway (69°24'30"N, 20°58'40"E, 850 m) one site with NW exposure and the high-arctic test region in Colesdalen on Svalbard (78°04'60"N, 15°15'00"E, 50 m) with SW exposure.

In each test region, we have chosen sites on mountain slopes that are above the climatic tree line, are steep (no

rock cliffs), are covering an elevational range of least 200 m, show a rich microtopography but no change in macroexposure, are 'easily' accessible and offer an opposing slope that permits to place the thermal camera. The lack of an opposing slope at the site in Colesdalen forced us to place the camera in the plain in front of the target slope.

Thermal imaging technology, microclimatic loggers and meteorological data

We used a thermal camera which screens 76.800 image points at 50 Hz (VarioCAM[®]; Infa Tec GmbH, Dresden, Germany). This camera records the long-wave infra-red in a spectral range from 7.5 to 14 μm on a micro bolometer array with 320 \times 240 sensors and transforms the radiation readings directly into temperature. The camera uses an auto-calibration routine, using an inbuilt near to ideal black body and software to correct for single image point deviation from black body temperature. In meteorology, this kind of temperature is often misleadingly called brightness temperature but reflects at an emissivity very close to 1.0 [0.98 for plants (Rubio *et al.*, 1997)], mainly the surface temperature of a body, and will therefore be referred as surface temperature in this article. The accuracy of the absolute temperature is ± 1 K, the relative differences between sensor readings have an accuracy of ± 0.1 K and the thermal resolution is 0.05 K. At 500 m distance this translates into an area of about 60 000 m^2 covered by the 76 800 individual temperature measurements or one reading point per 0.75 m^2 .

The thermal camera was placed on a heavy professional tripod (Manfrotto MN 161 MK2; Manfrotto, Bassano Del Grappa, Italy) to yield very stable images at repeated shots. To arrive at a sturdy connection between the thermal camera and the tripod, we used a customized metal camera socket on which we also fixed a telescopic sight (magnification of nine diameters) in order to better spot field marks.

For longer-term records of soil temperature in our target slopes, we used small water proof temperature loggers (iButtons; Maxim Integrated Products, Sunnyvale, CA, USA) which have a resolution of 0.5 K and enough memory to record 80 days with one temperature reading per hour. As a reference, we additionally placed at two sites (Furka Pass and Abisko) four of the more precise soil temperature logger (TidbiT[®] v2 Temp Logger Onset Computer Corporation, Bourne, MA, USA) in 10 cm soil depth which record hourly temperature readings for a period of 2–3 years with a resolution of 0.2 K. To record the meteorological data (air temperature, relative humidity, solar radiation), we had our own weather station (Vantage Pro2 Plus[™] with solar radiation sensor; Davis Instruments, Hayward, CA,

USA) within 1 km of all slopes at Furka Pass and for the subarctic-alpine sites we used a more mobile hand held weather station with a 4-channel data logger (LI-1400, Li-cor, Inc., Lincoln, NE, USA). Additionally, air humidity and air temperature at all sites were measured regularly with a whirling psychrometer during IR imaging campaigns.

Field data

In the centre of each target mountain slope (study site), a rock was marked with bright colour as visible target mark. The thermal imaging device was installed on the opposing slope (or plain for Colesdalen) and the exact position of the tripod was marked. The telescopic sight attached to the thermal imaging device allowed us to align the camera exactly with the visible mark in the target slope. This combination of the tripod position and telescopic sight assured that all images show exactly the same part of the target slope and made the data of different days easily comparable.

For each target slope, we recorded at least one (if possible more) diurnal series of thermal images (temperature readings) under clear sky conditions. The series of images started at midnight and ended 2 h after sunset. The time interval between two images of a series was 15 min (at Furka Pass a 1 min resolution was possible because of external power supply). Within each slope, we defined at least one horizontal and one vertical transect (three horizontal and three vertical transects on the NNW exposed slope of the Furka Pass, our core site) of a minimum length of 100 m (varying from 100 to 350 m). Along these transects every 10 m on horizontal and every 15 m on vertical transects a temperature logger was buried at a depth of 3 cm in the soil. We have specifically chosen 3 cm to capture the spatial and temporal variation of ground temperature in the centre of the top soil rooting zone. Many of these alpine plants (graminoids in particular) also have their apical meristems close to that depth. We will refer to this temperature as root zone temperature. We recorded the root zone temperature for 75 days (June 22, 2008–September 8, 2008) at the Furka Pass and 77 days (June 20, 2008–September 8, 2008) at Colesdalen which represented the main growing season for both sites in the study year 2008. At Abisko and Kåfjorddalen, we placed microclimatic loggers for only 7 (July 28, 2008–August 4, 2008) or 4 days (August 7, 2008–August 11, 2008), respectively, the periods during which we took thermal imaging at these sites. In total, we placed 86 iButtons on a NNW, 33 on a SSE and 54 on a W exposed slope at the Furka Pass. In Scandinavia, we buried 77 loggers in Colesdalen, 27 in Abisko and 29 in Kåfjorddalen.

To know the exact position of each micrologger in the thermal images a field assistant with a visible mark

walked along transects and a thermal image was taken from the opposing slope (position of thermal camera) at the position of each microclimatic logger. The precise position of each logger in the thermal images was marked by using the person as a 'warm spot' (the military purpose these devices had been developed for).

The meteorological data we recorded in the Swiss Alps had a temporal resolution of 10 min. In Scandinavia with the mobile LI-1400, the air temperature, relative humidity and solar radiation was recorded every 30 min. For logistic reasons (too difficult to get there and maintain a weather station), it was not possible to record the atmospheric data directly within the target slope, but at the position of the thermal camera (opposite slope). We assumed that these 2 m aboveground data are representative for the wider region, given the close distance (mostly < 500 m) and atmospheric turbulence. However, because of different insolation during morning and evening hours the opposing slopes might still influence their local air temperatures somewhat, an effect, small compared with the surface warming and presumably cancelled, when we consider long-term and full-day data sets.

Because it was impossible to map the vegetation of the whole slopes at a one pixel-thermal-image resolution, we decided to apply a transect-based approach. For the vegetation analysis, we used the same transects as for the microloggers. This allowed a maximum matching of data sets and assured an optimal spatial alignment with the thermal images. Along each transect, we recorded meter by meter, in 1 m² plots the percentage of vascular plant cover, the percentage of moss and lichens cover, the percentage of stone and bare ground cover and the vegetation height.

Data analysis

The thermal images of one series were aggregated to three different mean images. The first image represented a standard daytime interval from 07:00 to 20:00 hours local time ('standard'). The second is showing the conditions during the 6 h with highest insolation and daytime warming 12:00–18:00 hours ('full solar radiation'). The third, the coldest period, is before sunrise 00:00–06:00 hours ('dark period'). For this analysis, we defined the area within each image where there is no change in macroexposure (slope orientation) and excluded the rest.

We investigated the frequency distribution of surface temperatures in absolute and in relative values standardized by the air temperature of the corresponding time period and site. This standardization by 2 m air temperature allowed us direct comparisons of different sites (Scandinavia, Alps) and days, regardless of their

absolute temperature differences. Additionally, we placed at least hundred (up to 600) horizontal and vertical lines of data points (pixels) and fitted for each of these ‘transects’ a linear regression and calculated the variance and the residual variance of surface temperatures within a ‘transect’. The variance indicates the absolute spatial variation of temperature along a given transect, whereas the variance of the residuals gives us information about the spatial variation of temperature along transects after correcting for the possible bias caused by effects such as exposure or elevational range.

To analyze the root zone temperature data, we calculated different kinds of mean values for each micro-logger: The mean temperature in July and August, the total mean of the season (‘seasonal mean’, i.e., measuring period), the mean for hours with high potential solar heating (‘day-hours’, 11:00–17:00 hours), the mean of the hours with no direct insolation on the ground (‘night-hours’, 00:00–06:00 hours) and the mean of the clear sky sunshine hours (‘clear sky hours’, radiation $> 800 \text{ W m}^{-2}$, 133 h from June 22, 2008–September 8, 2008). The frequency distribution of the root zone temperatures was analyzed for each slope separately in absolute values and also in relative values, standardized by the mean air temperature at a given site and time period. For each transect, a linear regression analysis of the root zone temperatures (‘seasonal mean’, ‘day-hours’, ‘night-hours’, ‘clear sky hours’) was conducted to test for effects of elevation or exposure. Additionally the variance of root zone temperature along transects was calculated for ‘seasonal mean’, ‘day-hours’, ‘night-hours’ and ‘clear sky hours’. By a Fligner–Killeen test (Conover *et al.*, 1981), we approved the homogeneity of variance within the horizontal and vertical transects and compared the variances of the two groups. To exclude the possible bias that differences in variance are only mediated by elevation or exposure gradients, we also compared the residual variance of the linear regressions. To find the best correlation between infra-red surface temperatures, root zone temperatures and air temperature, we tested different time delays for root zone temperature ranging from 0 to 6 h. To check if spots (microhabitats) with on average warmer/colder infra-red surface temperature result in warmer/colder than average root zone temperatures, we analyzed the correlation of daily mean surface and root zone temperature for the same day.

The vegetation data (bare ground, vegetation height) was used as explanatory variables for the variation in surface and root zone temperatures. This allows a better interpretation and separation of microclimatic differences into effects by microtopography and effects related to land cover (plant morphology, density).

Results

Surface temperatures

The absolute surface temperature varied strongly between days and sites and will not be used for any analysis in this article. All sites showed large amplitudes of diurnal courses in surface temperature on bright days, with on average 11 K (up to 17 K) in the Alps and on average 16 K (up to 25 K) in the subarctic-alpine zone (Fig. 1). During clear sky mid-summer nights, the surface temperature dropped at all sites close to or even below freezing point. The spatial variation in surface temperature during clear nights (in the subarctic, clear sky periods with no direct insolation) was low at all sites and usually ranged between 0 and 5 K, but under direct solar radiation the spatial variation can easily increase up to 20 K within a given mountain slope (Fig. 1). Along a horizontal transect (same elevation), we found remarkable spatial surface temperature variation at all sites with $8.4 \pm 2.5 \text{ K}$ (mean \pm SD). This strong spatial variation was not distributed randomly but reflected the microtopography in a very precise way indicating a close relationship of micro-topography and surface temperature (Fig. 1). The effect is so strong that temperature signals scaled to a grey scale ‘build’ a landscape that cannot be distinguished from a black and white photograph of that alpine landscape.

During the 6 h with full solar radiation, the mean temperature differences between surface and air were mostly positive (the surface is warmer than the air) but varied with slope. The difference was only $0.32 \pm 2.11 \text{ K}$ (mean \pm SD) on the NNW exposed slope, but reached $4.4 \pm 1.3 \text{ K}$ on the W and $4.7 \pm 1.1 \text{ K}$ on the SSE exposed slope in the Alps (Fig. 2). This strong exposure effect was even more prominent in the subarctic-alpine sites with a positive $2.5 \pm 1.9 \text{ K}$ surface-air temperature difference on a NW slope in Kåfjorddalen, $8.7 \pm 1.9 \text{ K}$ at the SE slope in Abisko and $9.3 \pm 2.3 \text{ K}$ at the SW exposed slope in Colesdalen (Fig. 2).

During periods with clear sky and no direct insolation, the surface temperatures dropped by about 3–5 K below air temperature in the Alps and by about 7–8 K in the Subarctic and the effects of exposure were a lot weaker (Fig. 2). The ‘standard’ time interval from 7 to 20 h showed again, that predominantly north oriented slopes were colder than south slopes. In the Alps, the NNW exposed slope had in fact a negative surface-air temperature difference of $-2.3 \pm 1.3 \text{ K}$ for this 13 h period, whereas the W exposed slope was $-0.3 \pm 0.7 \text{ K}$ cooler than air temperature, and the SSE slope was with $3.9 \pm 1.0 \text{ K}$ clearly warmer than the air (Fig. 3). This 13 h means cover periods and slope areas with and without direct slope

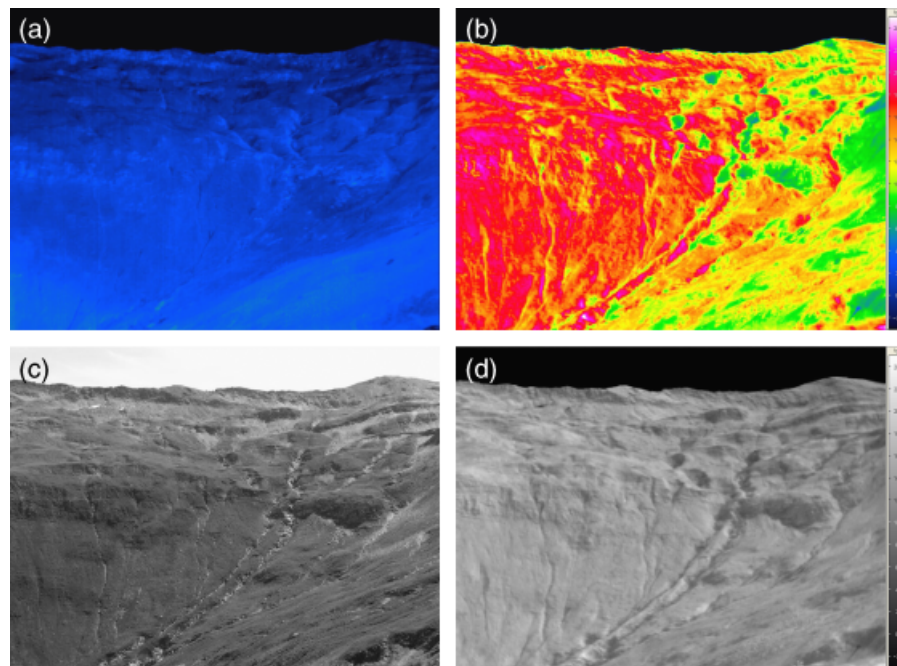


Fig. 1 Upper left image (a) represents a false colour image of surface temperature on a NNW exposed slope at the Furka Pass in the Swiss Alps on the August 29, 2008 during night (0–6 h), and the upper right image (b) shows data for the same slope under full direct solar radiation (12–18 h). Dark blue represents cold (2°C) and magenta hot (24°C) surface temperature. Lower left image (c) is an ordinary, visible light, greyscale photograph taken by a digital camera. Lower right (d) is the same image as upper right (b) but the false colour palette of surface temperature is change to greyscale (black, cold; white, hot).

insolation. Hence reflect the spatial and temporal integration over the full slope viewed by the camera.

In the subarctic alpine zone, all slopes were warmer than air temperature but the NW exposure led to only a $2.6 \pm 1.4\text{ K}$ warmer, compared with the $5.9 \pm 1.4\text{ K}$ warmer conditions on the SE slope and the $5.5 \pm 1.6\text{ K}$ warmer surface on the SW-slope (Fig. 3). Overall the surface temperature varies in space and time a lot more than does air temperature.

Under strong direct solar radiation, the spatial variation of surface temperature along transects was the same for horizontal and vertical transects and no general effects of elevation or exposure emerged. During periods with no insolation, the horizontal transects showed no trends whereas all vertical transects showed significantly decreasing surface temperature with increasing elevation (linear regression, $P < 0.05$) corresponding to a lapse rate of 0.6 K per 100 m of elevation. This resulted in a larger spatial variation of surface temperature along vertical than horizontal transects during night-time. But this effect disappeared when we corrected for the effect of elevation by analyzing the variance of residuals instead of total variance.

Surface temperatures are highly correlated with solar radiation and air temperature but show much larger amplitude than air temperature (Fig. 4). The time delay

of surface temperature compared with air temperature measured at a standard weather station varied strongly between sites and macroexposures. The surface temperature was delayed by 1 h for mostly south oriented slopes (SSE Furka, SE Colesdalen, SW Abisko) and by around 4 h for mostly N/W oriented slopes (NNW Furka, W Furka, NW Kåfjorddalen; Fig. 4).

The percentage of bare ground had a significant influence on surface temperature during dark periods (0–6 h, ANOVA; $df = 128$; $P < 0.05$) with more bare ground resulting in reduced radiative cooling whereas more plant cover leads to stronger night-time cooling (Fig. 5). Plant height also reduced the night-time surface temperature significantly (ANOVA; $df = 128$; $P < 0.05$). Moss and lichen cover had no influence on surface temperatures, and none of the vegetation parameters had an influence on surface heating (IR measurements) under full solar radiation (Fig. 5) at a given resolution of 2 m^2 per pixel. It is important to remember that IR images reflect the temperature of the uppermost surfaces, which may differ from temperatures within plant canopies.

Root zone temperatures

The mean root zone temperatures during the 2 warmest months in the Alps were significantly influence by slope

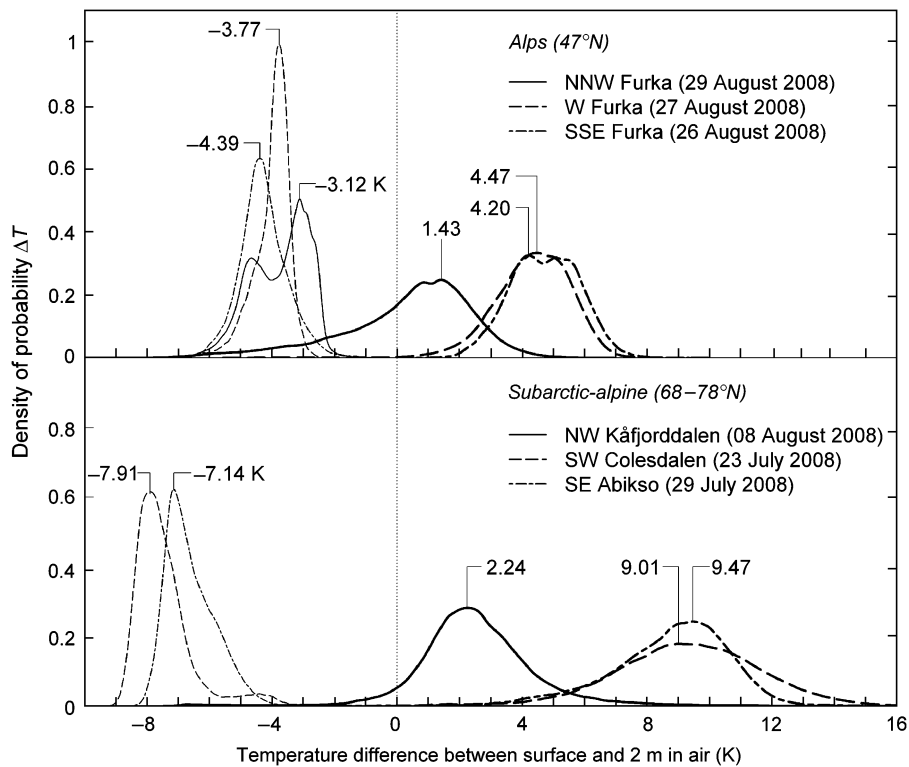


Fig. 2 Density distributions of surface temperatures (means over 6 h) standardized by mean air temperature of three different slopes in the Alps and Subarctic. Fine lines (left) represent data for the dark period (0–6 h) with the 6 h mean air temperature 2 m aboveground: NNW Furka 6.4 °C, W Furka 7.1 °C, SSE Furka 4.6 °C, SW Colesdalen 9.0 °C, SE Abisko 15.4 °C. Bold lines (right) show data for full solar radiation (12–18 h). During these records, the mean air temperature 2 m aboveground was: NNW Furka 12.8 °C, W Furka 11.1 °C, SSE Furka 10.2 °C, NW Kåfjorddalen 7.8 °C, SW Colesdalen 10.5 °C, SE Abisko 15.9 °C. In brackets the date of recording the thermal image series.

exposure (ANOVA; $df = 2$, $P < 0.01$) with 10.9 ± 0.9 °C (mean \pm SD) on SSE, 10.4 ± 0.9 °C on W and 9.3 ± 1.1 °C on NNW exposure in July and 11.4 ± 0.9 °C on SSE, 10.2 ± 0.9 °C on W and 8.8 ± 1.0 °C on NNW exposure in August. Irrespective of exposure, the root zone temperatures of all slopes were significantly warmer than the air temperature, which averaged at only 7.2 °C in July and 7.8 °C in August in the same area (Fig. 6). The only arctic site with continuous root zone temperature data (Colesdalen) averaged at 6.6 ± 1.0 °C in July and 5.8 ± 1.0 °C in August, clearly colder than the alpine sites in the temperate zone and only slightly warmer than the air temperature of 6.1 °C in July and 5.0 °C in August. In July and August, the root zone temperatures were always higher than the air temperatures at all sites and this difference increased with the intensity of solar radiation, resulting in smaller differences during ‘night-hours’ (0–6 h) than during ‘day-hours’ (12–18 h) and largest differences during ‘clear sky hours’ with more than 800 W m^{-2} radiation (Fig. 6).

