

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

Daniel Scherrer · Samuel Schmid · Christian Körner

Received: 9 June 2010 / Revised: 31 August 2010 / Accepted: 2 September 2010 / Published online: 6 October 2010  
© ISB 2010

**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-km<sup>2</sup>) to plot (1-m<sup>2</sup>) 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-m<sup>2</sup> 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-km<sup>2</sup> 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-km<sup>2</sup> (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-m<sup>2</sup> 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-m<sup>2</sup> 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-m<sup>2</sup> per pixel and 0.2-cm<sup>2</sup> 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-m<sup>2</sup> 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-m<sup>2</sup> plots) the inclination, exposure and surface structure (concave, convex or flat). By a grid-point intercept method applied to the 25-cm<sup>2</sup> 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-m<sup>2</sup> 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 <sup>a</sup>	Life form <sup>b</sup>	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

<sup>a</sup> Bas leaves concentrated in basal parts of plant, Mid leaves concentrated in middle parts of plant, Tus leaves concentrated in tussocks

<sup>b</sup> 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-m<sup>2</sup> 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-m<sup>2</sup>, 10-m<sup>2</sup> or 100-m<sup>2</sup> 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).

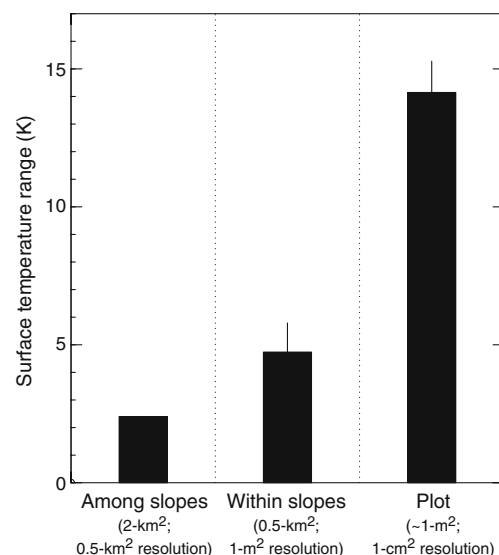
## Results

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

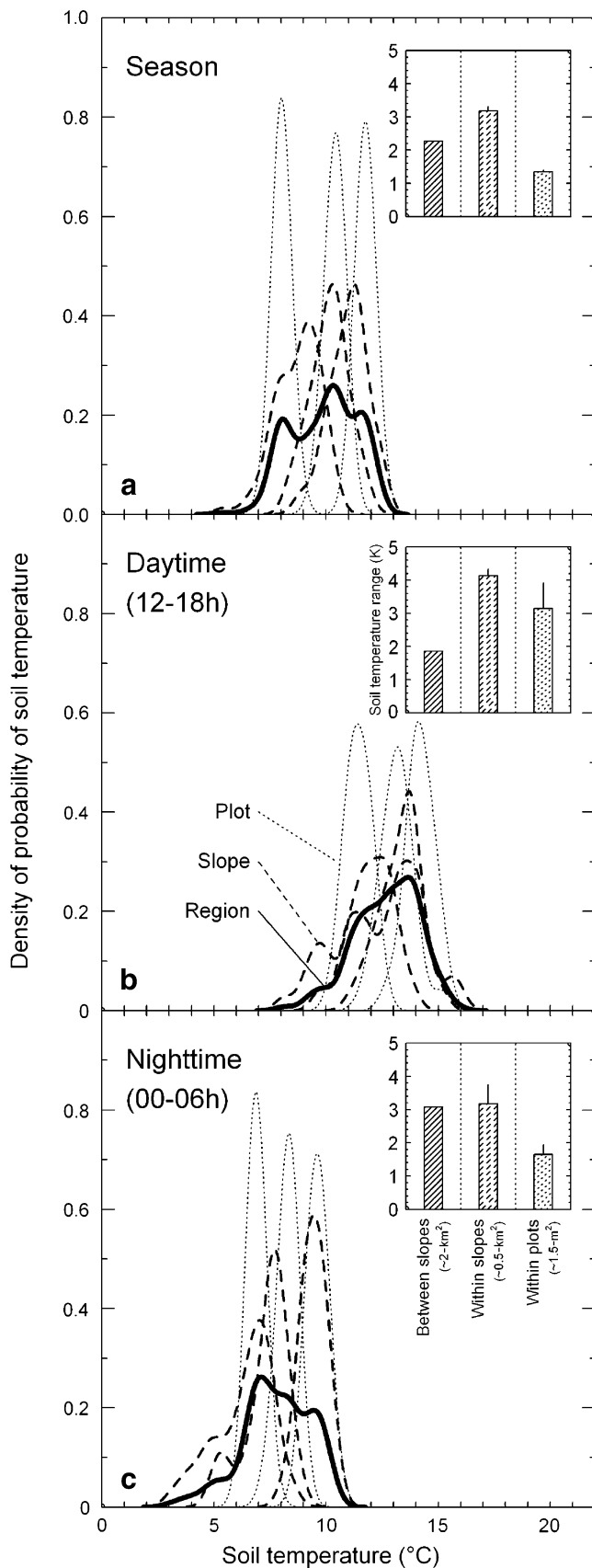
The difference in surface temperature among slopes was only 2.4 K while the range containing 90% of the data points within a given slope (c. 0.5-km<sup>2</sup>) was 4.8±1.06 K (mean ± SE) and 14.1±1.13 K within a 1-m<sup>2</sup> plot (Fig. 1). The range containing 90% of the data points was similar for all 1-m<sup>2</sup> 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 ± 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±0.13°C (mean ± SE) on the NNW, 10.1±0.12°C on the W and 11.0±0.11°C on the SSE exposed slope.

