



A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming

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Abstract. Induced by global warming, mountain plant species are migrating upwards. Species inhabiting the nival zone of today are threatened by competitors which move from the alpine zone towards the summits. The manner in which species move depends on their abilities to cope with microtopographical situations. We present a spatially explicit predictive model which draws scenarios of future species distribution patterns at a typical high mountain of the European Alps. The altitudinal temperature gradient is examined. Based on the lapse rate and on definitions of topographical niches of species, a +1 °C- and a +2 °C-warming scenario are modelled using a fine-scaled digital elevation model.

Nival species will lose area and become restricted to specific topographical situations. Alpine and subnival grassland species are predicted to expand their area, mainly along stable surface situations. Whether the migration will take place as a filling or a moving process is specific to the particular species. Overall, biodiversity is apparently not threatened on the decadal scale. In special cases, however, genetic losses are likely both on a local and on a regional scale.

Key words. Climate change, mountain vegetation, altitudinal gradient, predictive model, digital elevation model, European Alps.

INTRODUCTION

Many authors have suggested that mountain biota will move upwards as a result of global climate warming (e.g. Braun-Blanquet, 1957; Nilsson & Pitt, 1991; Ozenda & Borel, 1991). Concrete evidence of this phenomenon has already been provided (Gottfried *et al.* 1994; Grabherr *et al.* 1994, 1999; Pauli *et al.* 1996). The European Alps, like all mountain systems, show a clear altitudinal zonation of their vegetation (see, e.g. Grabherr, 1997). Most plant species are restricted to distinct altitudinal ranges, forming typical high mountain plant communities (e.g. Grabherr & Mucina, 1993) that are assembled in pronounced vegetation belts. Especially endemic species often show narrow altitudinal distribution patterns (Grabherr *et al.*, 1995). As mountains are cone-shaped, the uppermost vegetation units – species, as well as plant communities – are, in principle, threatened by more competitive species from below.

Upward migration, however, does not proceed

uniformly. Individual species move at different speeds (Grabherr *et al.*, 1995), and possess species-specific potentials to use migration paths. The most important features of plant migration paths in high mountains are relief and surface texture. Plants which are rock specialists move along stable ridges and crests, whereas specialists for unstable grounds can shift along screes. Gottfried *et al.* (1994) and Pauli *et al.* (1996) observed that the upward movement of species is most pronounced on mountains which offer both types of habitats.

The uppermost two altitudinal belts of the Alps, the so-called alpine and nival zone, are environments well suited for investigating such effects because they are more or less free of direct human impact. The main ecological driving force is climate, with temperature and the duration of the snow cover as key factors. The microclimatic patterns, however, are modified by pronounced microtopographical changes over short distances (Körner, 1995a). Species of these environments are strongly differentiated according to

their microtopographical niches (Gottfried *et al.* 1998). Most likely, this reflects the different capabilities of each species to deal with, firstly, topographical features, such as stability or instability, and, secondly, microclimatic features, such as temperatures near the surface or the length of the snow period. A general macro-climatic change leads to various changes in the microclimatic patterns. The manner in which plants follow these climatic changes in a spatial sense depends intrinsically on their abilities to move, i.e. to overcome topographical migration barriers. The phenomenon of upward migration must be viewed against this background.

Mountain macro-climatic features have been thoroughly studied (for a review, see Barry, 1992). Time series of climatic data from the highest weather station in Austria (at Sonnblick, 3106 m) showed essentially a warming trend similar to that observed globally (Auer *et al.* 1993). However, the microclimatic features of high mountain systems are understood rather poorly, mainly due to methodological difficulties of investigation and comparison. The altitudinal temperature gradient varies from season to season, mountain to mountain, and from one elevation section to the other (Wagner, 1930).

Here, we present a case study focusing on a typical high mountain of the Alps. Its altitudinal temperature gradient was determined. Based on this gradient and on the topographical niches of species, changes in species distribution patterns induced by climate warming were modelled at a resolution of 1 m²; this matches the fine-scaled ecological patterning of the specific environment under consideration.

STUDY AREA

The Schrankogel (3497 m, Austria) exhibits all typical features of a high siliceous mountain of the Alps. Figure 1(a) shows its south-, south-east-, and south-west-facing slopes. The immediate surroundings of the mountain are still heavily glaciated, although these glaciers are currently shrinking rapidly. The slope system is structured by pronounced ridges, intersected by hollows and gorges with wide debris cones at their bases (see also numbers indicated in Fig. 1b and in the figure caption). On stable surfaces, closed alpine swards reach up to about 2850–3000 m. From here up to 3100–3200 m the grassland disintegrates to pioneer swards. This transition zone is called the alpine-nival ecotone. Above it, the pioneer swards are replaced

by scattered nival vegetation, which is dominated by specialists for scree and rock habitats, low temperatures and long duration of snow cover. Even these species decline near the summit, and only a few plant individuals inhabit the immediate summit area. The model area (Fig. 1a,b) comprises all important situations of the slope system and is centred at the alpine-nival ecotone itself. The upper summit area was excluded because of its inaccessible slopes.