In contrast to the significant effect of exposure on mean root zone temperatures of complete slopes, the spatial variation of root zone temperature (using seasonal means)

within a slope (temperature differences among individual loggers within a slope) was not affected by slope direction (Fligner–Killeen test, $P = 0.45$; Fig. 6). Also during ‘day-hours’ and ‘clear sky hours’ with more than 800 W m^{-2} no differences in spatial variation of temperature was observed ($P > 0.1$, Fig. 6). Only in ‘night-hours’ the SSE exposed slope showed significantly lower variation ($P > 0.01$, Fig. 6). The high arctic site at Colesdalen showed a similar spatial variation of seasonal mean root zone temperature within a slope ($P = 0.5$). In all slopes the spatial temperature variation within a slope increased with solar radiation and was highest at ‘clear sky hours’ with more than 800 W m^{-2} .

A linear regression analysis of temperatures along transects revealed a directional change only in one out of seven horizontal transects for seasonal mean temperatures (decreasing temperature along E–W gradient; Furka Pass NNW exposure). This single transect included a part of the slope that receives morning shade through an adjacent mountain. Six out of seven vertical transects showed a temperature reduction with increasing elevation (linear regression, $P < 0.05$). The vertical transect on the SSE exposed slope on the Furka Pass

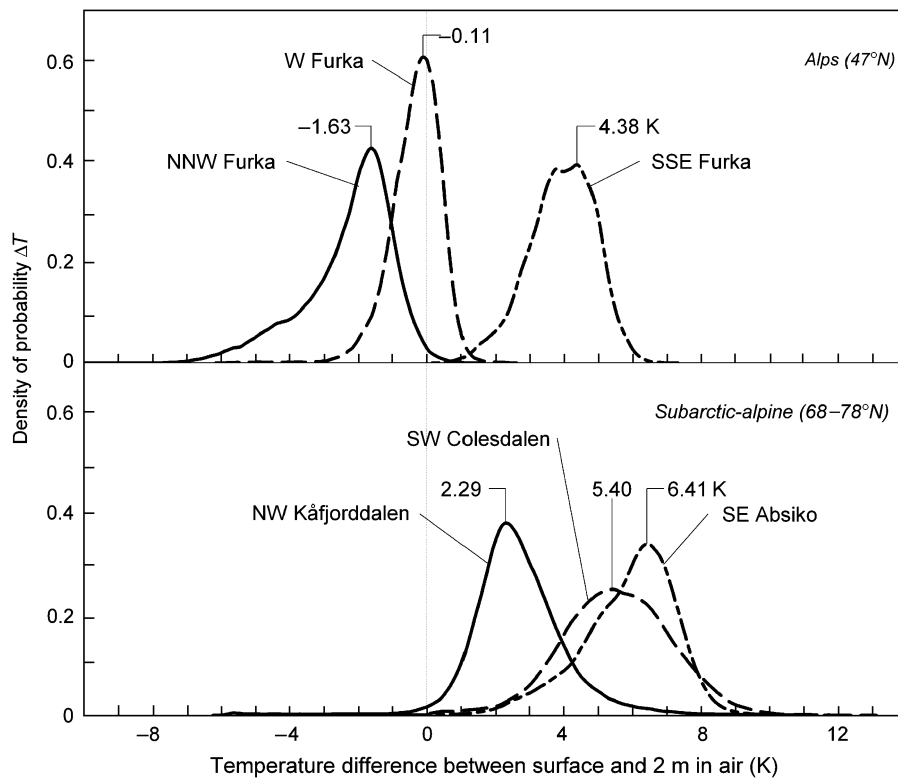


Fig. 3 Density distributions of mean surface temperatures standardized by air temperature of three different slopes in the Alps and the Subarctic during standard time interval (07–20 h). Mean air temperature 2 m above ground for these periods: NNW Furka 11.5 °C, W Furka 9.8 °C, SSE Furka 9.0 °C, NW Kåfjorddalen 6.6 °C, SW Colesdalen 10.5 °C, SE Absiko 15.4 °C.

showed no significant influence of elevation on root zone temperatures. The elevational effect on root zone temperature is stronger during periods without direct insolation ('night-hours') than during 'day-hours'.

For 'seasonal mean' temperatures and 'day-hours' all transects showed similar spatial temperature variation along a transect (temperature differences of individual loggers along a transect; $P > 0.7$), independently of transect length (100–350 m) or orientation (exposure, vertical or horizontal). During the clear sky 'night-hours', significant differences in spatial temperature variation along a transect occurred with higher variation on vertical than on horizontal transects (Welch's t -test, $P < 0.05$). This higher variation is mediated by the adiabatic lapse rate and if we correct for the elevation gradients on vertical transects the difference in variation disappears ($P = 0.22$). The spatial temperature variation along a transect was a lot stronger under direct solar radiation ('day-hours') than during the 'night-hours' ($P < 0.005$) with 5.3 ± 0.5 K (mean \pm SD) temperature difference during 'day-hours' along a 100 m horizontal transect. The differences in root zone temperature within a given slope are 4.0 ± 0.9 K in seasonal mean and 9.9 ± 1.8 K during 'clear sky hours' (NNW

exposure Furka Pass, Fig. 6). If we compare all exposures at the Furka Pass site which are located within 2 km² and 300 m of elevational range the observed spatial variation in root zone temperatures was 7.0 K in seasonal mean and 14.9 K during 'clear sky hours' while the air temperature difference mediated by elevation (adiabatic lapse rate) was about 2 K during this periods. There is a strong correlation of root zone and surface temperature, with the best fit at a 2 h delay of root zone compared with surface ($\text{cor} = 0.82$, $r^2 = 0.68$, $P < 0.0001$). This is true for all exposures and sites. But the time delay of root zone temperature compared with air temperature measured by a weather station strongly varies with exposure (Fig. 4). The best correlations resulted with a 3 h delay for the SSE slope and 6 h for the NNW and W slope on the Furka Pass in the Swiss Alps.

The percentage of bare ground had a significant influence on 'night-hours' root zone temperature ($P < 0.05$) with more bare ground resulting in stronger 'night-hours' cooling in the soil (in contrast to effects on surface temperature). A greater plant cover reduced 'night-hours' root zone cooling. Plant height had a tendency to reduce 'night-hours' cooling with increasing plant height ($P < 0.1$). The frequency of moss and

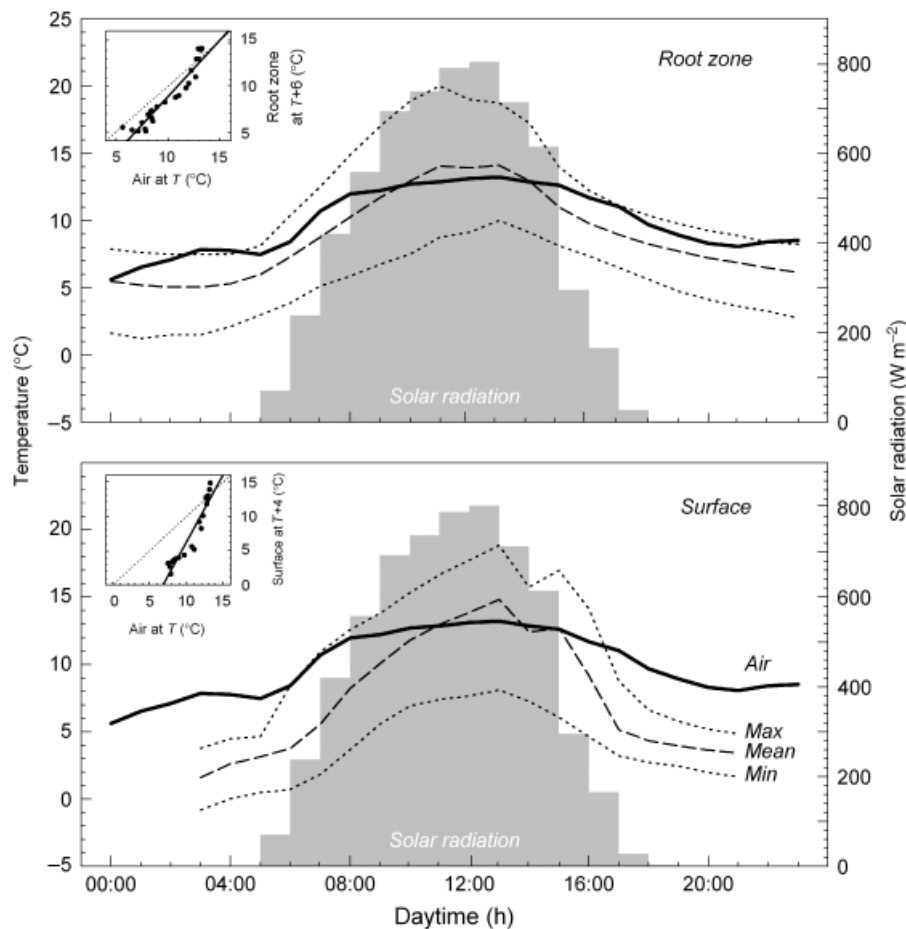


Fig. 4 Twenty-four hours course of root zone, surface (mean, min and max of each) and air temperature (2 m above ground). ‘Min’ and ‘Max’ refer to the coldest and warmest 5% of the measured temperatures. The small inset shows the correlation of air temperature and root zone or surface temperature corrected for the time delay caused by exposure and soil heat flux. All data for August 29, 2008; NNW exposed slope, Furka Pass, Swiss Alps.

lichen cover showed no influence on the root zone temperature. None of the vegetation parameters (plant cover, bare ground, plant height, moss and lichen cover) had a significant influence on root zone temperature under strong solar radiation.

Discussion

Our results clearly illustrate that surface temperatures strongly deviated from air temperature in temperate and subarctic-alpine regions with substantially warmer surface than air temperature under direct solar radiation and lower temperatures during periods without direct insolation at landscape scale. These deviations in temperature persisted over long periods on a given day and location, hence did not just reflect short-term fluctuations, and thus represent the relevant life conditions for alpine and arctic biota. Topography is the main

driver of these deviations, with plant cover exerting only a small modulating influence.

Surface temperature

The strong deviation of life conditions from meteorological data call for great caution with any projections with regard to climatic change effects in alpine terrain. Periodic deviations of plant and soil surface temperature from air temperatures, especially in low stature alpine vegetation, had been reported earlier (see ‘Introduction’). With the new thermal imaging technology, we were able to monitor entire landscapes over time with very high spatial resolution. The thermal images integrate over many plants, species and bare ground and yield a microhabitat temperature which reflect both topography as well as land cover effects. Additionally, we were able to aggregate information over time. The larger scale of the IR images explains why earlier

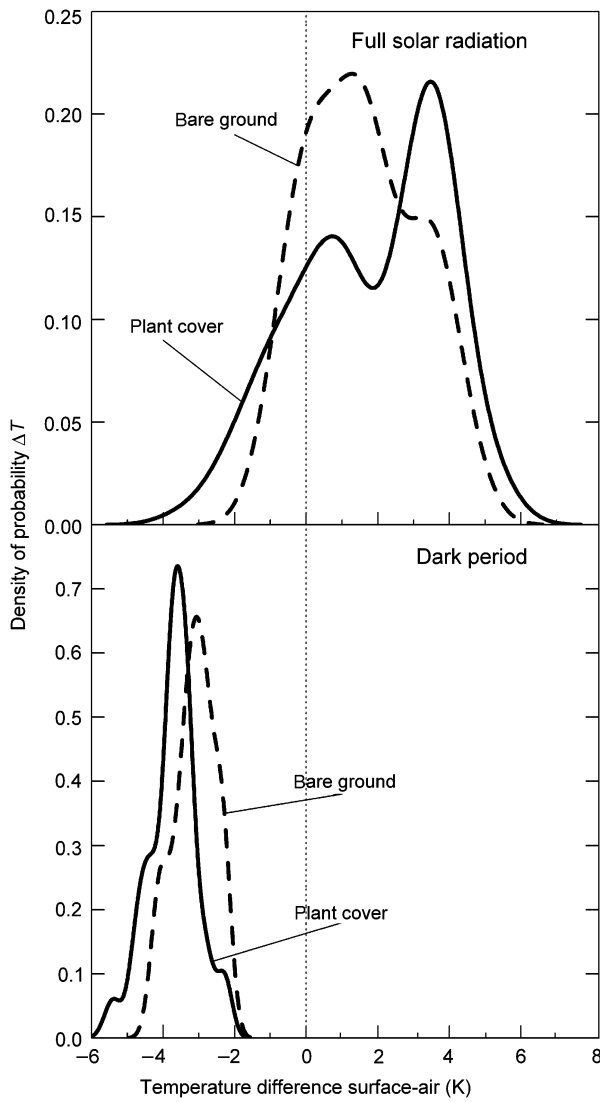


Fig. 5 Density distributions of surface temperatures standardized by air temperature of plots with more than 90% plant cover ('plant cover') and less than 40% plant cover ('bare ground'). The upper graph represents the 6 h with full solar radiation (12–18 h), the lower, the dark period (0–6 h). Example of a NNW exposed slope, Furka Pass, Swiss Alps on the August 29, 2008.

studies, which reported measurements on single plants, had arrived at even larger deviations from air temperature. Nevertheless, our data evidence significant thermal decoupling of vegetation from atmospheric conditions (2 m air temperature) at meter to kilometer scale. With increasing elevation the vegetation is closer attached to the ground and therefore the decoupling from atmospheric conditions generally increases with increasing elevation (Körner et al., 1983; Körner, 2003). The comparison of temperate and subarctic-alpine sites showed that the diurnal amplitude of surface

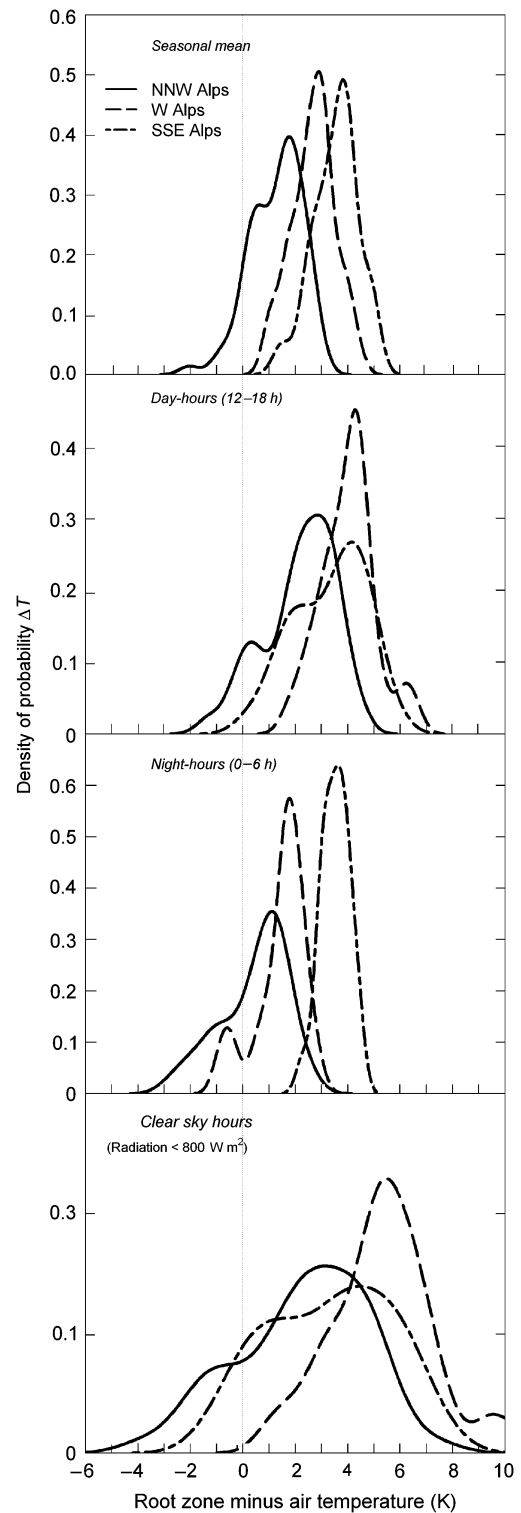


Fig. 6 Density distribution of the root zone temperatures standardized by air temperature for 'Seasonal mean' (June 22, 2008–September 8, 2008), 'Day-hours' (11–17 h; June 22, 2008–September 8, 2008), 'Night-hours' (0–6 h; June 22, 2008–September 8, 2008) and 'Clear sky hours' ($>800 \text{ W m}^{-2}$; June 22, 2008–September 8, 2008; 133 h).

temperature on bright days was twice that in air temperature in the temperate alpine zone, and four times that in air temperature in the subarctic-alpine zone. In part, this is because air temperature co-varies in the Arctic, but the low solar angles seem to contribute to this as well. The deviations of surface from air temperature are also much larger in the subarctic than in the temperate alpine zone both, under strong solar radiation and also during periods without direct insolation. While the daily mean temperatures in the temperate-alpine and subarctic-alpine regions are similar (Körner & Larcher, 1988) the diurnal courses are very different and therefore responsible for the stronger differences between surface and air temperature during clear sky days in the Subarctic. As shown by Körner *et al.* (2003) the alpine areas across Europe have a common thermal envelope. They found no latitudinal trend of seasonal length or mean temperature in alpine areas from the Mediterranean (37°N) to the Subarctic (68°N) and similar seasonal mean temperatures for most sites. Körner *et al.* (2003) suggest that the longer day length at the Scandinavian sites compensates for the reduced solar inclination compared with Mediterranean sites, the same effect we observed in our study.

We could quantify the well-known slope effects on nonforested land (Geiger, 1965; Barry, 1981; Körner, 2003) across a rich alpine topography. Exposure effects were stronger in subarctic-alpine than in temperate-alpine landscapes, presumably because of the lower solar angles in the Arctic. These effects become more pronounced during bright days (our 'standard' period; 13 h), simply because south exposed slope receives longer insolation (10 h) during that period than west or even north exposed slopes (only 4 h; a smaller radiation 'dose'). Under full solar radiation at mid-day in mid-summer, all slopes heat up to similar surface temperatures. This might be important for plant growth, given that the duration of favourable periods is more important than peak activity (Körner, 2003). Effects of exposure on surface temperature explain the differences in vegetation of opposing slopes (Zoller, 1992; Malyshev & Nimis, 1997). Therefore, exposure is a key variable in vegetation modelling in treeless terrain (Raupach & Finnigan, 1997; Bennie *et al.*, 2008). In contrast, exposure effects are very small on forested slopes (Beaman, 1962; Paulsen & Körner, 2001; Körner & Paulsen, 2004; Treml & Banas, 2008) owing to the fact that tree crowns rather than the slopes are interacting with solar radiation and trees are shading the ground and are also strongly coupled to atmospheric conditions.

The spatial variation of surface temperature within a given mountain slope adds to the strong thermal contrasts seen in alpine environments. Microtopography has a very large impact on microhabitat surface tem-

perature by influencing microexposure and wind (Körner, 2003). Microtopography effects overlap with overall slope effects so that slope effects either become enhanced or diminished, with the overall effect of microtopography exceeding that of slope and regional climate (Löffler *et al.*, 2006; Löffler & Pape, 2008). This leads to a very distinct mosaic of microhabitat temperatures, independently of the 2 m air temperature, likely contributing to the often sharp changes of alpine vegetation over short distances. Snow melt patterns are associated with the microtopography and will enhance the spatial arrangements of vegetation in alpine landscapes (Gjaerevoll, 1956; Friedel, 1961; Helm, 1982; Galen & Stanton, 1995; Körner, 2003; Schob *et al.*, 2009).

The adiabatic lapse rate had a direct effect on surface temperatures during periods without direct insolation, resulting in decreasing surface temperatures with increasing elevation. But this surface temperature gradient totally vanishes under direct solar radiation. Therefore microtopography effects on surface temperature are able (at the scale of meters) to mimic large elevation gradients and create, on small areas, microhabitat temperatures reflecting several hundred meters of elevation. The temperature ranges seen across a few meters match or exceed the rise in temperature predicted by IPCC (+ 3 K; Meehl *et al.*, 2007).

At the scale of the IR image resolution ($\approx 1 \text{ m}^2$) land cover had surprisingly little effect. Reduced night-time radiative heat loss of bare soil compared with dense vegetation was the most significant land cover effect. This is the result of heat flux within the soil, partly compensating for the radiative heat losses at the surface. In contrast, the upright plant structures are thermally decoupled from the soil and cool below air temperature in clear nights. Also the type of plant cover had hardly any effect. These results contradict many studies that found more pronounced heating of bare soil compared with closed vegetation and also greater warming in prostrate compared with more upright plants (Takasu, 1953; Salisbury & Spomer, 1964; Cernusca, 1976; Körner *et al.*, 1983; Körner & Cochrane, 1983; Gauslaa, 1984). A likely explanation is the fact that the vegetation at all our sites was quite low in stature (mostly < 25 cm) and that the thermal imaging amalgamated information for many plant species and structures (grasses, rosettes, dwarf scrubs) and therefore these differences of even finer scales are averaging out. At the meter-scale microtopography effects seem to outrange the influence of plant structure on surface temperature under strong solar radiation. Hence, at finer spatial resolution (< 1 m^2) we expect even greater deviations from air temperature than captures by these IR images.