The 1-m<sup>2</sup> plots showed large differences in their seasonal mean soil temperature with 8.0±0.28°C (mean ± SE) on the NNW, 10.4±0.34°C on the W and 11.7±0.30°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

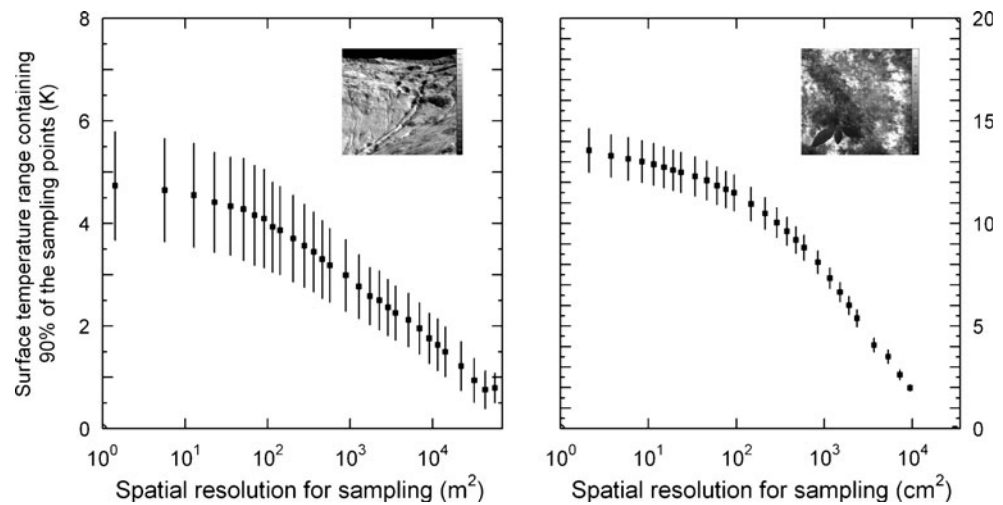


**Fig. 2** a Density distribution of seasonal mean soil temperatures for individual plots (1-m<sup>2</sup>; dotted lines), whole slopes (0.5-km<sup>2</sup>; dashed lines) and total region (2-km<sup>2</sup>; solid line). The inset shows the soil temperature range for three spatial scales (among slopes, 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-m<sup>2</sup> 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±5.3°C; mean ± SD), plants with leaves concentrated in middle parts of the stem had a medium leaf temperature (24.8±3.3°C), and tussocks (graminoids), exposing their long erect leaves to the wind, had the lowest leaf temperature (21.9±1.6°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-km<sup>2</sup>) and the *right panel* at plot scale (1-m<sup>2</sup>). The *insets* represent sample thermal images of a slope and a plot



