ORIGINAL ARTICLE

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

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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.

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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; Medellin *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. Gjærevoll, 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 km^2) 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 m^2 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 m^2 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

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

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 km^2 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 ± 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 ± 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 ± 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.
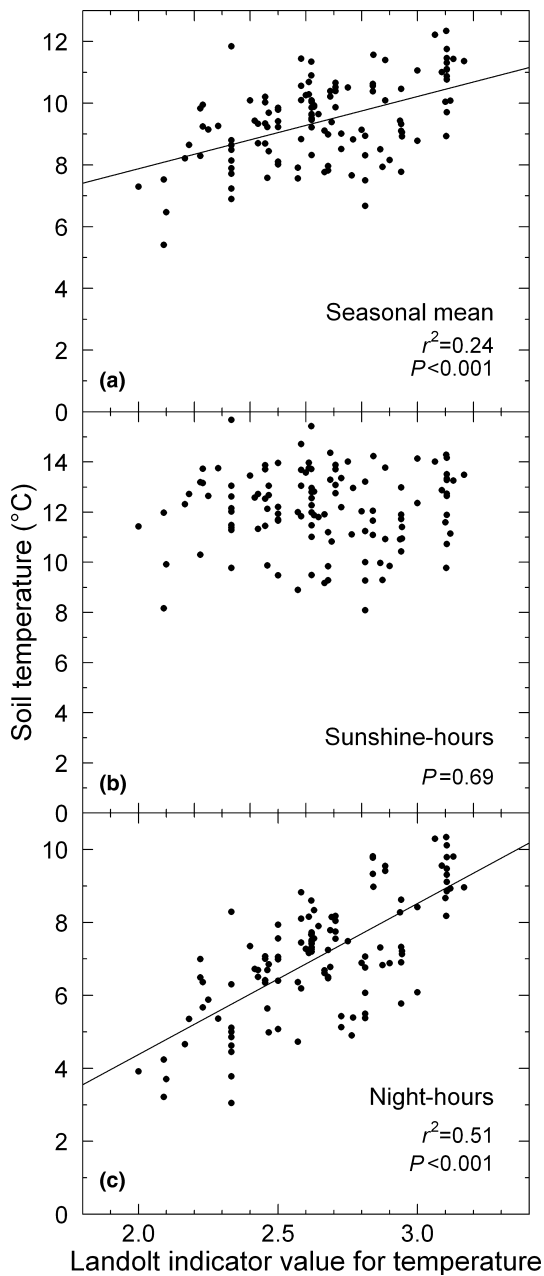
Figure 1 (a) Mean temperature indicator values per sampling plot (mean for all plant species present) and the seasonal mean soil temperature of the corresponding plot. (b) Mean temperature indicator values as in (a), plotted against the 'sunshine-hours' (radiation >800 W m^{-2}, 133 h). (c) As (b) but '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 ± 2.07 K (mean ± 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
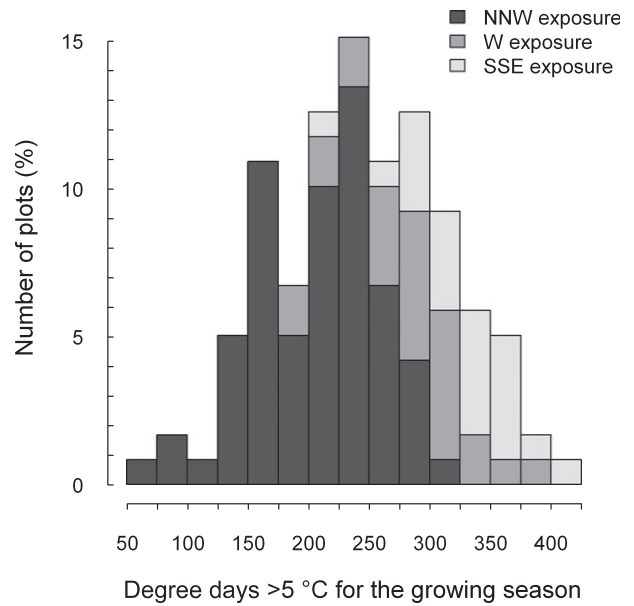

Figure 2 Degree days (>5 °C) for the complete (75 days) growing season for each soil temperature logger position on the north-north-west, west and south-south-east exposed slopes. The data were recorded from 22 June to 8 September 2008 at the Furka Pass in the Swiss Alps.