Soil temperatures

The influence of macroexposure (slope) on root zone temperature is consistent with the results of surface temperature and reflects solar incidence angles. South oriented slopes have longer periods of sunshine and steeper incidence angles than west or north oriented slopes. Increasing solar radiation correlates with the differences between root zone and air temperature. Root zone temperatures stayed warmer than the air temperature also during overcast or night-time periods because of heat storage. Belowground meristems are likely to profit from these generally warmer conditions (Körner, 2003). Meristem temperatures are clearly underestimated by air temperature, even during periods without sunshine. Similar to IR images, root zone temperatures showed a large within-slope variation, which increased with solar radiation. However, integrated across those microhabitat specific temperature conditions our elevational transects match expectations of a decreasing temperature with increasing elevation (0.6 K per 100 m). So, on average, higher elevation sites are colder than lower elevation sites at this larger scale. But the observed decrease in temperature with increasing elevation by 0.6 K per 100 m is >5 times smaller than the >3 K variation in temperature over short distances within such elevational transects. Microhabitat root zone temperature variations over distances of a few meters correspond to temperature differences otherwise found across an elevation range of 500 m.

The vegetation cover had only weak influence on root zone temperature and only affected temperature during 'night-hours', with more bare ground resulting in colder -3 cm root zone temperatures. This is the result of radiative cooling under clear sky conditions which is reduced under a closed plant cover. The correlation of surface temperature with root zone temperature is rather weak, which reflects the fact that the IR temperatures are means over >1 m², whereas the data loggers in 3 cm soil depth are averaging the influence of a few cm² of soil surface.

Conclusion

We documented large and persistent variation in microhabitat temperatures (root zone and surface) over large alpine terrain and systematic deviations of plant temperature from air temperature. These effects increased with solar radiation and mimic across a few meters, thermal contrasts in air temperature along elevation gradients of several hundred meter (or hundreds of kilometres in latitude). These consistent microhabitat temperature differences are larger than the temperature change predicted by IPCC (Meehl *et al.*, 2007). This

mosaic of temperature is likely to contribute to the patchy vegetation in treeless alpine landscapes and explain the lack of clear species limits such as those for tree taxa at the tree line. This temperature mosaics are offering refuges or stepping stones in a warming climate. Plants do not necessarily need to climb several hundred meters in elevation to find suitable new habitats in case of warming but may find conditions matching their 'thermal niche' over very short distances. In the light of these data, biodiversity of alpine landscapes may in fact be less endangered by climate change than is often assumed, although the abundance of certain habitat types will become reduced and additional factors such as changes in precipitation regime (snow cover duration, etc.) might influence the future plant species distribution as well. The data shown here thus challenge the stereotype of particularly sensitive and vulnerable alpine biota with respect to climatic warming. We advocate a more cautious treatment of this matter. Our results rather illustrate that rough high elevation terrain may in fact be more suitable to protect biodiversity under changing climatic conditions than most other, lower elevation types of landscapes, forests in particular. By their architecture, forest trees to a larger extent remove such beneficial topography effects (Paulsen & Körner, 2001) and experience temperatures much closer to ambient atmospheric conditions (Körner, 2003). Not surprisingly, their distributional patterns do track recent climatic warming well (Lenoir *et al.*, 2008).

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Chapter 3

Topographically controlled
thermal-habitat differentiation buffers
alpine plant diversity against climate
warming



Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming

Daniel Scherrer* and Christian Körner

Institute of Botany, University of Basel,
Schönbeinstrasse 6, CH-4056 Basel,
Switzerland

ABSTRACT

Aim We aim to: (1) explore thermal habitat preferences in alpine plant species across mosaics of topographically controlled micro-habitats; (2) test the predictive value of so-called ‘indicator values’; and (3) quantify the shift in micro-habitat conditions under the influence of climate warming.

Location Alpine vegetation 2200–2800 m a.s.l., Swiss central Alps.

Methods High-resolution infra-red thermometry and large numbers of small data loggers were used to assess the spatial and temporal variation of plant-surface and ground temperatures as well as snow-melt patterns for 889 plots distributed across three alpine slopes of contrasting exposure. These environmental data were then correlated with Landolt indicator values for temperature preferences of different plant species and vegetation units. By simulating a uniform 2 K warming we estimated the changes in abundance of micro-habitat temperatures within the study area.

Results Within the study area we observed a substantial variation between micro-habitats in seasonal mean soil temperature ($\Delta T = 7.2$ K), surface temperature ($\Delta T = 10.5$ K) and season length (>32 days). Plant species with low indicator values for temperature (plants commonly found in cool habitats) grew in significantly colder micro-habitats than plants with higher indicator values found on the same slope. A 2 K warming will lead to the loss of the coldest habitats (3% of current area), 75% of the current thermal micro-habitats will be reduced in abundance (crowding effect) and 22% will become more abundant.

Main conclusions Our results demonstrate that the topographically induced mosaics of micro-climatic conditions in an alpine landscape are associated with local plant species distribution. Semi-quantitative plant species indicator values based on expert knowledge and aggregated to community means match measured thermal habitat conditions. Metre-scale thermal contrasts significantly exceed IPCC warming projections for the next 100 years. The data presented here thus indicate a great risk of overestimating alpine habitat losses in isotherm-based model scenarios. While all but the species depending on the very coldest micro-habitats will find thermally suitable ‘escape’ habitats within short distances, there will be enhanced competition for those cooler places on a given slope in an alpine climate that is 2 K warmer. Yet, due to their topographic variability, alpine landscapes are likely to be safer places for most species than lowland terrain in a warming world.

Keywords

Climate change, indicator values, micro-habitat, snow distribution, soil temperature, species diversity, surface temperature, Switzerland, thermometry.

*Correspondence: Daniel Scherrer, Institute of Botany, University of Basel, Schönbeinstrasse 5, CH-4056 Basel, Switzerland.
E-mail: daniel.scherrer@unibas.ch

INTRODUCTION

Since the time of Theophrastus (*c.* 320 BC) plants have been known to be biological indicators for environmental conditions, and long before that as part of indigenous land-use skills. Recently, scientists have used the occurrence and abundance of different plant species to estimate environmental conditions and have attributed semi-quantitative ‘indicator values’ to each species (Ellenberg, 1974; Landolt, 1977). Such indicator values have the advantage that they do not rely on technical equipment and they represent integrated signals of plant–environment relationships under climate conditions that may otherwise strongly fluctuate over short periods of time and differ at fine spatial scales not captured by spot measurements (Wamelink *et al.*, 2002; Diekmann, 2003). Although the application of indicator values is often criticized because they are inferred from field experience and not from precise measurements (Økland, 1990; Dierschke, 1994), indicator values enjoy great popularity, especially in conservation biology and habitat monitoring (e.g. Kremen, 1992; Caro & O’Doherty, 1999; Jonsson & Jonsell, 1999; Medellín *et al.*, 2000; Niemi & McDonald, 2004), simply because they reflect habitat quality surprisingly well in most situations where species have unimodal relationships with the environment (Økland, 1990; Lawesson & Oksanen, 2002). Another great advantage of species-based indicator values (i.e. the environmental preferences of species) is that such values can be aggregated for many species (whole communities) and therefore, by considering community attributes, are likely to be more robust than the attributes of single species. The first quantitative indicator system for central Europe was developed by Ellenberg (1974), but there are many systems, for example the Landolt values for Switzerland (Landolt, 1977). This is important because the response of species may vary across large geographical gradients (Diekmann & Lawesson, 1999) and therefore the use of indicator values outside the region for which they were developed is a subject of considerable debate (Hill *et al.*, 2000), although the system seems to work well in most cases (e.g. Persson, 1981; Hill & Carey, 1997; Prieditis, 1997).

While indicator values aim to describe the most frequent association of a species with environmental conditions, the ecological niche of a given species is the result of the interplay of many environmental factors (Hutchinson, 1957). Hutchinson distinguished between the fundamental niche (the abiotic requirements of a species to maintain a positive population growth rate) and the realized environmental niche (the proportion of the fundamental niche in which a species has a positive population growth rate, given the constraining effects of biological interactions; Pulliam, 2000; Silvertown, 2004). In nature, we always observe the realized niche, while the fundamental niche can only be determined by experiment. However, along some environmental gradients, abiotic conditions may be more important than competition, and the margins of the realized niche may approximate the limits of the fundamental niche. Temperatures at high elevations are

likely to represent such a dominating environmental driver explaining species or even life-form limits (e.g. tree line formation; Körner, 1998; Körner & Paulsen, 2004).

The influence of air temperature on plant distribution is less obvious (not producing horizontal delineations such as the tree line) in the alpine belt, which is dominated by high topographic variability. Low-stature alpine vegetation is aerodynamically decoupled from atmospheric conditions (Körner, 2003). The temperature within the vegetation is controlled by aerodynamics and irradiance and thus co-dominated by micro-topography and plant morphology, resulting in a mosaic of micro-climates (Scherrer & Körner, 2010). Micro-topography also determines snow distribution on alpine slopes (Körner, 2003). These snow-melting patterns are highly conserved between years and exert a great influence on species composition by determining the length of the growing season (e.g. Gjørevoll, 1956; Friedel, 1961; Helm, 1982; Galen & Stanton, 1995; Körner, 2003; Schöb *et al.*, 2009).

Recently developed techniques such as thermal imaging of mountain slopes and miniature data loggers allow precise measurements of both surface and soil temperatures. They offer an opportunity to compare species thermal preferences based on the indicator values with actual micro-habitat conditions in alpine terrain. In this study we use infra-red thermometry, on-site micro data logging of soil temperatures and time series of snow-melting patterns in combination with Landolt indicator values (Landolt, 1977) to examine: (1) if different vegetation types and plant species occur in different micro-habitat temperatures; (2) if the observed micro-habitat temperatures match predictions derived from indicator values; and (3) if the Landolt indicator values for temperature reflect habitat temperature after snow-melt and/or season length as determined by snow-melt date. We also estimated (4) the potential loss and shift in abundance of micro-habitat temperatures within a small area under a 2 K warming scenario.

MATERIALS AND METHODS

Study sites

This project was carried out in the temperate-alpine zone near the Furka Pass in the Swiss central Alps (46°34′35″ N, 08°25′17″ E). Within the study area (about 2 km²) we chose three steep mountain slopes with north-north-west (centre at 2500 m a.s.l.), west (2480 m a.s.l.) and south-south-east (2430 m a.s.l.) exposures. All slopes are located well above the climatic tree line (which is at *c.* 2150 m a.s.l. in this region) and show strong variation in micro-topography but no variation in the general direction of slope exposure. The study sites cover an elevational range of 200 m on the south-south-east slope and 400–600 m on the other two slopes. Because of its large elevational amplitude, logistical reasons (power supply) and a field station for night measurements, we designated the north-north-west slope as our core site.

Field data

The surface temperature of the study slopes was measured with a thermal camera (VarioCAM[®]; Infra Tec GmbH, Dresden, Germany) which records the long-wave infra-red at a resolution of 76,800 image points and transforms the radiation directly into temperature. The recorded surface temperature mostly reflects vegetation canopy temperature in areas with >90% cover of alpine vegetation. The accuracy of the absolute temperature is ± 1 K and the relative differences between measurement fields (pixels) have a resolution of ± 0.1 K. To have an optimal angle of vision the thermal camera was placed on the opposite slope. For each target slope we recorded at least one (if possible more) diurnal series of thermal images under clear-sky conditions. The series of images had a temporal resolution of 15 min (time between two images), started at midnight and ended 2 h after sunset (for more details on the method used to record surface temperature see Scherrer & Körner, 2010). The spatial resolution of the thermal images was *c.* 0.75 m² per image point for all slopes.

Soil temperatures were recorded continuously with 173 small waterproof temperature loggers (iButtons; Maxim Integrated Products, Sunnyvale, CA, USA) which have a resolution of 0.5 K and record for 80 days with one temperature reading per hour. Within each of the three mountain slopes we defined at least one horizontal and one vertical transect (three horizontal and three vertical at our core site, the north-north-west exposed slope) of a minimum length of 150 m (varying from 150 to 350 m depending on topography). To capture the spatial and temporal variation of the temperature in the top-soil rooting zone we buried the loggers at a depth of 3 cm in the soil along the horizontal (one logger every 10 m) and vertical transects (one logger every 15 m). In total we placed 86 temperature loggers on the north-north-west, 33 on the south-south-east and 54 on the west exposed slopes, which recorded the soil temperature for 75 days (22 June to 8 September 2008). This 75-day period represented the main growing season at the Furka Pass during 2008. Additionally, standard meteorological data 2 m above ground (air temperature, air humidity, solar radiation) were recorded with a 10-min temporal resolution by our own weather station (Vantage Pro2 Plus[®] with a solar radiation sensor; Davis Instruments, Hayward, CA, USA) within the study area at 2445 m.

We took a photograph every third day from 1 June to 14 July 2008 to analyse the relative differences in season length of different plots within the mountain slopes. This permitted a comparison of the relative differences in season length given the fact that the spatial patterns of snow melt are highly conserved among years, even though the absolute date of snow melt (and therefore the absolute season length) varies strongly between years.

Along the transects of soil temperature loggers, we recorded metre by metre in 1 m² plots the percentage cover of vascular plant species, bryophytes, lichens and bare ground/stone. The vascular plants were identified to species level according to Binz & Heitz (1990) to provide a species list for each plot.

In total we had 531 plots on the north-north-west, 120 on the south-south-east and 238 on the west exposed slopes. For each vascular plant species an indicator value for temperature (values 1–5) was assigned according to Landolt (1977). The precise position of each plot in the thermal images was determined at a metre scale by using a person as a ‘warm spot’ (the military purpose for which these thermal cameras were developed).

Data analysis

The many thermal images of one time series were aggregated over time to three different mean images for each mountain slope. The first shows the coldest period before sunrise at 00:00–06:00 h (‘cold period’). The second represents the 6 h with highest insolation and daytime warming at 12:00–18:00 h (‘hot period’). The third image averages most of the daylight period from sunrise to sunset at 07:00–22:00 h (‘daylight period’). From each mean image we extracted the surface temperatures (pixels) corresponding to our 889 plots along the horizontal and vertical transects. To make the temperatures of different recording days (different air temperatures) comparable, we standardized the surface temperature by subtracting the mean air temperature (2 m above ground) of the corresponding period.

For each soil-temperature logger we calculated three different mean values. First, the mean temperature for the complete season (‘seasonal mean’); second, the mean for night hours (‘night-hours’, 00:00–06:00 h); and third, the mean for all clear sky sunshine hours (‘sunshine-hours’). As clear sky sunshine, we defined hours with more than 800 W m⁻² solar radiation according to our weather station, resulting in 133 h from 22 June to 8 September 2008. Additionally, we calculated the growing degree days (GDD; >5 °C) for the complete (75 days) growing season for each logger position. GDD was calculated on the basis of daily mean soil temperatures as

$$\text{GDD} = \sum_{i=1}^{75} \max[0, (T_i - T_0)],$$

where T_i is daily mean soil temperature and T_0 is the threshold value (5 °C), added up over time for $T_i > T_0$ (Tuhkanen, 1980). Even though we think a threshold value of 5 °C is most justified biologically, we also calculated GDD with different temperature thresholds (T_0) ranging from 0 to 10 °C.

The series of snow-melting photographs of the mountain slopes was used to determine visually the date of snow melt for each plot within the three slopes. The date was transformed into days of snow cover after 1 June 2008. The transformation was necessary because several plots (especially on the south-south-east slope) were already snow-free on 1 June 2008 when the sites could be first accessed and therefore no exact snow-melting date could be provided.

Based on the species lists, we calculated the mean Landolt indicator value for temperature (in the following called the temperature indicator value) of each plot. We used the mean instead of the median because we were interested in very small

differences within one alpine mountain slope, whereas studies dealing with median values are normally broad-scale comparisons of habitats. Therefore using the median would be inappropriate in this study where we are looking for fine-scale habitat differentiation of vegetation units and species. Linear regression was used to determine whether the mean temperature indicator value of a plot is correlated to its soil temperature ('seasonal mean', 'night-hours', 'sunshine-hours').

The mean soil temperature ('seasonal mean', 'night-hours', 'sunshine-hours') and surface temperature ('cold period', 'hot period', 'daylight period') were calculated separately for each plant species (mean temperature of all plots in which the plant species was present). Additionally the plant species were grouped according to their temperature indicator value (values 1 to 5) into five 'Landolt-T-Groups' and the mean soil and surface temperature for each group were calculated using the mean values of all species within a certain group. The mean surface and soil temperature of the five 'Landolt-T-Groups' were analysed by ANOVA and a Tukey honestly significant difference (HSD) test.

For each plant species the mean duration of snow cover after 1 June 2008 was calculated from the mean time of release from snow for all plots in which the plant species was present. Thereafter the plant species were assigned to the five 'Landolt-T-Groups' as above and the groups were analysed by ANOVA and a Tukey HSD test.

The similarity in species composition of the plots was examined by grouping the plots into different vegetation units using hierarchical cluster analysis. The clusters were constructed based on presence/absence of the species in the plots irrespective of their abundance. Plots with more than 70% of species in common were considered as belonging to the same cluster. For each vegetation unit we calculated the mean soil temperature ('seasonal mean', 'night-hours', 'sunshine-hours') and the mean temperature indicator value (mean of all plots within a cluster) and checked their relationship by regression analysis. By using regression, we tested if vegetation units that are less similar show larger temperature differences than closely similar vegetation types. For that purpose the distances in the hierarchical cluster dendrogram were arc-sine transformed because they reflected values between 0 and 1. The cluster analysis and all statistical analyses were performed with R 2.8.1 (R Development Core Team, 2008).

To quantify the potential losses and changes in thermal micro-habitat classes within the 2 km² study area due to climate warming we simulated a 2 K mean temperature increase. This was done by taking the current distributions of surface ('daylight period') and soil temperature ('seasonal mean') and shifting them by 2 K. Therefore only the mean temperature increased by 2 K while the variation in temperature stayed exactly the same. This parallel shift of temperatures is the best approximation because we have no data to assume or quantify a change in fine-scale temperature variation due to climate warming. By comparing the two temperature distributions ('current' and 'future') we can distinguish four different categories for the micro-habitat

temperatures. First, there are the coldest micro-habitat temperatures of the current distribution that are lost in the event of a 2 K warming ('lost', meaning no overlapping of the temperature distributions). The second category contains the cooler micro-habitat temperatures that are present in the current distribution as well as in the 2 K warming scenario but will decrease in their abundance ('decrease'). Third, there are the warmer micro-habitat temperatures of the current distribution that will increase in their abundance with a 2 K warming ('increase'); the fourth category contains the micro-climate temperatures that are warmer than the currently warmest habitats ('new').

RESULTS

We observed a remarkable variation in infra-red surface temperatures between the 889 plots, with a surface-air temperature difference of -0.26 ± 2.38 K (mean \pm SD; ranging from -4.9 to $+5.4$ K) during the 'daylight period' and 2.16 ± 2.46 K during the 'hot period'. During night-time without direct insolation ('cold period') the surface-air temperature difference was -3.98 ± 1.00 K.

The data from the 173 logger positions show a strong variation in soil temperature, with a 'seasonal mean' temperature for the complete slope of 9.68 ± 1.29 °C (mean \pm SD; ranging from 3.1 to 10.3 °C), a 'night-hours' soil temperature of 7.61 ± 1.58 °C and temperatures during 'sunshine hours' of 13.42 ± 2.49 °C (Fig. 1). This variation in seasonal mean temperatures between micro-habitats added up to large differences in GDD: 244 ± 71 GDD, ranging from 55 to 404 GDD. There was substantial variation within all slopes but generally the north-north-west exposed slope had lower GDD than the west and south-south-east exposed slopes (Fig. 2).

We recorded 174 vascular plant species (species are listed in Appendix S1 in Supporting Information). The mean number of vascular plant species per plot was 18.8 ± 10.0 (mean \pm SD). Most of the plant species had a temperature indicator value of 2 or 3 (88%), which is typical for alpine species, but plant species with values of 1, 4 and 5 were also present in the plots. The mean temperature indicator value of the plots matched the expectations for alpine landscapes and were between 2 and 3, except for some plots on the south-south-east slopes with values up to 3.2 (Fig. 1).

The linear regression model of the mean temperature indicator value per plot and the corresponding soil temperature showed a weak significant correlation of 'seasonal mean' temperatures ($P < 0.001$, $r^2 = 0.24$), no significant relationship during the 'sunshine-hours' ($P = 0.69$) and a strong relationship during the 'night-hours' ($P < 0.001$, $r^2 = 0.51$; Fig. 1). The linear model of the GDD >5 °C and the corresponding temperature indicator value per plot also showed a significant correlation similar to the results of 'seasonal mean' temperatures ($P < 0.001$, $r^2 = 0.23$). Additional temperature sums with thresholds ranging from 0 to 10 °C showed weaker or no correlation with the temperature indicator values.