## Discussion

### Within-plot variation

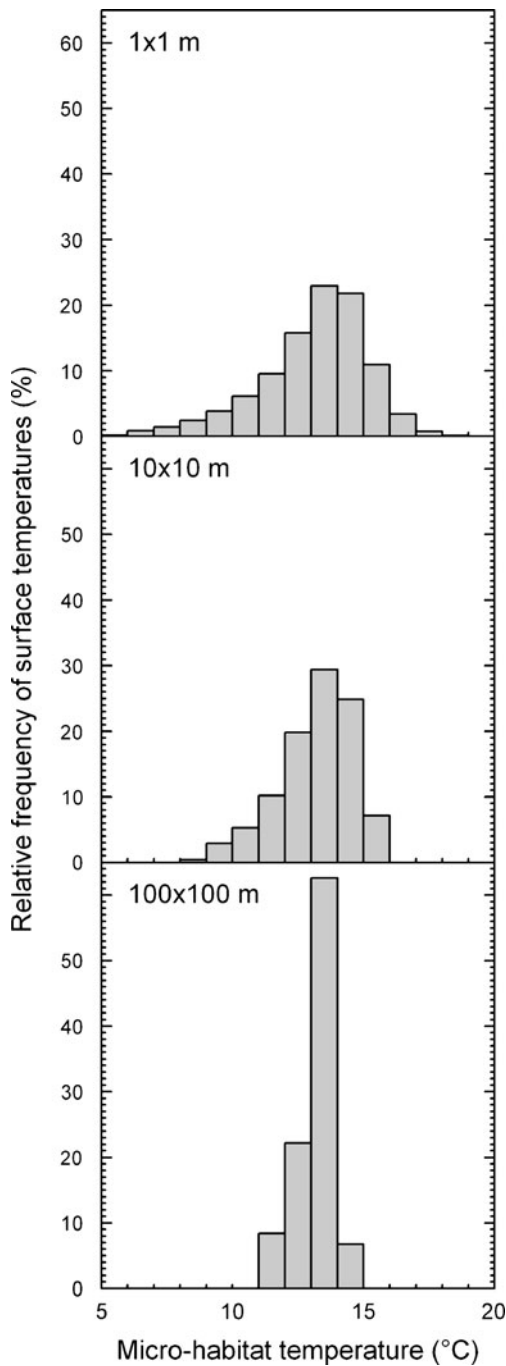
Our results show substantial variation in both surface and soil temperature on all three scales (among slopes, within slopes and within plots). The variation in surface temperature was highest on the finest scale (within plots) and independent of macro-exposure. This can partly be explained by a technical issue. For logistical reasons (only one thermal camera), it was impossible to monitor the 1-m<sup>2</sup> 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-m<sup>2</sup> 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-m<sup>2</sup> 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-m<sup>2</sup>) 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-cm<sup>2</sup> 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-m<sup>2</sup>; 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  $1 \times 1$  m to  $100 \times 100$  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 ( $1 \times 1$  m), less than 10% of the current micro-habitat conditions (climate space) disappear from a slope, while, at a lower resolution ( $100 \times 100$  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  $1 \times 1$  m resolution were not detected with a  $100 \times 100$  m resolution under current conditions. Therefore, we conclude that none of the micro-habitats identified with a  $100 \times 100$  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  $1 \times 1$  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.

**Acknowledgements** This work was carried out as part of the EC FP6 EcoChange (Challenges in Assessing and Forecasting Biodiversity and Ecosystem Changes in Europe, no. 066866 GOCE) project. Thanks to N. Zimmermann and A. Guisan for the data loggers, E. Hiltbrunner for logistical support and two anonymous reviewers for comments on the manuscript.