9.81 ± 1.16 °C (mean ± 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, $P < 0.001$,
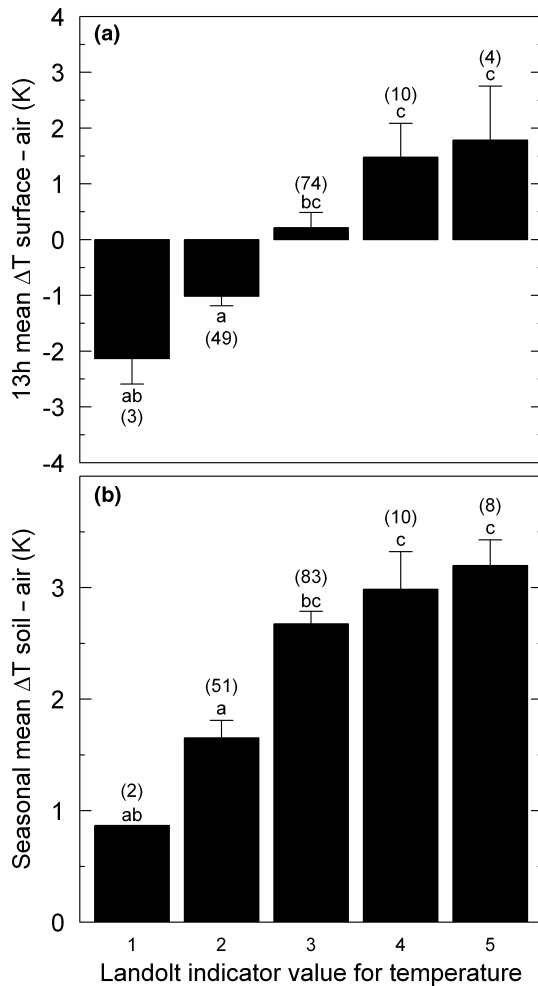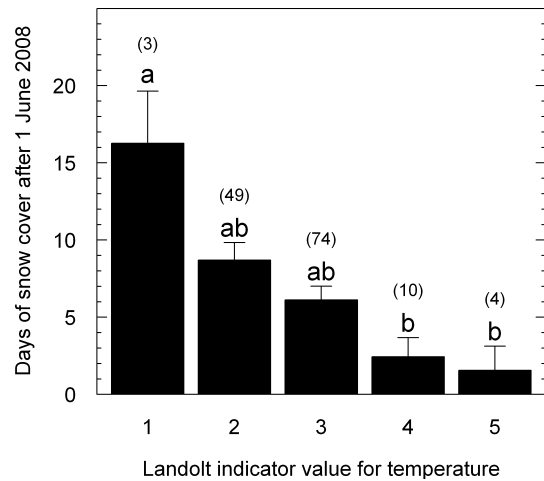
Figure 3 (a) Mean temperature difference ΔT (surface temperature minus air temperature; 07:00–20:00 h) per 'Landolt-T-Group' (all plant species assigned to the same indicator value for temperature according to Landolt, 1977). (b) Seasonal differences in mean soil temperature minus air temperature for 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.

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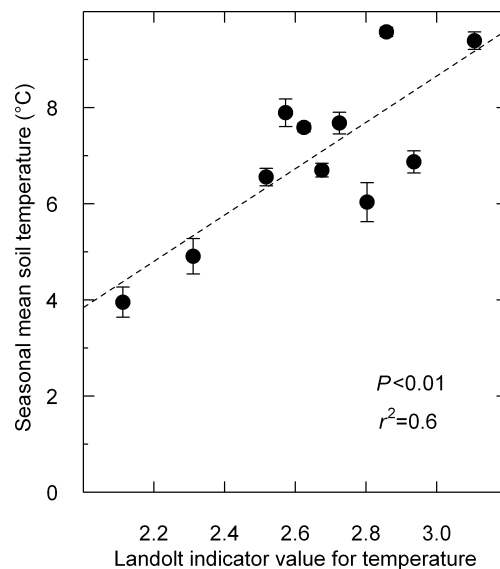
Figure 5 Correlation of the mean temperature indicator values of different vegetation units (cluster) and the corresponding soil temperature ('seasonal mean', 22 June to 8 September 2008). Each data point represents a vegetation unit and the error bars indicate the standard error.

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).

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
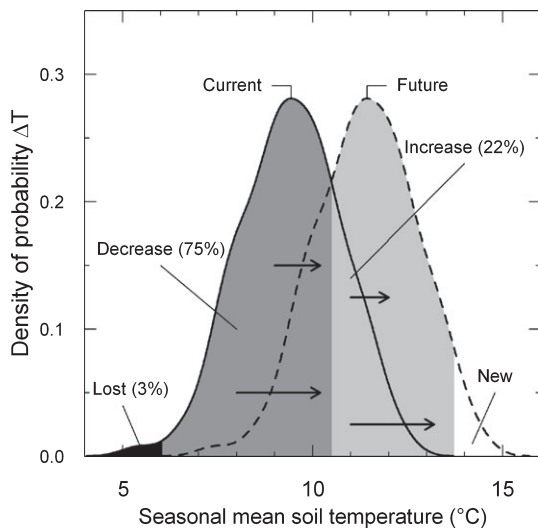
Figure 6 The density distribution of current 'seasonal mean' soil temperatures ('current') and in a 2 K warmer scenario ('future'). 'Lost' indicates the micro-habitat temperatures which disappear in a 2 K warmer scenario within our study area, 'decrease' indicates the micro-habitat temperatures that 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 °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 5–7 °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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