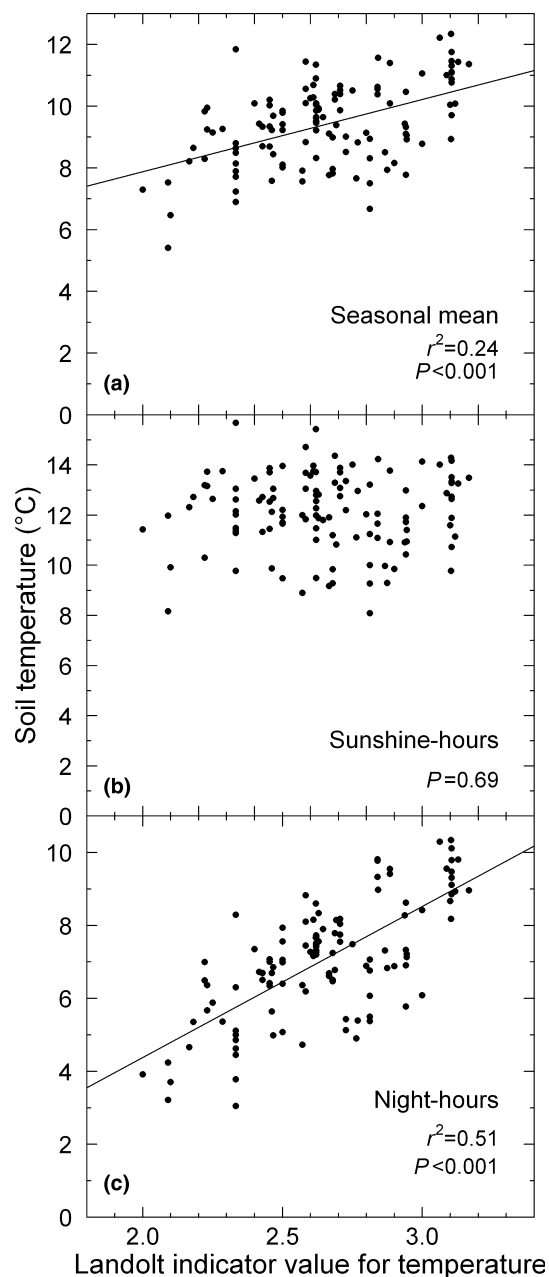


Figure 1 (a) Mean temperature indicator values per sampling plot (mean for all plant species present) and the seasonal mean soil temperature of the corresponding plot. (b) Mean temperature indicator values as in (a), plotted against the 'sunshine-hours' (radiation $>800 \text{ W m}^{-2}$, 133 h). (c) As (b) but 'night-hours' (00:00–00:06 h). Each data point represents a 1 m^2 vegetation plot. The data were recorded from 22 June to 8 September 2008 at the Furka Pass in the Swiss Alps.

There was strong variation in the plant species-specific mean surface temperature during the 'daylight period' with a surface–air temperature difference of $-0.16 \pm 0.07 \text{ K}$ (mean \pm SD) ranging from -3.2 K in *Saxifraga androsacea* to 5.0 K in *Geranium sylvaticum*. Also the 'seasonal mean' soil temperature showed species-specific variation with an overall mean of

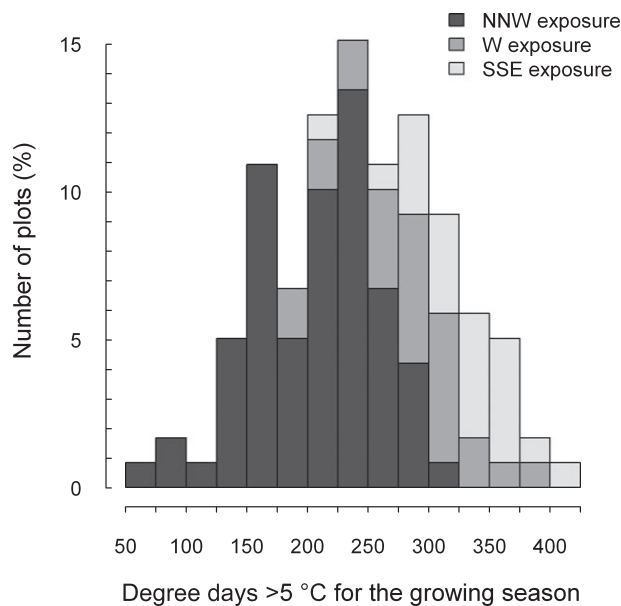


Figure 2 Degree days ($>5 \text{ °C}$) for the complete (75 days) growing season for each soil temperature logger position on the north-north-west, west and south-south-east exposed slopes. The data were recorded from 22 June to 8 September 2008 at the Furka Pass in the Swiss Alps.

$9.81 \pm 1.16 \text{ °C}$ (mean \pm SD) ranging from 6.9 °C for *Oxyria digyna*, a nival species, to up to 12.2 °C for *Lotus corniculatus*, which is not a typical alpine plant but rather a low-elevation species. This variation was not randomly distributed, but plant species with low temperature indicator values (1 or 2) grew in colder spots within a given mountain slope than plant species with higher temperature indicator values (3–5; Fig. 3).

The mean duration of snow cover after 1 June 2008 was 6.75 ± 7.33 days varying from 0 (south-south-east slope) to 32 days (north-north-west slope). Plant species with low temperature indicator values (1 or 2) had longer durations of snow cover than species with higher values (3–5; Fig. 4).

The hierarchical cluster analysis revealed 11 clear clusters with at least four plots per cluster. In total 82 plots (69%) were assigned to one of the 11 clusters. The remaining 37 plots formed clusters with fewer than three plots per cluster and were therefore excluded from further analysis. Even though the 11 vegetation units (clusters) were very distinct from each other they could not clearly be assigned to classical Braun-Blanquet vegetation types (Braun-Blanquet, 1964) (see Appendix S2). Not surprisingly, vegetation plots that are in close proximity to each other and on the same slope are more likely to have similar vegetation and therefore are in the same cluster, in part because of spatial autocorrelation. Nevertheless the clusters showed increasing soil temperature with increasing mean temperature indicator value ($P < 0.001$, adj. $r^2 = 0.51$, Fig. 5). The data show that there is a correlation of vegetation similarity and soil-temperature differences, with more differing clusters showing stronger soil-temperature differences than closely related vegetation units (linear regression, $P < 0.001$,

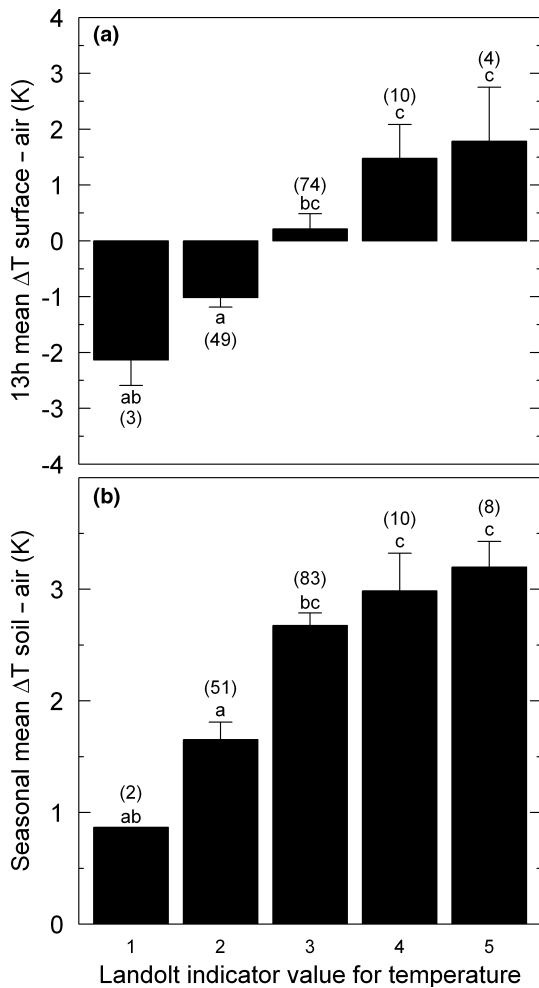


Figure 3 (a) Mean temperature difference ΔT (surface temperature minus air temperature; 07:00–20:00 h) per ‘Landolt-T-Group’ (all plant species assigned to the same indicator value for temperature according to Landolt, 1977). (b) Seasonal differences in mean soil temperature minus air temperature for the same ‘Landolt-T-Groups’. The numbers in brackets indicate the number of plant species within the different ‘Landolt-T-Groups’ (the letters above the bars indicate significant differences). The data were recorded in the year 2008 at the Furka Pass in the Swiss Alps.

adj. $r^2 = 0.35$). Therefore similar vegetation units occur at similar soil temperatures.

A rise in temperature of 2 K across all micro-habitats in alpine landscapes as surveyed here will cause the currently coldest micro-habitats to disappear. But the actual habitat area lost is small and represents 3% of the current land-area based on the soil-temperature data (seasonal mean, Fig. 6) and 9% based on surface-temperature data (daylight period data). The majority of the currently rather cool micro-habitats (75–80% of the alpine terrain) will decrease in their abundance under a 2 K warming scenario (Table 1). On the other hand, the currently warmest micro-habitats (10–22%) will increase in their abundance, and in a 2 K warmer climate 22% of the landscape will offer habitats even warmer than the currently warmest places within the study area (Table 1).

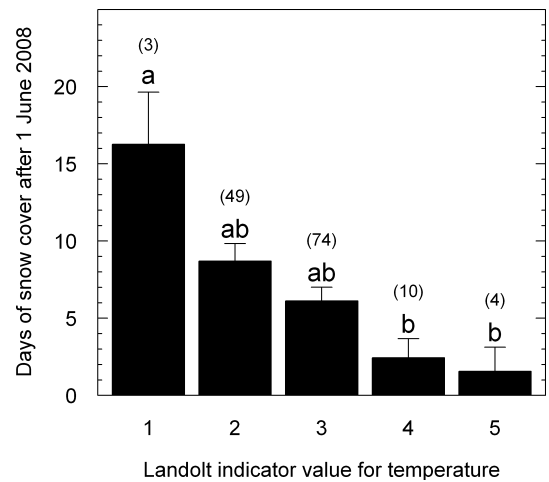


Figure 4 Mean number of days of snow-cover after 1 June 2008 for the five ‘Landolt-T-Groups’. The numbers in brackets indicate the number of plant species within the different ‘Landolt-T-Groups’ (the letters above the bars indicate significant differences). The data were recorded in the year 2008 at the Furka Pass in the Swiss Alps.

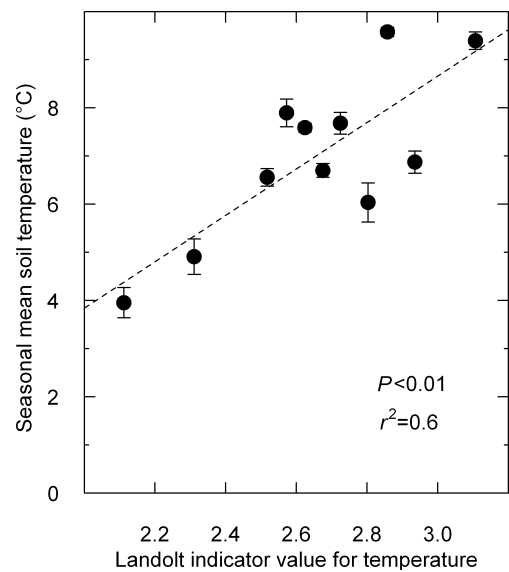


Figure 5 Correlation of the mean temperature indicator values of different vegetation units (cluster) and the corresponding soil temperature (‘seasonal mean’, 22 June to 8 September 2008). Each data point represents a vegetation unit and the error bars indicate the standard error.

DISCUSSION

The results of this analysis show that the substantial micro-habitat variation in surface and soil temperature within our 2 km² study area has a strong influence on local vegetation composition. As shown by Scherrer & Körner (2010), this micro-habitat variation of surface and soil temperature is mostly driven by micro-topography and slope orientation and

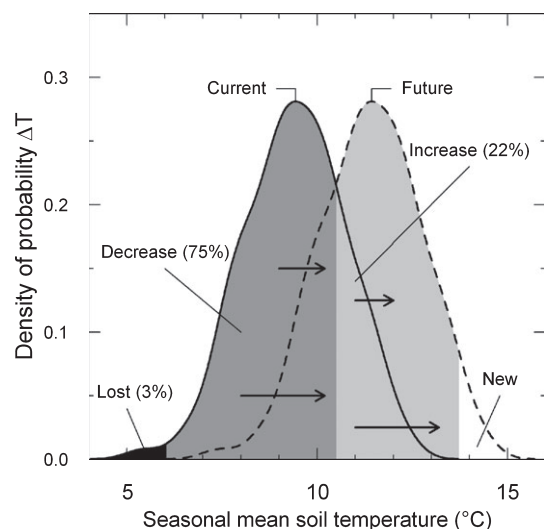


Figure 6 The density distribution of current 'seasonal mean' soil temperatures ('current') and in a 2 K warmer scenario ('future'). 'Lost' indicates the micro-habitat temperatures which disappear in a 2 K warmer scenario within our study area, 'decrease' indicates the micro-habitat temperatures that decrease in their abundance, 'increase' the ones that increase in abundance and 'new' the micro-habitat conditions that are warmer than the current warmest temperatures. The arrows indicate the direction of decreasing and increasing micro-habitat temperatures.

Table 1 The percentage of study plots falling into the categories 'lost' (micro-habitat temperatures that exist under current conditions but disappear with a 2 K warming), 'decrease' (micro-habitat temperatures that exist under current conditions and in the future but decrease in abundance), 'increase' (micro-habitat temperatures that increase in their abundance) and 'new' (micro-habitat temperatures that are warmer than the current warmest temperatures). The first number is based on surface temperature and the second on soil temperature measurements. 'Current' represents the current distribution and 'future' the distribution in a 2 K warmer scenario.

	Lost (%)	Decrease (%)	Increase (%)	New (%)
Current	9/3	80/75	10/22	0/0
Future	0/0	23/24	74/54	3/22

only marginally influenced by plant structure at the scale used in this study (low-stature alpine vegetation only). This indicates that the observed differences in surface and soil temperature between the vegetation types (and plant species) are not the effect of a plant-modulated environment but reflect different 'abiotic' thermal conditions. The correlation between the mean temperature indicator value and the mean soil temperature of the plots supports this habitat differentiation and demonstrates the power of indicator values. Even within a very small spatial area and a narrow range of indicator values (mean values between 2 and 3) the temperature indicator

values predicted the 'warm' and 'cold' spots remarkably well, bearing in mind that the realized niche is constrained by many more abiotic (e.g. soil moisture, nutrients) and biotic factors (e.g. competition) than just temperature (Hutchinson, 1957).

The fact that night-time soil temperatures correlated strongly with the mean temperature indicator values, while values for periods with high insolation did not, indicates that night-time temperatures are more important in determining plant species distribution than day-time or seasonal mean temperatures. In cold environments, freezing resistance and the risk of freezing during the growing period strongly influence the spatial pattern of plant distribution (Körner, 2003). We did not cover such extreme events of freezing during our survey, but we speculate that the mosaic of night-time soil temperatures correlates with the likelihood of exposure to such extreme events and therefore is a better proxy than day-time temperatures. A second possible explanation for the better match of temperature indicator values with night-time soil temperature is that growth (tissue formation) and development are more constrained during cold periods than is photosynthetic activity (Körner, 2003), and thus they exert an overriding influence on the spatial aggregation of plant species. A limitation of growth by photosynthetic products (sugar) in high-elevation plants is unlikely because, during daylight, air temperature is mostly $>7^{\circ}\text{C}$ and temperature within plant canopies is even higher (up to 30°C ; Takasu, 1953; Salisbury & Spomer, 1964; Cernusca, 1976; Larcher & Wagner, 1976; Körner & Cochrane, 1983; Scherrer & Körner, 2010). Körner & Diemer (1987) showed that high-elevation plants reach 50% of their photosynthetic capacity at 4°C and even night-time temperatures below freezing point hardly affect photosynthetic activity in the following day (Henrici, 1921; Blagowestschenski, 1935; Mark, 1975; Körner, 2003). While photosynthetic activity is only possible during periods with daylight and is probably not limited by temperature, growth and development involve 24-h processes, known to be very sensitive to temperature (Körner & Woodward, 1987; Woodward & Friend, 1988). Körner & Woodward (1987) showed that leaf extension in alpine plants approaches zero at close to 0°C (and in lowland plants at $5\text{--}7^{\circ}\text{C}$) and such low temperatures were regularly experienced in the field during this study. The spatial variation in 'night-hours' mean soil temperatures (up to 7 K within our study area) might therefore result in large differences in periods suitable for leaf/shoot extension. GDD values illustrate that specific threshold temperatures for certain biological processes can significantly enhance effective thermal contrasts among micro-habitats. In this study the GDD values added up to large differences (50 to 400) but the correlation with the temperature indicator value was almost the same as for 'seasonal mean' soil temperatures. Körner & Paulsen (2004) showed that mean growing season temperature gives better results than sum measurements such as degree-hours in determining the position of the tree line.

Our results show that the ranking of plant species according to their presumed temperature demands made by Landolt

(indicator values from 1 to 5) corresponds to the observed mean soil and surface temperature differences between the 'Landolt-T-Groups'. In particular, the two typical alpine groups (indicator values 2 and 3) occur at significantly different micro-climate temperatures (both surface and soil) even within a single mountain slope. The group of mostly nival species (indicator value 1) and the subalpine/lowland species (indicator values 4 and 5) were present very rarely within our alpine study site and were not significantly different (Fig. 3). But they show a clear trend of increasing site temperature with increasing temperature indicator values. This demonstrates the usefulness of ecological indicator values even on a single mountain slope in the topographically diverse alpine landscape, dominated by a mosaic of micro-climatic habitats.

A similar pattern was observed for the duration of snow cover, which is correlated with the 'Landolt-T-Groups', with a declining season length from lowland/subalpine species (temperature indicator values 4 and 5) to nival species (temperature indicator value 1). This indicates that the temperature indicator values not only represent the seasonal mean soil and surface temperatures of a habitat but also the length of the growing season, which is known to influence strongly the species composition (Gjærevoll, 1956; Friedel, 1961). Even within single snow-beds, the time course of snow disappearance dominates the vegetation (Galen & Stanton, 1995; Schöb *et al.*, 2009). The combination of these two environmental parameters (growing season length and temperature) within one indicator value is not surprising, because first these indicator values are based on field experience and not on precise measurements and second, at broader scales, season length and mean temperature are likely to be correlated in the temperate zone. However, the nature of conditions for life in the snow-bed might not be as well described by temperature indicator values as by growing season temperatures, because late disappearance of snow is often associated with rather warm conditions during the remaining, short summer, given the often sheltered habitat conditions, low vegetation cover and dark soil surfaces (Körner, 2003). Many studies show that snow-bed communities are also poorly represented by other indicator values, such as the nitrogen indicator value of Ellenberg (1974) which is normally a reliable indicator of nutrient availability and productivity (Ellenberg, 1992; Hill & Carey, 1997; Schaffers & Sykora, 2000).

The results for vegetation units (clusters) showed that there is a positive correlation of mean temperature indicator values and the mean soil temperature of the vegetation units. It is important to note that we derived the vegetation units (clusters) by clustering species without any plant sociological filtering. Therefore the distance between vegetation units in the cluster dendrogram simply reflects their similarity in species composition and therefore the number of species they have in common. Our data show a strong negative correlation of 'number of plant species in common' and soil temperature difference between vegetation units. Therefore we conclude that the more similar two vegetation units are, the more similar are the soil temperatures. This might sound trivial, but

it demonstrates that temperature directly influences the species assemblages in alpine landscapes at the metre scale, and therefore explains part of the often patchy distribution of different vegetation types in such environments.

Altogether, our results show that the thermal mosaics of alpine landscapes create fine-scale habitats that are inhabited by species with different thermal preferences. Since micro-habitats differ not only in temperature but also in soil type and nutrient and water availability as well as wind exposure the variation in micro-environmental conditions becomes further enhanced. As stressed by Nogués-Bravo *et al.* (2007), most dynamic and lapse-rate based statistical climate models (global climate models/regional climate models) are not able to account for the complex, topography-driven patterns of temperature and other regional climate features. Randin *et al.* (2009) showed for the central Alps that species distribution models based on the commonly used climate data at $10' \times 10'$ (16×16 km in the central Alps) resolution (New *et al.*, 2002) predict higher rates of habitat loss than models based on 25×25 m cells, and therefore might largely underestimate the persistence of plant species in alpine landscapes with a high topographic variability. In contrast to these results for the central Alps, Trivedi *et al.* (2008) found higher projected extinction rates with fine-resolution models (50×50 m) for mountains in central Scotland than on a European macroscale (50 km resolution). Presumably, this is due to the fact that the alpine life-zone is confined to plateau-shaped summits in central Scotland, whereas in the central Alps the alpine belt is enclosed by the subalpine and nival belt. Hence, the area of alpine terrain is relatively small in the central Scottish mountains and is poorly represented at a European scale, and summit vegetation cannot escape to higher elevations. The data shown here are for metre-scale variation, and much of this differentiation is smoothed out at a 50 m scale. Altogether, our major concern with all models (independent of the scale they are using) is that their predictions are based on weather station data, often downscaled to the desired grid size. Although the algorithms employed might be very sophisticated and high-resolution digital elevation models are used to incorporate adiabatic lapse rates and regional climate (e.g., Zimmermann & Kienast, 1999; Randin *et al.*, 2006, 2009; Trivedi *et al.*, 2007) they still predict meteorological (2 m air) rather than actual life conditions. It is therefore questionable whether such data reflect the actual alpine environment, with the majority of organisms living in micro-habitats strongly decoupled from atmospheric conditions and interacting with micro-topography at the centimetre to metre scale. Our simple 2 K warming scenario demonstrates this. Within our study area, we observe a substantial variation of surface and soil temperature around a given mean air temperature. Our results show that by shifting this distribution into a world that is 2 K warmer, the resulting habitat loss will affect less than 10% of the micro-habitats within our kilometre-scale test areas. Only the species confined to the coldest micro-habitats will have to move to higher elevations (or adapt), but the majority of the species will find suitable thermal habitats (as rated by their current

habitat preferences) in a distance of just a few metres. Therefore the extinction of species will be overestimated by broad-scale, isotherm-based models. However, the abundance of thermally suitable micro-habitats will be reduced for most species within the study area, and therefore competition for the remaining cooler places will increase. The large variation of micro-climatic conditions in alpine landscapes will still buffer the impacts on biodiversity by offering stepping stones and refugia, rather than forcing all species upslope in order to track climatic warming.