## References

- Algar AC, Kharouba HM, Young ER, Kerr JT (2009) Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography* 32:22–33
- Araújo MB, Guisan A (2006) Five (or so) challenges for species distribution modelling. *J Biogeogr* 33:1677–1688
- Araújo MB, New M (2007) Ensemble forecasting of species distributions. *Trends Ecol Evol* 22:42–47
- Araújo MB, Pearson RG, Thuiller W, Erhard M (2005a) Validation of species-climate impact models under climate change. *Glob Chang Biol* 11:1504–1513
- Araújo MB, Whittaker RJ, Ladle RJ, Erhard M (2005b) Reducing uncertainty in projections of extinction risk from climate change. *Glob Ecol Biogeogr* 14:529–538
- Bahn M and Körner C (2003) Recent increases in summit flora caused by warming in the Alps. In: Nagy L, Grabherr G, Körner C, Thompson DBA (eds) *Alpine diversity in Europe*. Springer, New York, pp 437–441
- Bakkenes M, Alkemade JRM, Ihle F, Leemans R, Latour JB (2002) Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Glob Chang Biol* 8:390–407
- Beniston M (2006) Mountain weather and climate: A general overview and a focus on climatic change in the Alps. *Hydrobiologia* 562:3–16
- Beniston M, Fox DG, Adhikary S, Andresson R, Guisan A, Holten JJ, Ines J, Maitima J, Price M, Tessier L (1996) The impacts of climate change on mountain regions. In: *Second Assessment Report of the Intergovernmental Panel on Climate Change (IPPC)*. Cambridge University Press
- Beniston M, Diaz HF, Bradley RS (1997) Climatic change at high elevation sites: an overview. *Clim Change* 36:233–251
- Billings WD, Mooney HA (1968) Ecology of arctic and alpine plants. *Biol Rev Camb Philos Soc* 43:481–529
- Cernusca A (1976) Structure of forest stand, bioclimatology and energy economy of dwarf shrub communities in the Alps. *Oecol Plant* 11:71–101
- Charpentier MA, Groffman PM (1992) Soil-moisture variability within remote-sensing pixels. *J Geophys Res Atmos* 97:18987–18995
- Colwell RK, Brehm G, Cardelus CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322:258–261
- Cornelissen JHC, Lavorel S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H (2003) A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust J Bot* 51:335–380
- Cosma S, Richard E, Miniscloux F (2002) The role of small-scale orographic features in the spatial distribution of precipitation. *Q J R Meteorol Soc* 128:75–92
- Currie DJ (1991) Energy and large-scale patterns of animal-species and plant-species richness. *Am Nat* 137:27–49
- Diaz HF, Grosjean M, Graumlich L (2003) Climate variability and change in high elevation regions: past, present and future. *Clim Change* 59:1–4
- Elith J, Graham CH, Anderson RP, Dudik M, Ferrier S, Guisan A, Hijmans RJ, Huettmann F, Leathwick JR, Lehmann A, Li J, Lohmann LG, Loiselle BA, Manion G, Moritz C, Nakamura M, Nakazawa Y, Overton JM, Peterson AT, Phillips SJ, Richardson K, Scachetti-Pereira R, Schapire RE, Soberon J, Williams S, Wisz MS, Zimmermann NE (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29: 129–151
- Field R, Hawkins BA, Cornell HV, Currie DJ, Diniz-Filho JAF, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Turner JRG (2009) Spatial species-richness gradients across scales: a meta-analysis. *J Biogeogr* 36:132–147
- Fischer AG (1960) Latitudinal variations in organic diversity. *Evolution* 14:64–81
- Grabherr G, Gottfried M, Pauli H (1994) Climate effects on mountain plants. *Nature* 369:448
- Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. *Ecol Lett* 8:993–1009
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecol Modell* 135:147–186
- Hawkins BA, Field R, Cornell HV, Currie DJ, Guegan JF, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology* 84:3105–3117
- Herrick JE, Range JE (2005) *Monitoring manual for grassland, shrubland and savanna ecosystems*. USDA-ARS Jornada Experimental Range, Las Cruces, N.M
- Hills RC, Reynolds SG (1969) Illustrations of soil moisture variability in selected areas and plots of different sizes. *J Hydrol* 8:27–47
- Hutchinson GE (1957) Population studies - animal ecology and demography - concluding remarks. *Cold Spring Harb Symp Quant Biol* 22:415–427