METHODS

Altitudinal temperature gradients

Thirty-three temperature loggers (TINYTAG) were used to measure the altitudinal temperature lapse rate. They consist of a thermistor and a minicomputer combined in a box measuring 5 × 6 cm. The instruments were mounted so that they measure the air or snow temperature at 1–3 cm above the relief surface. This departs from the common approach of measuring air temperatures 2 m above the surface and ensures that exactly those temperatures which are effective for plant life were measured. Direct solar radiation to the thermistor was avoided. The devices were distributed over the entire slope system, from 2900 up to 3475 m. In this paper we use the first available annual series from 13 August 1997 to 11 August 1998, with a sampling interval of 1.5 h (i.e. 16 counts per day). Separately for each instrument the following indices were calculated from these series (Fig. 2): *annual mean*, averaging all 5824 measurements (in Fig. 2 termed as annual 24 h mean to distinguish from other indices); *annual daytime mean*, averaging measurements from 9 am to 4.30 pm; *annual night-time mean*, averaging measurements from 9 pm to 4.30 am; *monthly mean* (in Fig. 2 termed as monthly 24 h mean); *monthly daytime mean* and *monthly night-time mean*, averaging measurements within the same time span as for the annual indices, but separated for each month. The altitudinal temperature lapse rates were calculated by linear regressions of these indices with the elevations at which the instruments were placed. The correlation coefficients (labelled as R of lapse rate) are included in Fig. 2. Figure 3 shows three typical gradient patterns.

Warming scenarios for species distribution patterns

In a previous study we established around 1000 permanent plots (1 × 1 m each) within the model area