CONCLUSIONS

This study quantified the mosaic nature of thermal conditions for life in an alpine environment. We demonstrated the power of semi-quantitative ecological plant indicator values as derived from expert knowledge in detecting different abiotic habitat conditions in alpine terrain. Indicator values offer a 'low tech' method to account for the variety of micro-environments that support the high biodiversity of alpine landscapes.

Topographic variability of steep alpine terrain creates a multitude of fine-scale thermal habitats that is mirrored in plant species distribution. Across distances of a few metres we observed seasonally stable soil and plant surface temperature differences that exceed the range of warming in IPCC projections for the next 100 years. These local thermal contrasts lead to the lack of clear species or life-form limits (isolines) such as the tree line. Within a short distance, on the same elevation, we find 'subalpine', 'alpine' and 'nival' species depending on the micro-environmental conditions of their habitats.

The results of this study warn against projections of the responses of alpine plant species to climatic warming that adopt a broad-scale isotherm approach. We suggest that alpine terrain is, in fact, for the majority of species, a much 'safer' place to live under conditions of climate change than is flat terrain which offers no short-distance escapes from the novel thermal regime.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of the 174 vascular plant species recorded in the study.

Appendix S2 List of the 11 vegetation units (clusters).

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BIOSKETCHES

Daniel Scherrer is a PhD candidate at the University of Basel, where his research focuses on alpine plant ecology, micro-climatology and plant–water relationships.

Christian Körner (PhD thesis on the ecology of alpine plant–water relations, 1977, Innsbruck, Austria) was appointed full chair for botany at the University of Basel in 1989. His main research interests are the functional ecology of alpine plants, the tree line phenomenon and the influence of elevated CO₂ on a broad suite of biota, forests in particular (the Swiss canopy crane project). Ch. Körner is editor in chief of *Oecologia* (Springer) and chairs the Global Mountain Biodiversity Assessment, GMBA, of DIVERSITAS. <http://pages.unibas.ch/botschoen/koerner/index.shtml>.

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Chapter 4

Elevational species shifts in a warmer climate are overestimated when based on weather station data

Elevational species shifts in a warmer climate are overestimated when based on weather station data

Daniel Scherrer · Samuel Schmid · Christian Körner

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Abstract Strong topographic variation interacting with low stature alpine vegetation creates a multitude of micro-habitats poorly represented by common 2 m above the ground meteorological measurements (weather station data). However, the extent to which the actual habitat temperatures in alpine landscapes deviate from meteorological data at different spatial scales has rarely been quantified. In this study, we assessed thermal surface and soil conditions across topographically rich alpine landscapes by thermal imagery and miniature data loggers from regional (2-km²) to plot (1-m²) scale. The data were used to quantify the effects of spatial sampling resolution on current micro-habitat distributions and habitat loss due to climate warming scenarios. Soil temperatures showed substantial variation among slopes (2–3 K) dependent on slope exposure, within slopes (3–4 K) due to micro-topography and within 1-m² plots (1 K) as a result of plant cover effects. A reduction of spatial sampling resolution from 1 × 1 m to 100 × 100 m leads to an underestimation of current habitat diversity by 25% and predicts a six-times higher habitat loss in a 2-K warming scenario. Our results demonstrate that weather station data are unable to reflect the complex thermal patterns of aerodynamically decoupled alpine vegetation at the investigated scales. Thus, the use of

interpolated weather station data to describe alpine life conditions without considering the micro-topographically induced thermal mosaic might lead to misinterpretation and inaccurate prediction.

Keywords Alpine · Soil temperature · Spatial scale · Suitable climate space · Surface temperature · Thermometry

Introduction

The alpine life zone is dominated by strong topographic variation and extreme climatic conditions forcing plants and animals to a high degree of specialisation and adaptation (Billings and Mooney 1968; Körner and Larcher 1988; Körner 2003). The steep environmental gradients and the reduction in land area with increasing elevation supposedly cause alpine environments to be particularly sensitive to global warming (Beniston et al. 1996; Diaz et al. 2003; Beniston 2006). In addition, most climate warming scenarios predict higher than average warming in most alpine areas (Meehl et al. 2007; Nogués-Bravo et al. 2007). The Alps warmed by +1.5 K compared with the global average of +0.7 K during the last century and therefore are often considered as particularly threatened (Beniston et al. 1997; Theurillat and Guisan 2001; Schröter et al. 2005; Nogués-Bravo et al. 2007). It is widely believed that the recent and future climate warming is driving species ranges polewards and towards higher elevations (Beniston et al. 1996; Theurillat and Guisan 2001; Walther 2004; Colwell et al. 2008) and may cause regional species extinctions. In fact, there is evidence of upslope migration of plant species in the Alps (Grabherr et al. 1994; Walther et al. 2002, 2005; Pauli et al. 2007; Lenoir et al. 2008) as well as evidence for substantial resistance to climatic forcing in plants inhabiting

D. Scherrer (✉) · C. Körner
Institute of Botany, University of Basel,
Schönbeinstrasse 6,
4056 Basel, Switzerland
e-mail: daniel.scherrer@unibas.ch

S. Schmid
Institute of Plant, Animal and Agroecosystem Sciences,
ETH Zurich,
Universitätsstrasse 2,
8092 Zurich, Switzerland

the same location over thousands of years (Steinger et al. 1996; Bahn and Körner 2003).

Species distribution models (SDMs; Guisan and Zimmermann 2000; Guisan and Thuiller 2005) have been employed to project the impact of future climate change on species distributions (Bakkenes et al. 2002; Thomas et al. 2004; Thuiller et al. 2005; Randin et al. 2009). SDMs statistically fit the environmental niche (Hutchinson 1957; Kearney and Porter 2004) by relating abiotic habitat conditions with occurrences of a species (Guisan and Thuiller 2005; Araújo and Guisan 2006). Strong impacts on biodiversity and species abundance have been predicted (Bakkenes et al. 2002; Thuiller et al. 2005), especially in mountain ranges.

Yet the predicted habitat loss in mountainous regions strongly depends on model selection (Araújo et al. 2005b; Algar et al. 2009) and the spatial resolution of the SDMs (Trivedi et al. 2008; Randin et al. 2009). Scherrer and Körner (2010a) showed that in alpine landscapes there is substantial variation in actual plant surface and soil temperature within 1-km² test areas, not reflected in the commonly referred to 2-m-aboveground air temperature. The thermal mosaic created by micro-topography, in fact, offers suitable habitats for many species with different thermal preferences requiring hardly any migration for a 2-K warming scenario (Scherrer and Körner 2010b). This results from both geo-diversity (topography) as well as aerodynamic decoupling of low stature alpine vegetation from atmospheric conditions at a centimetre scale (Körner 2003). Most models work on interpolated weather station data at much larger scales, with the noteworthy exception of an attempt for a small-scale resolution by Randin et al. (2009). Although not based on actual plant temperatures, this study revealed the significance of scale. Given the key role of spatial sampling resolution of climatic conditions to describe patterns of current micro-habitats, fact-based life conditions need to be assessed, the aim of the work presented here.

Modern thermal imagery techniques and miniature data loggers allow us to record surface and soil temperature data at high spatial resolution across rough alpine terrain. In this study we recorded surface (plant canopy) and soil temperature (root zone) data at different spatial resolutions ranging from centimetre to kilometre scale. This data were used (1) to partition the surface and soil temperature variation into among-slopes, within-slope and centimetre scale variation, (2) to identify the most influential factors for surface and soil temperature at different spatial scales, (3) to quantify the observed variation in surface temperature dependent on spatial sampling resolution, and (4) to estimate the projected habitat loss under climate warming scenarios and the dependence of predictions on spatial resolution. This information will improve predictions of future habitat

conditions and thus reduce uncertainties in projected habitat distribution.

Materials and methods

Study sites

The study area is situated in the temperate-alpine zone near the Furka Pass in the Swiss Central Alps (46°34'35"N, 08°25'17"E), well above the climatic tree line (which is at c. 2,150 m in this region). Within an area of about 2-km² (study area), we chose three steep mountain slopes with NNW (centre at 2,500 m), W (2,480 m) and SSE (2,430 m) exposure. All slopes showed strong variation in micro-topography but no change in macro-exposure and covered elevation ranges of 400–600 m on the NNW and W slope and 200 m on the SSE slope. Within each slope, we defined four 1-m² plots (near the centre) which were used for detailed small-scale measurements. For logistical reasons (power supply, road access) and a field station for night measurements, we designated the NNW slope as our core site.

Field data

The surface temperatures of the study slopes and plots were measured with a thermal camera (VarioCAM®; Infra Tec, Dresden, Germany) which records the long-wave infra-red at a resolution of 76,800 image points and transforms the radiation directly into temperature. The accuracy of the absolute temperature is ± 1 K and the relative differences between measurement fields (pixels) have a resolution of ± 0.1 K. To create mean thermal images (integrated over time) of whole slopes, the thermal camera was placed on the opposite slope (to have optimal angle of vision), and for each target slope, we recorded at least one (if possible more) diurnal series of thermal images under clear sky conditions. The series of images had a temporal resolution of 15 min (time between two images), started at midnight and ended 2 h after sunset. The detailed surface temperature of the twelve 1-m² plots (four per slope) was recorded three times during the growing season (16 July 2009, 18 August 2009 and 08 September 2009) by placing the camera directly over the centre of each plot (90° angle and fixed distance). The ground resolution for the slope measurements was about 0.75-m² per pixel and 0.2-cm² for the plot measurements.

Longer-term soil temperature within slopes and plots was recorded with 281 small waterproof temperature loggers (iButtons; Maxim Integrated Products, Sunnyvale, CA, USA) which have a resolution of 0.5 K and record for 80 days with one temperature reading per hour. To capture

the spatial and temporal variation of the soil temperature within each of the three mountain slopes, we defined at least one horizontal and one vertical transect (three horizontal and three vertical ones at our core site, the NNW exposed slope) of a minimum length of 150 m (varying from 150 to 350 m depending on topography). The loggers were buried in the top soil rooting zone at a depth of 3 cm along the horizontal (one logger every 10 m) and vertical transects (one logger every 15 m). In total, we placed 86 temperature loggers on the NNW, 33 on the SSE and 54 on the W exposed slope along transects which recorded the soil temperature for 75 days (22 June–8 September 2008). Additionally, to get an impression of the small-scale variation of top soil temperature, we placed 36 loggers within one 1-m² plot per slope (20×20 cm grid) which recorded the soil temperature for 75 days in 2009 (29 June–13 September 2009). These 75-day periods represented the main growing season at the Furka Pass in the study years 2008 and 2009. Standard meteorological data 2 m above the ground (air temperature, air humidity, solar radiation) were recorded with a 10-min temporal resolution by a weather station (Vantage Pro2 Plus™ with solar radiation sensor; Davis Instruments, Hayward, CA, USA) within the study area at 2,445 m.

To identify the most influential abiotic factors on soil temperature at the centimetre scale, we measured (at the position of each logger within the 1-m² plots) the inclination, exposure and surface structure (concave, convex or flat). By a grid-point intercept method applied to the 25-cm² above each logger (1×1 cm grid, 36 points; modified from Herrick and Range 2005), we measured the specific cover of each vascular plant species, mosses, lichens, litter and rocks, the percentages of bare ground and the mean and maximum vegetation height. Additionally, functional classifications of plant species (classifica-

tions for functional group, growth form, life form, stem growth type, leaf distribution) were performed following Cornelissen et al. (2003).

Data analysis

The many thermal images of one time series were aggregated to a mean image representing the 6 h with highest insolation and daytime warming ('day time', 1200–1800 hours). By aggregating over time, we averaged out short-term fluctuations and obtained more reliable information about the micro-climatic conditions within a given slope (Scherrer and Körner 2010a). Because the time series were not recorded on the same day, we standardised the surface temperature of a slope by subtracting the air temperature 2 m above the ground for the corresponding period. This makes the data of different days more easily comparable. From the detailed thermal images of the 1-m² plots, we extracted leaf temperature of eight individuals for 14 different plant species. All the species are common in the study area and prominent in at least one of the study slopes (the 14 species are listed in Table 1).

For each soil temperature logger, we calculated three different mean values: first, the mean temperature for the complete measuring period ('seasonal mean'), second, the mean for night hours (0000–0600 hours), and third, the mean for day hours (1200–1800 hours).

We analyzed the surface and soil temperature variation on three different scales: first, the regional variation (variation among whole slopes), second, the within-slope variation, and third, the within-plot variation. For each slope, we calculated a mean surface temperature during 'day time' and the mean soil temperatures for seasonal mean, night-hours and day-hours. These mean slope temperatures were then compared to obtain the among-slopes variation. The within-slope and within-plot

Table 1 Plant species-specific leaf temperatures of 14 selected plant species with different growth forms (mean ± sd)

Plant species	Growth form ^a	Life form ^b	Leaf temperature (°C)
<i>Sesleria caerulea</i>	Tus	Hem	21.4±1.7
<i>Elyna myosuroides</i>	Tus	Hem	21.9±1.5
<i>Carex curvula</i>	Tus	Hem	22.5±1.4
<i>Helictotrichon versicolor</i>	Mid	Hem	22.5±1.1
<i>Gentiana punctata</i>	Mid	Hem	23.3±4.1
<i>Trifolium alpinum</i>	Bas	Hem	23.3±1.9
<i>Leontodon helveticus</i>	Bas	Hem	23.9±2.7
<i>Anthyllis vulneraria</i>	Mid	Hem	24.0±2.2
<i>Polygonum viviparum</i>	Mid	Geo	25.4±3.5
<i>Aster alpinus</i>	Mid	Hem	26.8±3.4
<i>Geum montanum</i>	Mid	Hem	26.9±2.5
<i>Homogyne alpina</i>	Bas	Hem	27.3±2.0
<i>Dryas octopetala</i>	Bas	Cha	32.3±3.6
<i>Saxifraga paniculata</i>	Bas	Cha	34.0±4.7

^a Bas leaves concentrated in basal parts of plant, Mid leaves concentrated in middle parts of plant, Tus leaves concentrated in tussocks

^b Geo geophyte, Hem hemicryptophyte, Cha chamaephyte

variation was calculated by taking 90% of the data points (loggers, IR-pixels) within one slope and plot, respectively. We excluded the 5% of the lowest and highest values to exclude bias due to extreme values of single data points such as, for example, stones heating up to 80°C under strong insolation. This was done separately for surface temperature during ‘day time’ and soil temperature during seasonal mean, night-hours and day-hours. To identify the most important physical and biological factors influencing the small-scale pattern of soil temperature within our 1-m² plot we conducted a correlation analysis of the recorded parameters (see above) and the seasonal mean, night-time and day-time soil temperatures.

While the soil temperature data (loggers) represent point measurements, the IR images deliver integrated data over an area (slope, plot). This allowed us to artificially manipulate (decrease) the spatial resolution of our IR images. For example, we can observe the same slope with a 1-m², 10-m² or 100-m² resolution just by aggregating pixel information. By doing this, we not only lose information but also decrease the surface temperature variation observed within a slope and thus underestimate the real micro-climatic variation. We therefore analyzed the variation within each slope and plot at different spatial resolutions by randomly sampling 10,000 points per resolution, slope and plot respectively. This results in a correlation of the spatial resolution of sampling and the observed variation in surface temperature.

To quantify the losses of micro-habitats within a single mountain slope dependent on the sampling resolution, we simulated mean temperature increases of 2, 3 and 4 K. This was done by taking the current distribution of surface temperature at 1×1, 5×5, 10×10, 25×25 and 100×100 m resolution and shifting the temperatures by the desired temperature increase. This way, only the mean temperature was increased, while the spatial variation of temperatures stayed the same. By comparing (overlapping) the two temperature distributions (current and future), we can estimate the micro-habitat temperatures of the current distribution that are lost in a warmer climate assuming a similar air-surface temperature correlation and similar solar forcing. We excluded the coldest and warmest 5% of the recorded micro-habitats to avoid conditions that are extremely rare and therefore biologically not significant on the applied scale of this study. This was done for the different spatial resolutions (1×1, 5×5, 10×10, 25×25 and 100×100 m) and the three warming scenarios (2, 3 and 4 K).

Results

On clear sky days during day time, we observed increasing variation in surface temperature with increasing resolution.

The difference in surface temperature among slopes was only 2.4 K while the range containing 90% of the data points within a given slope (c. 0.5-km²) was 4.8 ± 1.06 K (mean \pm SE) and 14.1 ± 1.13 K within a 1-m² plot (Fig. 1). The range containing 90% of the data points was similar for all 1-m² plots, irrespective of their macro-exposure (NNW, W, SSE).

The soil temperature data showed a different pattern. The largest variation in soil temperature was always found within a slope, with a range containing 90% of the data points of 3.2 ± 0.14 K (mean \pm SE) for seasonal mean, 3.2 ± 0.58 K during night-hours and 4.1 ± 0.20 K during day-hours (Fig. 2). The within-plot soil temperature range containing 90% of the data points was larger during day-hours with 3.2 ± 0.77 K than for the seasonal mean, with 1.4 ± 0.05 K, and night-hours with 1.65 ± 0.29 K (Fig. 2). The differences among slopes were 2.3 K for seasonal mean, 3.1 K during night-hours and 1.9 K during day-hours (Fig. 2). The macro-exposure had no significant influence on the within-slope or within-plot variation of soil temperature, but significantly influenced the mean soil temperatures of slopes with a seasonal mean of $8.7 \pm 0.13^\circ\text{C}$ (mean \pm SE) on the NNW, $10.1 \pm 0.12^\circ\text{C}$ on the W and $11.0 \pm 0.11^\circ\text{C}$ on the SSE exposed slope.