- Jackson RB, Caldwell MM (1993) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74:612–614
- Kaspar TC, Bland WL (1992) Soil-temperature and root-growth. *Soil Sci* 154:290–299
- Kearney M, Porter WP (2004) Mapping the fundamental niche: physiology, climate, and the distribution of a nocturnal lizard. *Ecology* 85:3119–3131
- Körner C (1998) A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115:445–459
- Körner C (2003) *Alpine plant life*, 2nd edn. Springer, Berlin
- Körner C, Cochrane P (1983) Influence of plant physiognomy on leaf temperature on clear midsummer days in the Snowy Mountains, Southeastern Australia. *Acta Oecol, Oecol Plant* 4:117–124
- Körner C, Demoraes J (1979) Water potential and diffusion resistance in alpine cushion plants on clear summerdays. *Oecol Plant* 14:109–120
- Körner C, Larcher W (1988) Plant life in cold climates. In: Long SF, Woodward FI (eds) *Plants and temperature*. The Company of Biology, Cambridge, pp 25–57
- Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *J Biogeogr* 31:713–732
- Körner C, Allison A, Hilscher H (1983) Altitudinal variation of leaf diffusive conductance and leaf anatomy in heliophytes of montane New-Guinea and their interrelation with microclimate. *Flora* 174:91–135
- Larcher W, Wagner J (1976) Temperature limits of CO<sub>2</sub> uptake and temperature resistance of leaves of alpine plants during growing season. *Oecol Plant* 11:361–374
- Larcher W, Kainmuller C, Wagner J (2010) Survival types of high mountain plants under extreme temperatures. *Flora* 205:3–18
- Lenoir J, Gegout JC, Marquet PA, de Ruffray P, Brisse H (2008) A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320:1768–1771
- Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao ZC (2007) Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) *Climate change 2007: The physical science basis*. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, pp 747–845
- Nogués-Bravo D, Araújo MB, Errea MP, Martínez-Rica JP (2007) Exposure of global mountain systems to climate warming during the 21st Century. *Glob Environ Change Hum Policy Dimens* 17:420–428
- Pauli H, Gottfried M, Reier K, Klettner C, Grabherr G (2007) Signals of range expansions and contractions of vascular plants in the high Alps: observations (1994–2004) at the GLORIA master site Schrankogel, Tyrol, Austria. *Glob Chang Biol* 13:147–156
- Pearson RG, Thuiller W, Araújo MB, Martínez-Meyer E, Brotons L, McClean C, Miles L, Segurado P, Dawson TP, Lees DC (2006) Model-based uncertainty in species range prediction. *J Biogeogr* 33:1704–1711
- Pearson RG, Raxworthy CJ, Nakamura M, Peterson AT (2007) Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. *J Biogeogr* 34:102–117
- Randin CF, Dirnbock T, Dullinger S, Zimmermann NE, Zappa M, Guisan A (2006) Are niche-based species distribution models transferable in space? *J Biogeogr* 33:1689–1703
- Randin CF, Engler R, Normand S, Zappa M, Zimmermann NE, Pearman PB, Vittoz P, Thuiller W, Guisan A (2009) Climate change and plant distribution: local models predict high-elevation persistence. *Glob Chang Biol* 15:1557–1569
- Reynolds SG (1974) A note on the relationship between size of area and soil moisture variability. *J Hydrol* 22:71–76
- Reynolds HL, Hungate BA, Iii FSC, D'Antonio CM (1997) Soil heterogeneity and plant competition in an annual grassland. *Ecology* 78:2076–2090
- Salisbury FB, Spomer GG (1964) Leaf temperatures of alpine plants in the field. *Planta* 60:497–505
- Scherrer D, Körner C (2010a) Infra-red thermometry of alpine landscapes challenges climatic warming projections. *Glob Chang Biol* 16:2602–2613
- Scherrer D, Körner C (2010b) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *J Biogeogr*. doi:10.1111/j.1365-2699.2010.02407.x
- Schröter D, Cramer W, Leemans R, Prentice IC, Araújo MB, Arnell NW, Bondeau A, Bugmann H, Carter TR, Gracia CA, de la Vega-Leinert AC, Erhard M, Ewert F, Glendinning M, House JJ, Kankaanpää S, Klein RJT, Lavorel S, Lindner M, Metzger MJ, Meyer J, Mitchell TD, Reginster I, Rounsevell M, Sabate S, Sitch S, Smith B, Smith J, Smith P, Sykes MT, Thonicke K, Thuiller W, Tuck G, Zaehle S, Zierl B (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science* 310:1333–1337
- Smith WK, Geller GN (1979) Plant transpiration at high elevations - theory, field-measurements, and comparisons with desert plants. *Oecologia* 41:109–122
- Sommer JH, Kreft H, Kier G, Jetz W, Mutke J, Barthlott W (2010) Projected impacts of climate change on regional capacities for global plant species richness. *Proc R Soc Lond B* 277:2271–2280
- Steinger T, Körner C, Schmid B (1996) Long-term persistence in a changing climate: DNA analysis suggests very old ages of clones of alpine *Carex curvula*. *Oecologia* 105:94–99
- Takasu K (1953) Leaf temperature under natural environments (Microclimatic study V). *Meml Coll Sci B* 20:179–188
- Theurillat JP, Guisan A (2001) Potential impact of climate change on vegetation in the European Alps: a review. *Clim Change* 50:77–109
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. *Nature* 427:145–148
- Thuiller W, Araújo MB, Pearson RG, Whittaker RJ, Brotons L, Lavorel S (2004) Biodiversity conservation: uncertainty in predictions of extinction risk. *Nature* 430:34
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proc Natl Acad Sci USA* 102:8245–8250
- Trivedi MR, Berry PM, Morecroft MD, Dawson TP (2008) Spatial scale affects bioclimate model projections of climate change impacts on mountain plants. *Glob Chang Biol* 14:1089–1103
- Walther GR (2004) Plants in a warmer world. *Perspect Plant Ecol Evol Syst* 6:169–185
- Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Walther GR, Beissner S, Burga CA (2005) Trends in the upward shift of alpine plants. *J Veg Sci* 16:541–548
- Zimmermann NE, Kienast F (1999) Predictive mapping of alpine grasslands in Switzerland: Species versus community approach. *J Veg Sci* 10:469–482