The 1-m² plots showed large differences in their seasonal mean soil temperature with $8.0 \pm 0.28^\circ\text{C}$ (mean \pm SE) on the NNW, $10.4 \pm 0.34^\circ\text{C}$ on the W and $11.7 \pm 0.30^\circ\text{C}$ on the SSE slope. Therefore, we used macro-exposure as a random factor for the analysis of the influence of surface and vegetation structure on the within-plot soil temperature variation. Otherwise, the strong signal of macro-exposure would have covered all effects of small-scale temperature variation. The most influential factors for within-plot seasonal mean soil temperature were inclination (ANOVA,

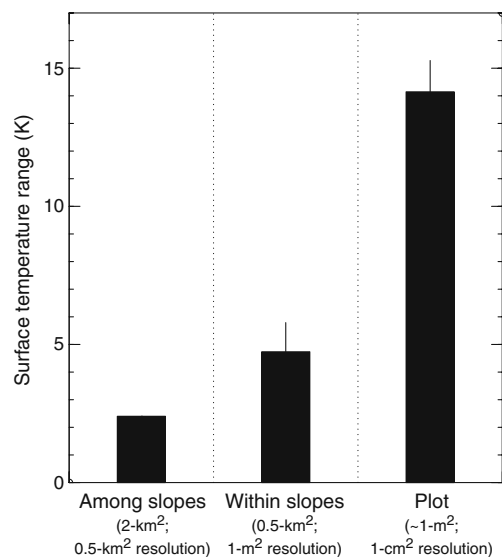


Fig. 1 Surface temperature range at three different scales and sampling resolutions (mean, SE). The data were collected on clear sky days during June 2008 and June 2009 from 1200 to 1800 hours

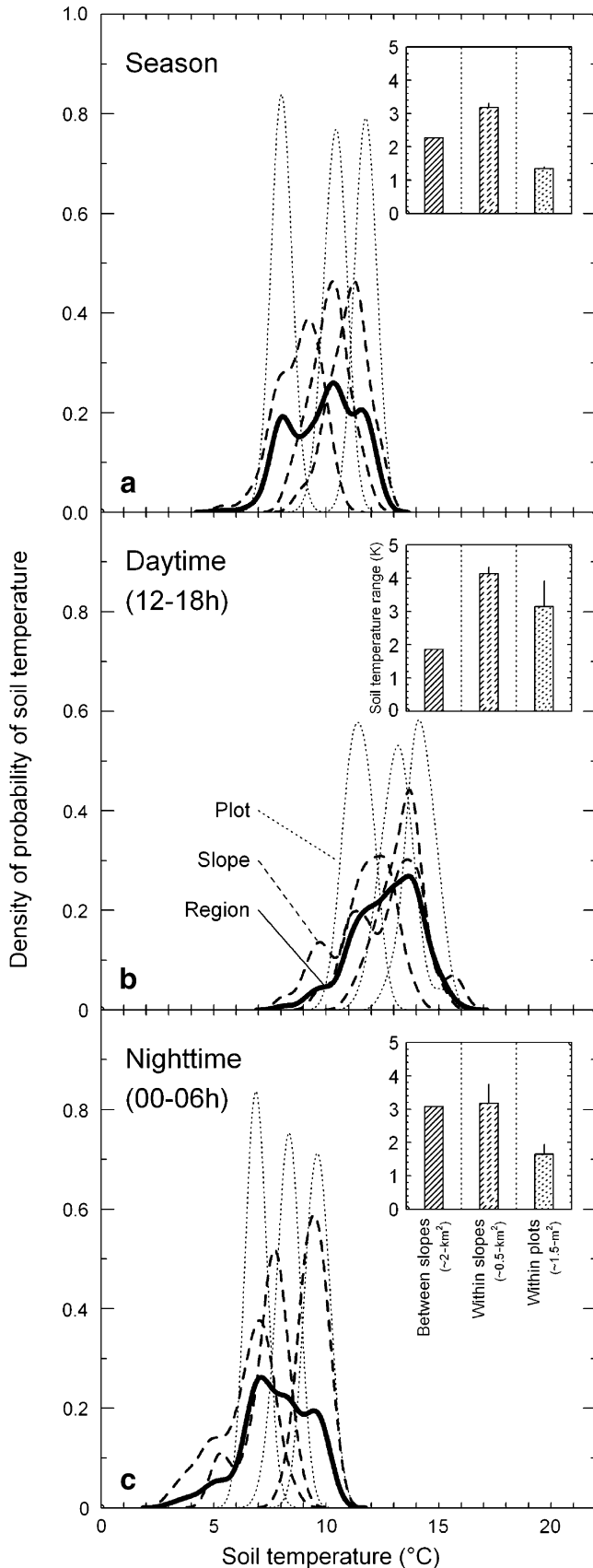
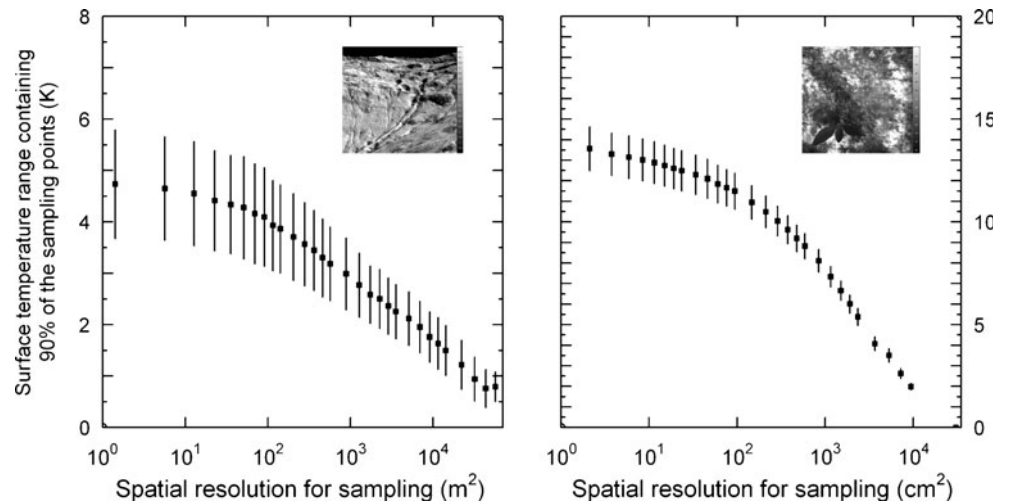


Fig. 2 a Density distribution of seasonal mean soil temperatures for individual plots (1-m²; dotted lines), whole slopes (0.5-km²; dashed lines) and total region (2-km²; solid line). The inset shows the soil temperature range for three spatial scales (among slopes, within slopes, within plots). b The same information, but for daytime mean temperatures, and c for night-time mean temperatures. The data for the 1-m² plot level were collected from 29 June to 13 September 2009 and for the slope level from 22 June to 8 September 2008

$p < 0.001$), followed by plant canopy cover, and mean vegetation height ($p < 0.05$). During day-hours with bright sky insolation the influence of inclination, canopy cover and mean vegetation height was strongest while there was no effect on night-time soil temperature. Plant species identity as well as the functional group, life form, stem growth type and leaf distribution of the plants had no consistent influence on small-scale soil temperature. Only the growth form (namely cushion versus tussock) had a tendency to influence day-hours soil temperature but this was likely the result of a strong correlation of percent cushion and tussock plants respectively and mean vegetation height. The leaf temperatures of all 14 plant species were higher than concurrent air temperature 2 m above the ground (c. 16°C) and showed significant differences among species (Table 1). These differences basically could be explained by the different plant architecture: plants with leaves concentrated close to the soil surface (mainly rosette plants) had the highest leaf temperature ($28.2 \pm 5.3^\circ\text{C}$; mean \pm SD), plants with leaves concentrated in middle parts of the stem had a medium leaf temperature ($24.8 \pm 3.3^\circ\text{C}$), and tussocks (graminoids), exposing their long erect leaves to the wind, had the lowest leaf temperature ($21.9 \pm 1.6^\circ\text{C}$; Table 1).

The artificial manipulation of spatial resolution on both slope and plot level led to an exponential decrease of surface temperature variation with decreasing resolution (Fig. 3). As expected, the spatial sampling resolution had absolutely no influence on the estimated mean surface temperature of both the plot and slope. The reduction of the spatial resolution from 1×1 m to 100×100 m strongly narrowed the distribution of the observed surface temperatures (Fig. 4). This led to an underestimation of the true habitat variability within the study area. With decreasing spatial resolution, a substantial part of currently existing micro-habitat conditions were cooler or warmer than the detected range of temperatures (Table 2). A decreasing sampling resolution led to an increase in the proportion of current micro-habitats (suitable climate space) that would disappear in the event of a warmer climate (Table 3), especially if the spatial resolution was lower than 10×10 m. As expected, the fraction of current micro-habitats that disappeared within a given slope under climate warming scenarios increased with increasing temperature difference (Table 3).

Fig. 3 Observed surface temperature range as a function of spatial resolution of sampling (means, SD). The *left panel* shows data at slope scale (0.5-km²) and the *right panel* at plot scale (1-m²). The *insets* represent sample thermal images of a slope and a plot



Discussion

Within-plot variation

Our results show substantial variation in both surface and soil temperature on all three scales (among slopes, within slopes and within plots). The variation in surface temperature was highest on the finest scale (within plots) and independent of macro-exposure. This can partly be explained by a technical issue. For logistical reasons (only one thermal camera), it was impossible to monitor the 1-m² plots for longer time intervals (6 h) and we only have repeated snapshots. Therefore, some of the observed variation in surface temperature would likely average out in longer term means. But the strong variation in surface temperature at the centimetre scale illustrates the important effect of radiative heating in aerodynamically decoupled systems such as alpine vegetation (Körner 2003). Many studies have shown that leaf temperatures in alpine landscapes largely deviate from 2 m above the ground air temperature (e.g., Takasu 1953; Salisbury and Spomer 1964; Cernusca 1976; Larcher and Wagner 1976; Körner and Cochrane 1983; Larcher et al. 2010; Scherrer and Körner 2010a). Our results show that plant species were warmer than the air temperature (Table 1), and that growth form directly influences the leaf temperature as had been shown in the studies cited above. Upright plant structures such as tussock leaves are far better coupled to the atmosphere and therefore are closer to 2 m above the ground air temperature than rosette leaves attached to the ground (e.g. Körner and Demoraes 1979; Körner et al. 1983; Körner and Cochrane 1983). With thermal imagery, these differences are directly accessible within one image. Leaf temperature provides information about physiological processes such as rate of photosynthesis, respiration or tissue formation. Additionally, leaf temperature can be used as an indicator for evaporative forcing (Smith and Geller 1979). By comparing species-specific leaf temperatures under dry and moist conditions,

one can identify the species most affected by water shortage (Schmid, unpublished data).

Within single plots, we observed consistent seasonal (75-day) mean soil temperature differences of several K depending on topography and plant structure. The variation in soil temperature within a 1-m² plot was three times higher during day-time than night-time. Night-time soil heat flux averages out most of the variation within a 1-m² area, while under strong insolation, there are up to 4 K soil temperature differences at the centimetre scale. The dominant factor on the smallest scale was slope inclination, defining the solar incidence angle and therefore the energy balance of the inclined surface. Also, the vegetation height and vegetation cover had a significant influence on soil temperature at the centimetre scale. Both factors increase the shading of the soil and therefore reduce the amount of direct radiation reaching the ground. These shading effects on soil temperature are well documented in forests and are one of the factors which explain sharp tree lines (Körner 1998; Körner and Paulsen 2004). Root zone temperatures are known to be important for root growth, root development and nutrient uptake (Kaspar and Bland 1992; Körner 2003).

Within-slope variation

Within slopes, we observed substantial soil and surface temperature variation independent of macro-exposure. As was shown by Scherrer and Körner (2010a), these micro-climates are mainly the effect of micro-topography and only marginally influenced by plant structure (within the small stature alpine vegetation). Even though the soil and surface temperatures show the same micro-climatic patterns, the quality of their signals differs. The within-slope surface temperatures represent larger scale integrated measurements. All the leaf surface temperatures within one pixel (around 1-m²) are averaged on this scale. Therefore, the thermal image of a slope directly delivers micro-climate

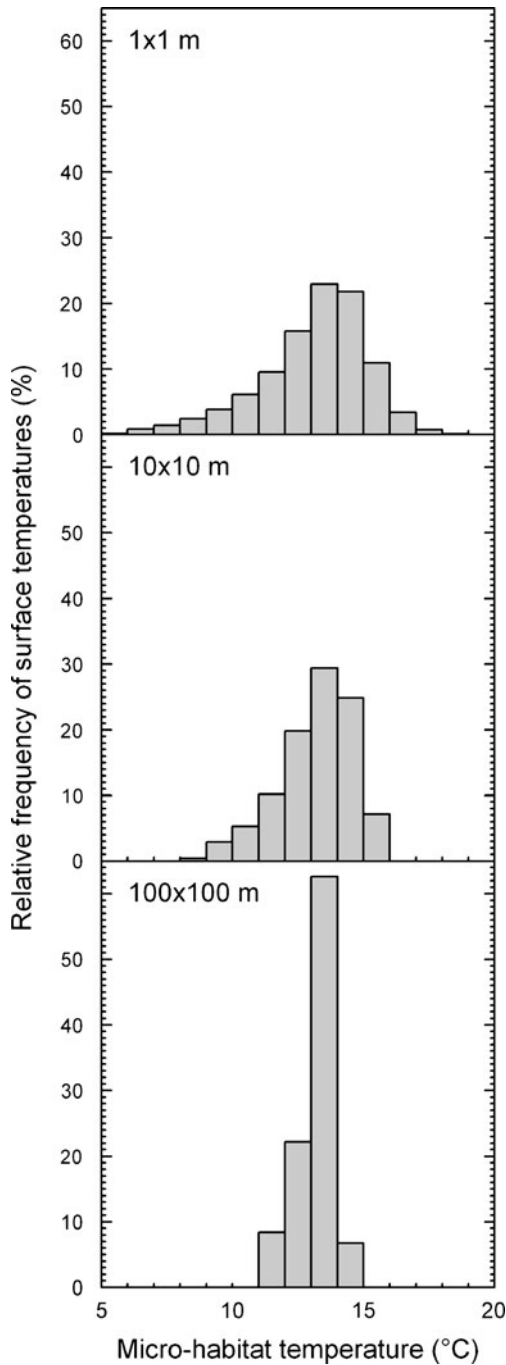


Fig. 4 The observed micro-habitat temperatures based on surface temperature measurements at different spatial scales (1×1 m, 10×10 m, 100×100 m)

temperatures at metre scale, only marginally influenced by the dominating life form (Scherrer and Körner 2010a). For technical and logistical reasons, the thermal imaging data were only available for selected days and not continuously, but we assume the quality of the observed micro-climatic pattern within slopes is retained and only the absolute range varies with irradiance.

Table 2 Fraction of undetected thermal micro-habitat conditions dependent on spatial sampling resolution based on IR surface temperatures of three alpine slopes (mean ± SD)

Spatial resolution (m)	Undetected conditions (%)
1×1	-
5×5	0
10×10	1.8±0.4
25×25	9±2.8
100×100	22.5±6.3

Soil temperature measurements in the upper rooting zone, on the other hand, were continuously measured over a 75-day period and therefore show consistent seasonal differences of micro-habitats. But the loggers only integrate over an area of c. 100-cm² and therefore represent point measurements not necessarily representative of the surroundings at metre scale (distance between loggers >10 m). About 30–50% of the soil temperature variation observed within a slope, achieved by spreading the loggers all over the slope, would also be recorded within a single plot (1-m²; Fig. 2). The within-slope variation of soil temperature therefore reflects a combined signal of centimetre scale influences (inclination, vegetation cover, vegetation height) and metre-scale factors such as topography.

Among-slope variation

The among-slope variation was quite similar for surface and soil temperature with south-exposed slopes about 2–3 K warmer than north-exposed slopes. These differences reflect the effects of macro-exposure on the incoming radiation dose due to incidence angle, the duration of direct insolation, and self-shading, respectively. Here, the information from the surface and soil temperature measurements are similar, both delivering mean slope temperatures by aggregating information (pixel, logger) within a slope.

Table 3 Fraction of the coldest thermal micro-habitat conditions that are assumed to disappear under different climate warming scenarios depending on spatial sampling resolution based on IR surface temperature data of three alpine slopes (mean ± SD)

Spatial resolution (m)	2 K scenario habitat loss (%)	3 K scenario habitat loss (%)	4 K scenario habitat loss (%)
1×1	7.5±0.9	20.3±8.0	40.4±19.0
5×5	16.8±9.9	40.0±22.2	57.5±30.0
10×10	17.4±7.6	42.8±20.1	67.1±24.3
25×25	44.1±24.3	68.1±25.6	86.2±11.3
100×100	64.7±28.9	95.5±3.7	100±0.0

All three spatial scales influence both mean surface and soil temperatures, as well as their variation. As shown by Scherrer and Körner (2010b), the distribution of micro-habitat temperatures correlate with the assemblages of plant species to vegetation units. Sampling or describing alpine landscapes, dominated by the high variation in micro-topography, with a crude spatial resolution might therefore be dangerous as highlighted by our climate warming modelling experiment.

Manipulation of spatial sampling resolution

In this study, we re-sampled the mountain slopes at different spatial resolutions and made simple predictions for warmer climates. The results show that the spatial resolution of sampling strongly biases the outcome of any prediction of climate warming. This bias is mostly the result of a narrowing of the range of micro-habitats, leading to an underestimation of the range of current habitat conditions and an overestimation of the percentage of micro-habitats lost in the event of climate warming. By decreasing the spatial resolution from 1×1 m to 100×100 m, we lose almost 25% of the current thermal micro-habitats found within a single slope at highest resolution (Table 2). A 2-K climate warming scenario revealed that, based on the high resolution data (1×1 m), less than 10% of the current micro-habitat conditions (climate space) disappear from a slope, while, at a lower resolution (100×100 m), more than 60% would be predicted to disappear (Table 3). In fact, the 10% of current micro-habitat conditions that might disappear under moderate climate warming (2 K) at the 1×1 m resolution were not detected with a 100×100 m resolution under current conditions. Therefore, we conclude that none of the micro-habitats identified with a 100×100 m sampling grid will disappear under a moderate 2-K climate warming within a single slope. The climate warming scenarios of 3 and 4 K yielded similar results with up to 100% predicted micro-habitat loss within our study slopes at low resolutions but only c. 40% at high 1×1 m resolution. Apart from habitats disappearing within an area due to climate warming, there will also be a large proportion of habitats decreasing and increasing in their abundance (Scherrer and Körner 2010b). The proportion of these habitats is also strongly dependent on the sampling resolution. Changes in micro-habitat abundance will change the competitive situation for many species and may exert biodiversity effects different in nature from those implied by large-scale shifts of isotherms and associated large-scale migration needs. While, due to climate warming, the coldest habitats within a given area will disappear, new warmer habitats will emerge as the area stays constant and new species might replace those which are lost, resulting in no changes in species richness at all.

In this study, we artificially manipulated the spatial resolution of our data (plant canopy and soil temperature) by aggregating information, in contrast to most models which base their predictions on interpolated and down-scaled meteorological data. Although the modern algorithms employed might be very sophisticated and high resolution digital elevation models are used to incorporate local and regional climate (Zimmermann and Kienast 1999; Guisan and Thuiller 2005; Randin et al. 2006, 2009), we have two major concerns: first, most of the climate models used predict meteorological conditions 2 m above the ground and it is therefore questionable whether such data reflect the actual alpine life conditions, with the majority of organisms living in micro-habitats strongly decoupled from atmospheric conditions and strongly interacting with micro-topography at the centimetre to metre scale. Second, the field data used for interpolation might not be representative for a wider region. As shown, there is strong variation in surface and soil temperature but also soil moisture (Hills and Reynolds 1969; Reynolds 1974; Charpentier and Groffman 1992), nutrient availability (Jackson and Caldwell 1993; Reynolds et al. 1997) and precipitation (Cosma et al. 2002) are known to vary at small spatial scales. The environmental envelope achieved by interpolation might therefore strongly differ from real environmental conditions.

The popularity of species distribution models to predict climate warming impacts on biodiversity and species distribution have led to an ongoing debate about model selection (Elith et al. 2006; Pearson et al. 2006; Araújo and New 2007), validation (Araújo et al. 2005a; Araújo and Guisan 2006; Pearson et al. 2007), uncertainty (Thuiller et al. 2004; Araújo et al. 2005b; Pearson et al. 2006), transferability (Randin et al. 2006) and spatial scale (Trivedi et al. 2008; Randin et al. 2009). Apart from SDMs predicting the potential distribution of each species individually, based on their climatic envelope, other models directly predict species richness based on macroecology theory (Fischer 1960; Currie 1991; Hawkins et al. 2003). These models directly correlate various environmental conditions (mainly climatic variables) with regional species richness. While these models often predict lower extinction rates than SDMs (Algar et al. 2009; Sommer et al. 2010), they also seem to be prone to scale issues (Field et al. 2009), with insufficient correlation at small scales. The current debate about modelling future biodiversity and species distribution in mountains leads to numerous new approaches and improved methods, but the modelling community tends to keep their focus mostly on model technical issues and often ignores the source of the data used for modelling. It is important to keep in mind that almost all models discussed here use weather station data for their projections. As shown here and in previous works,

this is highly inappropriate for aerodynamically decoupled vegetation such as low stature alpine heath. The correlation of weather station data and real climate conditions for a plant species might strongly vary among life forms, depending on their aerodynamic coupling to the atmosphere. The more strongly an ecosystem is decoupled from atmospheric conditions by topography and vegetation structure, the more thermal micro-habitat variation is observed (Scherrer and Körner 2010a). The number of these micro-habitats that are detected depends on the methods and spatial scale used to collect the climate data. The quality (spatial resolution) of this data might drastically influence or even bias the result of projections, independent of the modelling approach. These scale effects might be less important when the centre of species distributions is modelled, but they distort the results when modelling extinctions near niche boundaries. Based on this study, we advocate not only consideration of the uncertainty and variability in biodiversity projections caused by model technical issues but also the need to account for the effects of the quality and spatial scale of the climate data used. The data presented here re-confirm that alpine habitats are in fact more suitable for organisms to cope with climatic change than had commonly been assumed.

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Chapter 5

Summary and General Conclusion

Summary and general conclusion

Aim

This thesis investigated the thermal patterns in alpine landscapes at different spatial scales. By accumulating a large amount of surface (plant canopy) and soil (root zone) temperature data the following key questions were addressed: (1) Do surface and soil temperatures in the alpine life zone deviate from 2 m above ground air temperature and if so, by how much? (2) To what degree does the variation in surface and soil temperature depend on spatial scale (plot, slope, region) and what are the driving forces? (3) Is the observed thermal mosaic associated with vegetation patterns? (4) How does the spatial resolution of climate data influence the observed and predicted (climate warming projections) micro-habitat distribution?

The understanding of the interplay of solar radiation, topography and vegetation leading to the thermal micro-habitat mosaic of alpine landscapes might help us to better assess the vulnerability of alpine ecosystems in a warming climate. Additionally, the data collected on small scale variation of temperature might help to improve larger scale models that are currently unable to reflect the meter to meter scale pattern.

Deviation of surface and soil temperature from air temperature

Surface temperatures show strong positive (2-9 K) and negative (3-8 K) deviations from 2 m above ground air temperature on bright days and clear nights, respectively. Seasonal mean root zone temperatures are consistently 2-4 K above air temperature during summer (Scherrer & Körner, 2010). As to be expected, macro-exposure directly influenced mean surface and soil temperature with south oriented slopes being warmer than west or north slopes. These results indicate that 2 m above ground air temperature cannot directly be associated with plant life conditions. On cloudy or rainy days the surface temperatures are closer to air temperature, yet our results still demonstrate that life conditions of low stature alpine vegetation may be considerably more favourable than would be expected from climate station data across the season.

Surface and soil temperature variation at different spatial scales

We observe substantial soil and surface temperature variation at all tested spatial scales. At a few centimetres distance we find seasonal mean soil temperature differences of 1.5 K, mostly dependent on inclination, vegetation cover and vegetation height. There is also large leaf temperature variation at the centimetre scale, mainly influenced by growth form. Within a single slope micro-topography effects lead to a surface temperature variation of c. 5 K on clear sky days. The within-slope soil temperature differences are c. 3.5 K, composed of micro-topography (c. 2 K) and centimetre scale cover effects (c. 1.5 K). The among-slope effects are explained by macro-exposure, with south slopes c. 2.5 K warmer than north slopes both for surface and soil temperature (Scherrer & Körner, 2010; Scherrer *et al.*, 2010).

Thermal mosaic and assemblage of plant species

The described mosaic of thermal micro-habitat conditions directly influences the assemblage of plant species. Within a single slope we find plant communities with a high proportion of ‘nival’ species (low mean Landolt indicator value for temperature) in colder places than plant communities with high temperature indicator values (mostly ‘sub-alpine’ species). Since macro-exposure modulates the seasonal mean temperature, a higher proportion of ‘sub-alpine’ and ‘montane’ plant species is found on a warmer south slope than on north or west slopes (Scherrer & Körner, 2011).

Low spatial resolution leads to an underestimation of today’s habitat diversity

By artificially decreasing the spatial resolution within a given grid of pixels of the thermal images we exponentially lose information about the micro-habitat variation. At 1 x 1 m² a surface temperature range

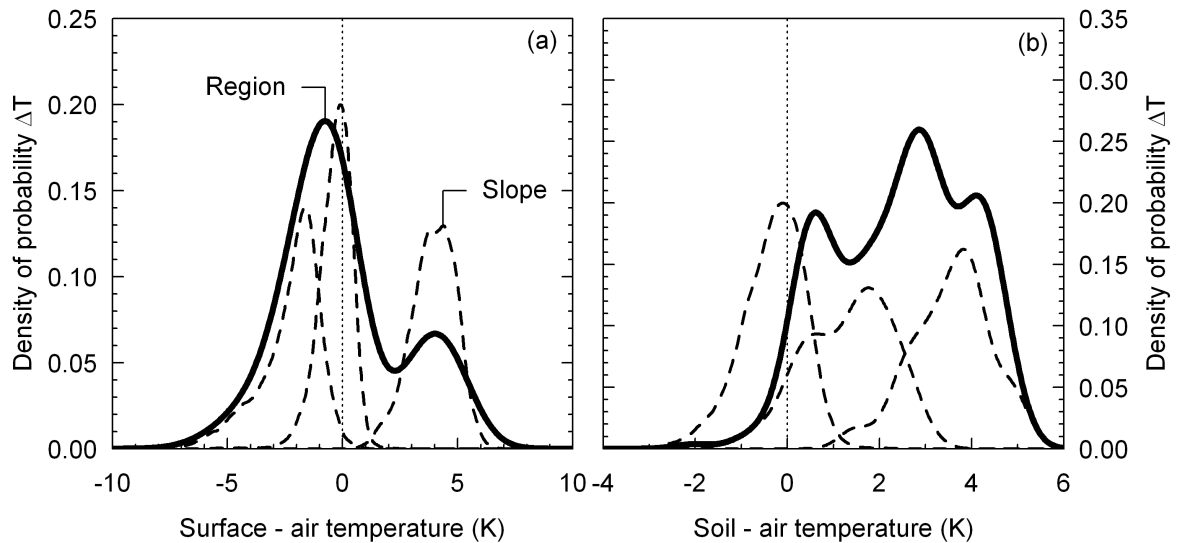


Figure 1: (a) Density distribution of surface minus air temperature for the region (2 km^2) and each contributing slope separately (NW, W, SE exposure from left to right). Surface temperature data are mean values of clear sky days from 7 to 20 h. (b) Density distribution of seasonal mean soil minus air temperature for the region and each slope as in (a). Soil temperature data was collected from June 22, 2008 to September 8, 2008 and from June 29, 2009 to September 13, 2009.

of 11 K is obtained while at a $100 \times 100 \text{ m}^2$ resolution the observed range is reduced to 4 K. In fact, at a $100 \times 100 \text{ m}^2$ resolution we over or underestimate the thermal micro-habitat conditions of 25% of the study area. Therefore every fourth micro-habitat is no longer represented at the $100 \times 100 \text{ m}^2$ resolution and not even considered when making climate warming projections based on this data (Scherrer *et al.*, 2010).

The spatial resolution not only influences our picture of the current micro-habitat distribution, but also directly influences the projected habitat loss due to climate warming, the lower the spatial resolution the higher the proportion of habitats that are assumed to disappear.

As simple as this model for predicting future habitat distribution might be, the assumption that a 2 K warming will shift all microhabitat temperatures by 2 K is hard to falsify. Low resolution models are likely to underestimate the habitat diversity and therefore tend to overestimate the extinction risk of species in patchy areas with high topographic variability and steep environmental gradients. High resolution models might predict persistence in areas too small to shelter populations viable in the longer term. Also strong fragmentation and crowding effects in remaining habitat patches might be a problem not accurately considered by high resolution models, even in taxas adapted to naturally fragmented landscapes such as the alpine life zone. However, a substantial number of new habitats will emerge, offering conditions for low elevation species to expand their range

and therefore the species richness within any given area might stay the same.

Final conclusions

The results of this study show that the alpine landscapes with their steep slopes and highly variable micro-topography build a meter-scale thermal mosaic closely interacting with plant species. The thermal mosaic offers a wide range of micro-habitats inhabited by various plant communities depending on their specific thermal habitat preferences, as evidenced by the close match with known temperature preferences (indicator values). The high heterogeneity of both alpine vegetation and micro-habitat conditions (temperature, soil moisture, duration of snow cover) might make alpine biodiversity less vulnerable to climate warming impacts than is commonly assumed and predicted by large scale isotherm based models. The small scale mosaic of micro-habitats offers both refuge habitats as well as stepping stones, and therefore buffers alpine species diversity against the effects of a rise in atmospheric temperature.

In my opinion it would be worthwhile to incorporate the observed thermal mosaic into models predicting alpine species distribution. One possible method of doing this would be to construct models at finer spatial scale (e.g., Trivedi *et al.*, 2008; Randin *et al.*, 2009). Unfortunately, the data on species distribution and climate are not available at fine spatial resolutions for most regions of the world. To collect

such micro-climate and species distribution data at high spatial resolution for larger areas is almost impossible and the calculation of meter-scale models for larger areas would absorb many resources. Another possibility would be to use frequency distributions of (micro-) climatic conditions instead of single point data. A certain point in the landscape (for example a 4x4 km² area) would then not have a single value as, for example, 850 mm annual precipitation and 4.3 °C seasonal mean temperature, but host frequency distributions such as 850 ± 130 mm (mean ± sd) annual precipitation and 4.3 ± 4 °C seasonal mean temperature using empirical matrices as elaborated here. While the mean values would be interpolated by weather station data, the standard deviation should strongly depend on topography parameters. Rough terrains, such as alpine landscapes, likely have a larger spatial variation in seasonal mean temperature than flat terrain (for example tundra).

Describing a raster point in the landscape as a frequency distribution instead of a single values might more realistically describe the heterogeneity of landscapes especially in mountainous terrain and largely influence the model projections. Given that temperature is the major driver of niche-based models for alpine terrain, incorporating frequency distributions of thermal habitat conditions at otherwise standard applications of means for precipitation etc. might produce much better approximations to real world conditions.

In the light of the data presented in this thesis it is obvious that predicting the changes in heterogeneous alpine terrain is complex either by modeling, experiments or "educated guessing". However, in my opinion all approaches and scales have their fields of applicability as long as one is aware of the potential biases. Only the combination of larger and small scale approaches allows an overall picture of alpine biodiversity and its future changes due to climate warming. However, with this thesis we can offer frequency distributions of surface and soil temperatures within a km² area for alpine landscapes, incorporating effects of slope exposure (NW, W, SE), micro-topography and vegetation cover effects (Figure 1).

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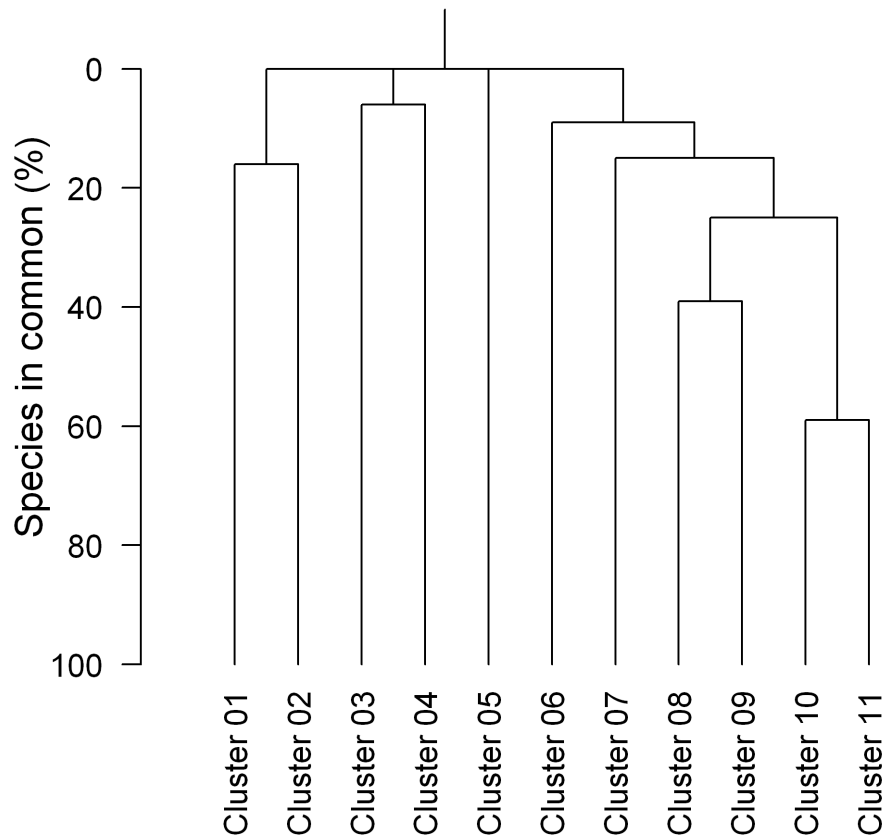
Chapter 6

Appendix and supplementary material
to chapters 2-4

List of vascular plant species (Appendix S1)

<i>Achillea atrata</i>	<i>Festuca rubra</i>	<i>Polytrichum norvegicum</i>
<i>Achillea erba-rotta</i>	<i>Festuca varia</i>	<i>Potentilla aurea</i>
<i>Achillea nana</i>	<i>Festuca violacea</i>	<i>Potentilla crantzii</i>
<i>Adenostyles alliariae</i>	<i>Galium anisophyllum</i>	<i>Potentilla grandiflora</i>
<i>Adenostyles glabra</i>	<i>Galium pumilum</i>	<i>Primula farinosa</i>
<i>Agrostis alpina</i>	<i>Gentiana acaulis</i>	<i>Primula hirsuta</i>
<i>Agrostis schraderiana</i>	<i>Gentiana campestris</i>	<i>Pulsatilla alpina</i>
<i>Alchemilla alpina</i>	<i>Gentiana nivalis</i>	<i>Pulsatilla sulphurea</i>
<i>Alchemilla fissa</i>	<i>Gentiana punctata</i>	<i>Pulsatilla vernalis</i>
<i>Alchemilla hybrida</i>	<i>Gentiana purpurea</i>	<i>Ranunculus alpestris</i>
<i>Alchemilla pentaphylla</i>	<i>Gentiana ramosa</i>	<i>Ranunculus glacialis</i>
<i>Alchemilla vulgaris</i>	<i>Geranium sylvaticum</i>	<i>Ranunculus montanus</i>
<i>Alchemilla xanthochlora</i>	<i>Geum montanum</i>	<i>Rumex alpestris</i>
<i>Androsace chamaejasme</i>	<i>Geum reptans</i>	<i>Sagina linnaei</i>
<i>Androsace obtusifolia</i>	<i>Globularia elongata</i>	<i>Salix helvetica</i>
<i>Antennaria carpatica</i>	<i>Gnaphalium hoppeanum</i>	<i>Salix herbacea</i>
<i>Antennaria dioica</i>	<i>Gnaphalium norvegicum</i>	<i>Salix reticulata</i>
<i>Anthoxanthum alpinum</i>	<i>Gnaphalium supinum</i>	<i>Salix retusa</i>
<i>Anthoxanthum odoratum</i>	<i>Gypsophila repens</i>	<i>Salix serpyllifolia</i>
<i>Anthyllis vulneraria</i>	<i>Hedysarum hedysaroides</i>	<i>Saussurea alpina</i>
<i>Arenaria ciliata</i>	<i>Helianthemum nummularium</i>	<i>Saxifraga aizoides</i>
<i>Arnica montana</i>	<i>Helictotrichon versicolor</i>	<i>Saxifraga aizoon</i>
<i>Aster alpinus</i>	<i>Hieracium angustifolium</i>	<i>Saxifraga androsacea</i>
<i>Aster bellidiastrum</i>	<i>Hieracium piliferum</i>	<i>Saxifraga biflora</i>
<i>Aster bellidiastrum</i>	<i>Homogyne alpina</i>	<i>Saxifraga bryoides</i>
<i>Bartsia alpina</i>	<i>Hutchinsia alpina</i>	<i>Saxifraga moschata</i>
<i>Biscutella levigata</i>	<i>Juncus jacquinii</i>	<i>Saxifraga seguieri</i>
<i>Botrychium lunaria</i>	<i>Juncus trifidus</i>	<i>Saxifraga stellaris</i>
<i>Calluna vulgaris</i>	<i>Juniperus nana</i>	<i>Scabiosa lucida</i>
<i>Campanula barbata</i>	<i>Koeleria hirsuta</i>	<i>Sedum alpestre</i>
<i>Campanula cochleariifolia</i>	<i>Leontodon helveticus</i>	<i>Sedum atratum</i>
<i>Campanula scheuchzeri</i>	<i>Leontodon hispidus</i>	<i>Sedum montanum</i>
<i>Campanula thyrsoides</i>	<i>Leucanthemopsis alpina</i>	<i>Selaginella selaginoides</i>
<i>Cardamine resedifolia</i>	<i>Leucanthemum vulgare</i>	<i>Sempervivum montanum</i>
<i>Carex curvula</i>	<i>Ligusticum mutellina</i>	<i>Sempervivum tectorum</i>
<i>Carex foetida</i>	<i>Linaria alpina</i>	<i>Senecio doronicum</i>
<i>Carex sempervirens</i>	<i>Loiseleuria procumbens</i>	<i>Sesleria caerulea</i>
<i>Cerastium arvense</i>	<i>Lotus corniculatus</i>	<i>Sibbaldia procumbens</i>
<i>Cerastium uniflorum</i>	<i>Luzula alpinopilosa</i>	<i>Silene acaulis</i>
<i>Cetraria islandica</i>	<i>Luzula campestris</i>	<i>Silene vulgaris</i>
<i>Cirsium spinosissimum</i>	<i>Luzula lutea</i>	<i>Soldanella pusilla</i>
<i>Crepis aurea</i>	<i>Luzula spicata</i>	<i>Solidago virg-aurea</i>
<i>Crepis pyrenaica</i>	<i>Minuartia sedoides</i>	<i>Thesium alpinum</i>
<i>Deschampsia flexuosa</i>	<i>Minuartia verna</i>	<i>Trifolium alpinum</i>
<i>Diphasiastrum alpinum</i>	<i>Myosotis alpestris</i>	<i>Trifolium badium</i>
<i>Doronicum clusii</i>	<i>Myosotis versicolor</i>	<i>Trifolium nivale</i>
<i>Draba aizoides</i>	<i>Nardus stricta</i>	<i>Trifolium pratense</i>
<i>Dracocephalum austriacum</i>	<i>Oxyria digyna</i>	<i>Trifolium thalii</i>
<i>Dryas octopetala</i>	<i>Parnassia palustris</i>	<i>Trisetum spicatum</i>
<i>Elyna myosuroides</i>	<i>Pedicularis foliosa</i>	<i>Vaccinium myrtillus</i>
<i>Erigeron alpinus</i>	<i>Pedicularis kernerii</i>	<i>Vaccinium uliginosum</i>
<i>Erigeron uniflorus</i>	<i>Pedicularis verticillata</i>	<i>Vaccinium vitis-idaea</i>
<i>Euphrasia minima</i>	<i>Petasites paradoxus</i>	<i>Valeriana officinalis</i>
<i>Euphrasia rostkoviana</i>	<i>Phleum alpinum</i>	<i>Veronica alpina</i>
<i>Festuca alpina</i>	<i>Phyteuma betonicifolium</i>	<i>Veronica bellidioides</i>
<i>Festuca cf. rubra</i>	<i>Phyteuma hemisphaericum</i>	<i>Veronica fruticans</i>
<i>Festuca halleri</i>	<i>Poa alpina</i>	
<i>Festuca pulchella</i>	<i>Poa laxa</i>	
<i>Festuca quadriflora</i>	<i>Polygonum viviparum</i>	

List of vegetation units (cluster) (Appendix S2)

**Cluster 1**

Alchemilla vulgaris
Androsace obtusifolia
Antennaria carpatica
Anthoxanthum odoratum
Arnica montana
Aster alpinus
Botrychium lunaria
Campanula barbata
Carex sempervirens
Cerastium arvense
Crepis pyrenaica
Deschampsia flexuosa
Erigeron alpinus
Euphrasia rostkoviana
Galium anisophyllum
Gentiana campestris
Geum montanum
Gnaphalium norvegicum
Helictotrichon versicolor
Homogyne alpina
Juncus jacquinii

Juncus trifidus
Leontodon hispidus
Luzula campestris
Phleum alpinum
Phyteuma tetonicifolium
Poa alpina
Potentilla crantzii
Primula farinosa
Sempervivum montanum
Sempervivum tectorum
Senecio doronicum
Silene vulgaris
Solidago virg-aurea
Thesium alpinum
Trifolium alpinum
Trifolium pratense
Vaccinium myrtillus
Vaccinium vitis-idaea

Cluster 2

Agrostis alpina
Androsace obtusifolia

Anthoxanthum odoratum
Arnica montana
Biscutella levigata
Botrychium lunaria
Campanula scheuchzeri
Carex sempervirens
Erigeron alpinus
Erigeron uniflorus
Euphrasia minima
Festuca varia
Gentiana campestris
Gentiana nivalis
Geum montanum
Helictotrichon versicolor
Juncus trifidus
Koeleria hirsuta
Leucanthemum vulgare
Potentilla grandiflora
Pulsatilla vernalis
Sempervivum tectorum
Senecio doronicum
Sesleria caerulea

Silene vulgaris
Trifolium alpinum
Trifolium nivale
Trifolium thalii
Veronica bellidioides

Cluster 3

Agrostis alpina
Carex curvula
Cetraria islandica
Elyna myosuroides
Helictotrichon versicolor
Hieracium piliferum
Loiseleuria procumbens
Phyteuma hemisphaericum
Polygonum viviparum
Primula hirsuta
Salix serpyllifolia
Saxifraga bryoides
Silene acaulis
Veronica bellidioides

Cluster 4

Cerastium uniflorum
Doronicum clusii
Elyna myosuroides
Ranunculus glacialis
Salix retusa
Saxifraga bryoides
Saxifraga seguieri
Silene acaulis
Veronica bellidioides

Cluster 5

Agrostis schraderiana
Campanula scheuchzeri
Carex curvula
Gentiana ramosa
Geum montanum
Helictotrichon versicolor
Homogyne alpina
Juncus trifidus
Leontodon helveticus
Leucanthemopsis alpina
Ligusticum mutellina
Loiseleuria procumbens
Phyteuma hemisphaericum
Polygonum viviparum
Salix serpyllifolia
Sempervivum montanum
Soldanella pusilla
Trifolium alpinum

Cluster 6

Agrostis schraderiana
Bartsia alpina
Campanula scheuchzeri
Cirsium spinosissimum
Doronicum clusii
Festuca alpina
Galium anisophyllum

Gentiana purpurea
Geum montanum
Helictotrichon versicolor
Homogyne alpina
Juncus jacquinii
Ligusticum mutellina
Polygonum viviparum
Potentilla aurea
Ranunculus montanus
Salix reticulata
Salix retusa
Vaccinium myrtillus
Vaccinium uliginosum

Cluster 7

Agrostis alpina
Alchemilla pentaphyllea
Bartsia alpina
Carex curvula
Cetraria islandica
Elyna myosuroides
Euphrasia minima
Gentiana punctata
Helictotrichon versicolor
Homogyne alpina
Juncus trifidus
Leontodon helveticus
Leucanthemopsis alpina
Loiseleuria procumbens
Salix herbacea
Salix retusa
Soldanella pusilla

Cluster 8

Agrostis schraderiana
Anthoxanthum odoratum
Bartsia alpina
Cetraria islandica
Festuca alpina
Gentiana punctata
Geum montanum
Helictotrichon versicolor
Homogyne alpina
Juncus jacquinii
Leontodon helveticus
Ligusticum mutellina
Salix herbacea
Salix reticulata
Salix retusa
Soldanella pusilla
Trifolium badium

Cluster 9

Agrostis schraderiana
Alchemilla vulgaris
Anthoxanthum odoratum
Bartsia alpina
Campanula scheuchzeri
Carex curvula
Carex foetida
Cetraria islandica

Cirsium spinosissimum
Crepis aurea
Euphrasia minima
Gentiana punctata
Geum montanum
Gnaphalium supinum
Helictotrichon versicolor
Homogyne alpina
Juncus jacquinii
Juncus trifidus
Leontodon helveticus
Leucanthemopsis alpina
Ligusticum mutellina
Luzula alpinopilosa
Luzula lutea
Phleum alpinum
Ranunculus montanus
Salix herbacea
Soldanella pusilla
Trifolium badium
Veronica alpina

Cluster 10

Agrostis schraderiana
Alchemilla alpina
Anthoxanthum odoratum
Bartsia alpina
Campanula scheuchzeri
Cirsium spinosissimum
Euphrasia minima
Euphrasia sp.
Gentiana purpurea
Geum montanum
Helictotrichon versicolor
Homogyne alpina
Juncus jacquinii
Leontodon helveticus
Ligusticum mutellina
Phleum alpinum
Poa alpina
Polygonum viviparum
Potentilla aurea
Pulsatilla sulphurea
Ranunculus montanus
Salix herbacea
Salix serpyllifolia
Soldanella pusilla

Cluster 11

Alchemilla pentaphyllea
Anthoxanthum odoratum
Campanula scheuchzeri
Festuca alpina
Gentiana purpurea
Geum montanum
Helictotrichon versicolor
Homogyne alpina
Juncus jacquinii
Leontodon helveticus
Leontodon hispidus
Ligusticum mutellina

Nardus stricta
Phleum alpinum
Phyteuma hemisphaericum

Poa alpina
Potentilla aurea
Soldanella pusilla

Trifolium badium

Functional classifications of plant species (Appendix S3)

Table 1: Classifications for **functional group**(graminoid [gra], forb [for], legume [leg]), **growth form** (basal leaves [bas], leaves in the middle part of the plant [mid], leaves in the top part of the plant [top], tussock [tus], cushion [cus]), **life form** (therophyte [the], geophyte [geo], hemicryptophyte [hem], chamaephyte [cha]), **stem growth type** (stem erect [ere], stem ascending [asc], stem prostrate [pro], without evident stem [wit]) and **leaf distribution** (rosette plant [ros], semi-rosette plant [sem], leaves distributed regularly along stem [dis]).)

Plan species	Functional group	Growth form	Life form	Stem growth type	Leaf distribution
<i>Carex curvula ssp. curvula</i>	gra	tus	hem	ere	sem
<i>Helictotrichon versicolor</i>	gra	mid	hem	ere	sem
<i>Leontodon helveticus</i>	for	bas	hem	ere	ros
<i>Geum montanum</i>	for	mid	hem	ere	sem
<i>Nardus stricta</i>	gra	tus	hem	ere	sem
<i>Ligusticum mutellina</i>	for	mid	hem	ere	sem
<i>Gentiana punctata</i>	for	mid	hem	ere	sem
<i>Homogyne alpina</i>	for	bas	hem	ere	ros
<i>Soldanella pusilla</i>	for	bas	hem	asc	ros
<i>Euphrasia minima</i>	for	top	the	ere	dis
<i>Trifolium alpinum</i>	leg	bas	hem	ere	ros
<i>Phyteuma hemispaericum</i>	for	mid	hem	ere	sem
<i>Luzula lutea</i>	gra	mid	hem	ere	sem
<i>Leucanthemopsis alpina</i>	for	bas	hem	ere	ros
<i>Sempervivum montanum</i>	for	bas	cha	ere	ros
<i>Anthoxanthum alpinum</i>	gra	mid	hem	ere	sem
<i>Potentilla aurea</i>	for	mid	hem	asc	sem
<i>Gnaphalium supinum</i>	for	mid	hem	ere	sem
<i>Luzula alpinopilosa</i>	gra	mid	hem	ere	sem
<i>Festuca violacea</i>	gra	tus	hem	ere	sem
<i>Campanula scheuchzeri</i>	for	top	hem	asc	dis
<i>Alchemilla fissa</i>	for	mid	hem	ere	sem
<i>Ranunculus montanus</i>	for	mid	hem	asc	sem
<i>Salix reticulata</i>	for	bas	cha	pro	dis
<i>Alchemilla pentaphyllea</i>	for	mid	hem	asc	sem
<i>Cirsium spinosissimum</i>	for	mid	hem	ere	sem
<i>Trifolium badium</i>	leg	mid	hem	ere	sem
<i>Salix retusa</i>	for	bas	cha	pro	dis
<i>Aster bellidiastrum</i>	for	bas	hem	ere	ros
<i>Campanula barbata</i>	for	mid	hem	ere	sem
<i>Selaginella selaginoides</i>	for	top	cha	asc	dis
<i>Sesleria caerulea</i>	gra	tus	hem	ere	sem
<i>Festuca quadriflora</i>	gra	tus	hem	ere	sem
<i>Euphrasia rostkoviana</i>	for	top	the	ere	dis
<i>Polygonum viviparum</i>	for	mid	geo	ere	sem
<i>Aster alpinus</i>	for	mid	hem	ere	sem
<i>Elyna myosuroides</i>	gra	tus	hem	ere	sem
<i>Saxifraga paniculata</i>	for	bas	cha	ere	ros
<i>Pulsatilla vernalis</i>	for	bas	hem	ere	ros
<i>Carex curvula ssp. rosae</i>	gra	tus	hem	ere	sem
<i>Pedicularis verticillata</i>	for	mid	hem	ere	sem
<i>Draba aizoides</i>	for	bas	cha	ere	ros
<i>Anthyllis vulneraria ssp. alpestris</i>	leg	mid	hem	ere	sem
<i>Primula farinosa</i>	for	bas	hem	ere	ros
<i>Carex sempervirens</i>	gra	tus	hem	ere	sem
<i>Agrostis alpina</i>	gra	tus	hem	ere	sem
<i>Gentiana campestris</i>	for	top	the	ere	dis
<i>Dryas octopetala</i>	for	bas	cha	pro	dis

List of important thermal images

This Appendix presents the most important aggregated (mean) thermal images mentioned in the thesis as false colour images. The Appendix includes thermal images at slope, plot and individual plant level.

Thermal images of slopes in the Swiss Alps

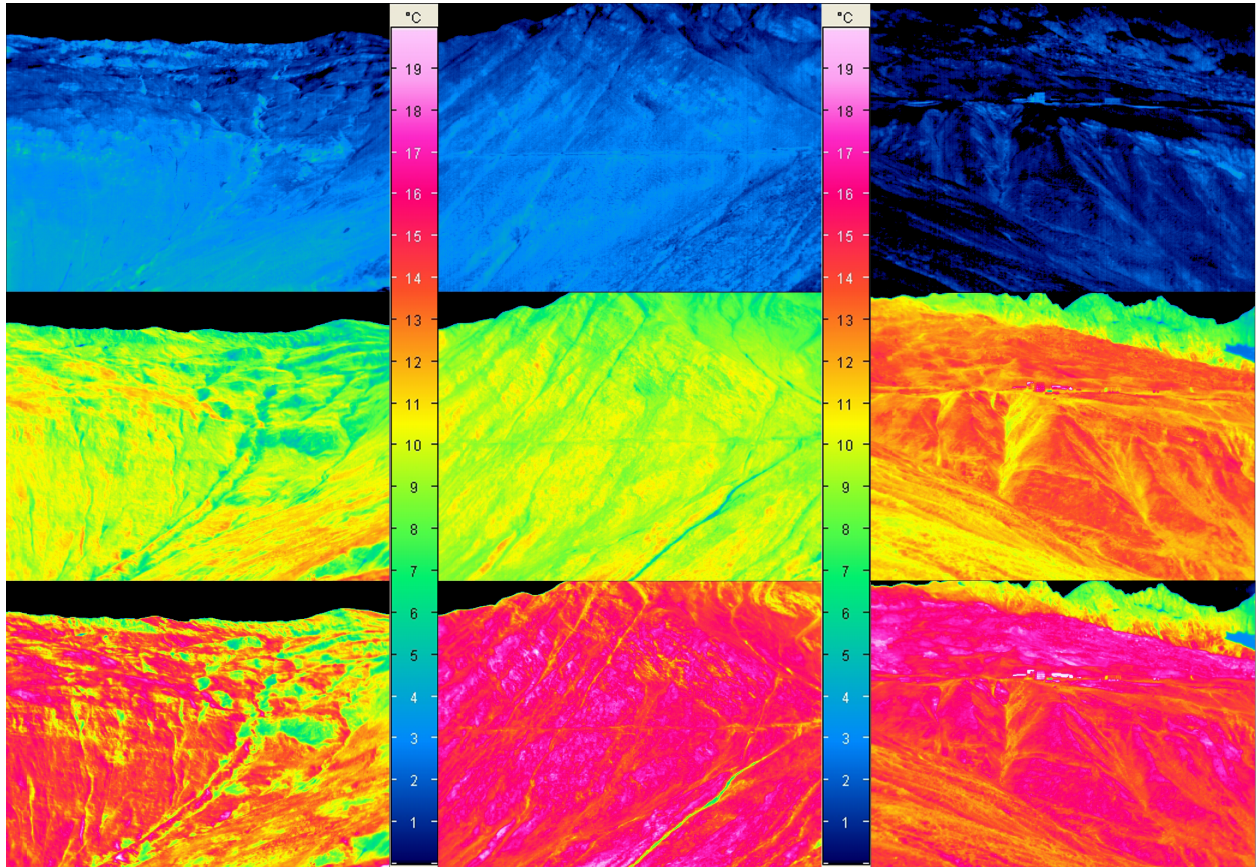


Figure 1: The first column (left) shows thermal images for a NNW, the second column (middle) for a W and the third column (right) for a SSE exposed slope at the Furka Pass in the Swiss Alps. The top row represents mean thermal images from 00-06h ('night-time'), the middle row from 07-20h and the bottom row from 12-18h ('day-time'). All thermal images were recorded from August 27, 2008 to August 29, 2008.

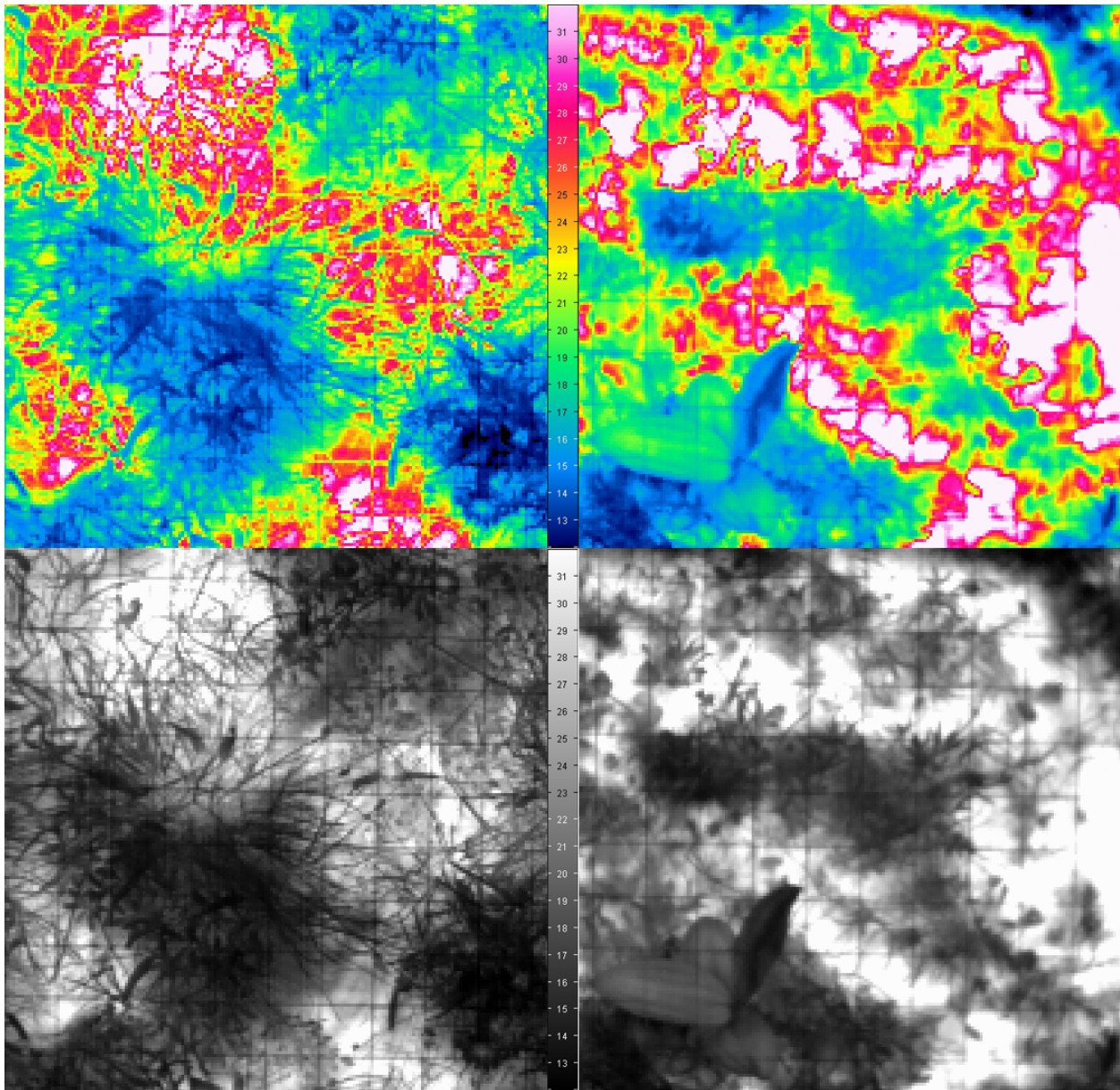
Thermal images of 0.25 m² plots in the Swiss Alps

Figure 2: Two examples of 0.25 m² plots with different vegetation types. Top row shows the thermal images in a red to blue colour scale. Bottom row shows the same thermal images in a grey scale. Both images were recorded on July 16, 2009.

Thermal images of individual plant species in the Swiss Alps

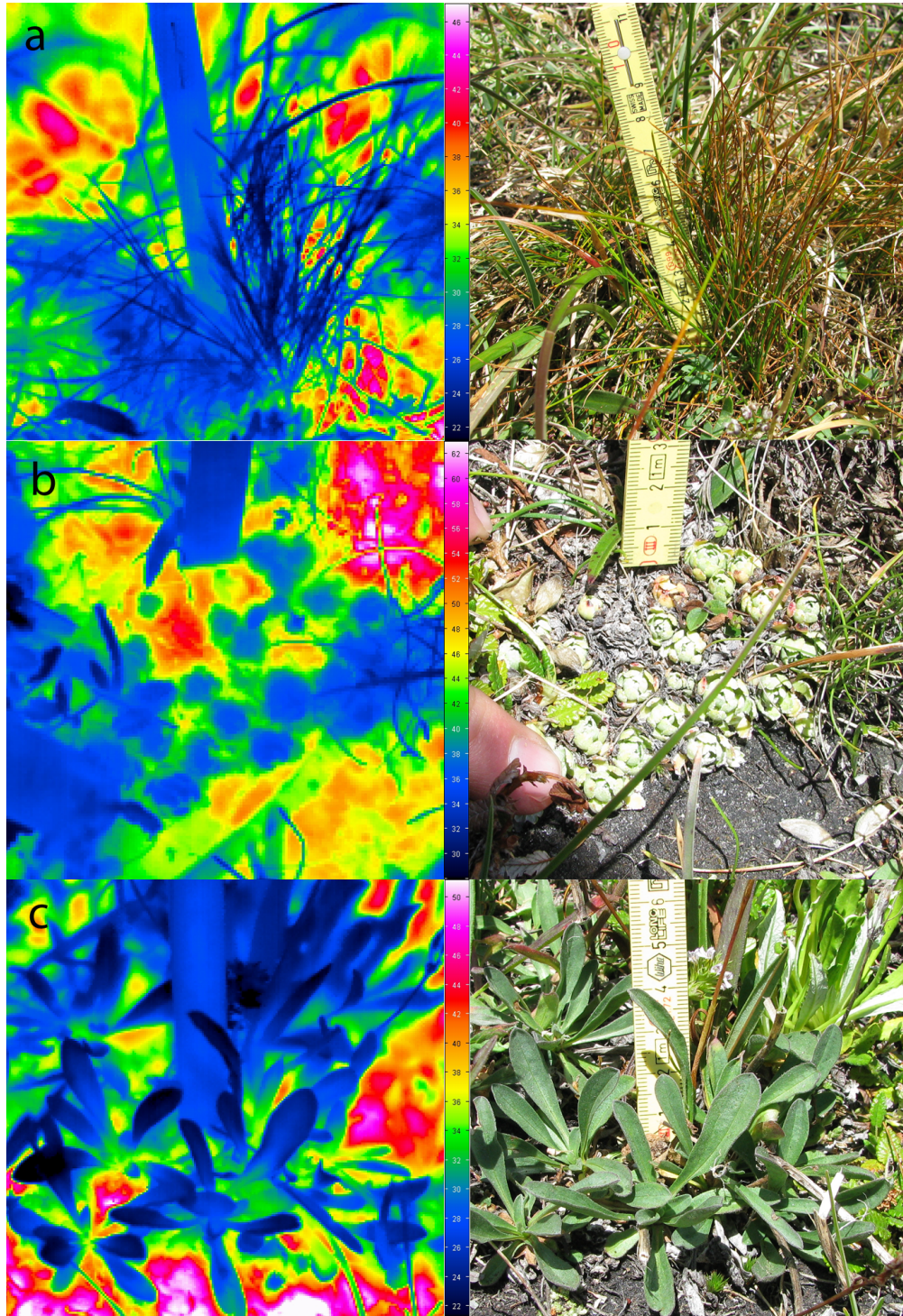


Figure 3: Thermal images and the corresponding visual light image for (a) *Elyna myosuriodes*, (b) *Saxifraga paniculata* and (c) *Aster alpinus*. All images were recorded on July 18, 2009 under clear sky conditions.

Chapter 7

Curriculum Vitae

Curriculum Vitae

Name	Daniel Scherrer
Date of birth	11.11.1981
Place of birth	Basel
Nationality	Switzerland (Krummenau)

Education

2007-2010	PhD position at the Institute of Botany, University of Basel, Switzerland. ‘Infra-red thermometry in alpine terrain’, supervised by C Körner
2005-2007	Master of Science in Ecology, University of Basel, Switzerland. ‘Local extinction risk, colonisation probability, and spatial spread of the alpine <i>Geum reptans</i> on a glacier foreland in the Swiss Alps’, supervised by J Stöcklin
2002-2005	Bachelor of Science in Biology, University of Basel, Switzerland
2000	High school leaving exam

Professional experience

2009	Teaching assistant in graduate course Ecology (Introduction to R)
2009	Teaching assistant in undergraduate course Ecology (Blockkurs Pflanzenökologie)
2004-2005	Teaching assistant in undergraduate course Informatics (Werkzeuge der Informatik)
2005	Teaching assistant in undergraduate course Informatics (Programmieren I&II)

Conferences

2010	International conference on Global Change and the World’s Mountains in Perth, Scotland. ‘Topography driven niche differentiation buffers alpine biodiversity against climate warming impact’
2009	GfÖ-Jahrestagung in Bayreuth, Germany. ‘Infra-red thermometry evidences life conditions in alpine terrain at landscape scale’
2007	Popbio2007 in Basel, Switzerland. ‘Local extinction risk, colonisation probability, and spatial spread of the alpine <i>Geum reptans</i> on a glacier foreland in the Swiss Alps’

Publications

2010

Scherrer D, Körner Ch (2010): Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Global Change Biology*, **16**, 2602-2613

Scherrer D, Körner Ch (2011): Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406-416

Scherrer D, Schmid S, Körner Ch (2010): Elevational species shifts in a warmer climate are overestimated when based on weather station data. *International Journal of Biometeorology*, *in press*

Scherrer D, Stoll P, Stöcklin J (2010): Local extinction risk, colonisation probability, and spatial spread of the alpine *Geum reptans* on a glacier foreland in the Swiss Alps. *OIKOS*, *submitted*