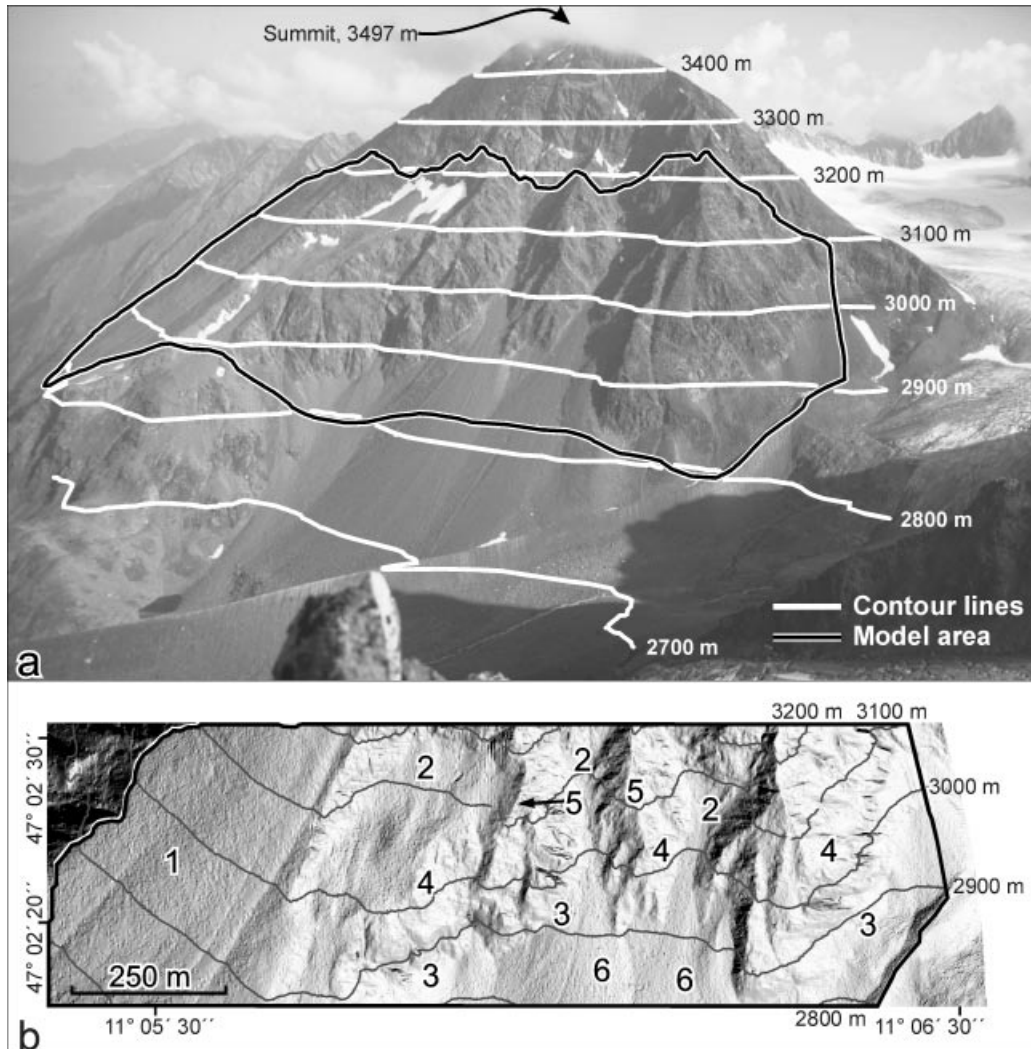


Fig. 1. a) Slope system of Schrankogel (Tyrol, Austria), oblique view from the south-east. In the foreground the pronounced crest of the moraine of Schwarzenbergferner; b) vertical view of the model area (thick black line). Digital elevation model (1×1 m horizontal resolution, 0.1 m vertical tolerance), shaded from south-east. Thin black lines=contour lines. Numbers indicate the following important topographical situations: 1=well pronounced, south-west slope, rich in stable and unstable scree; 2=hollows with scree; 3=downslope areas below major ridges which structure the main slope; 4=upslope areas on major ridges; 5=ridge tops; 6=wide debris cones below major ridges.

to start a monitoring programme of climate change-induced migration effects. In each of these quadrats (hereafter referred to as *sampled plots*) the cover of each vascular plant was recorded. The study is described in more detail in Gottfried *et al.* (1998) and Pauli *et al.* (1998).

Gottfried *et al.* (1998) used a fine-scaled digital

elevation model (DEM) and a geographical information system (GIS; ARC/INFO; ESRI, 1995) to extrapolate the vegetation patterns found in the sampled plots to all 1×1 m pixels (hereafter referred to as *predicted plots*) of the entire model area (consisting of a total of about 650 000 pixels; Fig. 1). First, topographical niches of the species were defined by a

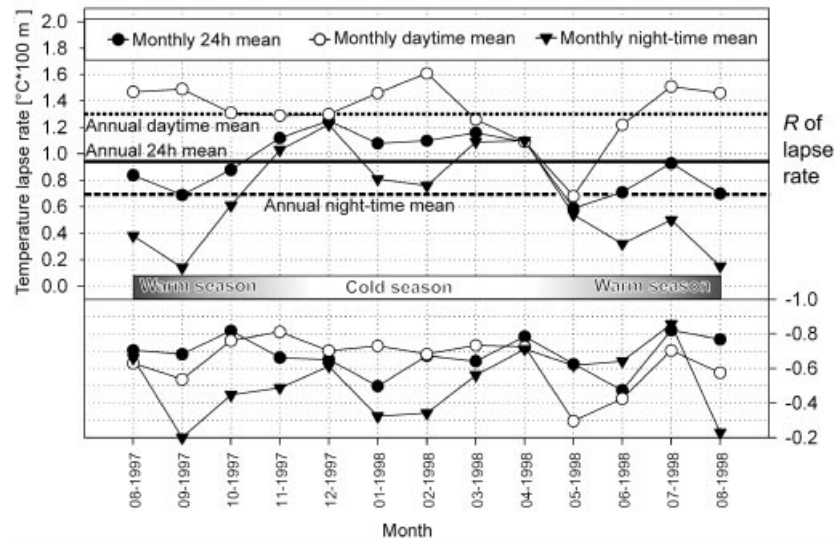


Fig. 2. Top: annual and monthly means of the altitudinal temperature gradient. Bottom: correlations of monthly means with altitude (R of lapse rate).

direct gradient analysis of the sampled plot data using canonical correspondence analysis (CCA; ter Braak, 1986). This method aims to interpret observed species distribution patterns by relating them to observed environmental gradients. The environmental gradients are weighted according to their importance in explaining the dispersion in the species data. Their weights are indicated by 'canonical coefficients', a measure related to regression coefficients. From the DEM, numerous topographical descriptors were derived using GIS methods; these descriptors of environmental gradients included altitude, slope, aspect, upslope area, distance to ridges, distance to runoff paths, relief roughness, etc. Moreover, these descriptors were calculated for several levels of resolution to include effects of microtopography, as well as of macro-topography, into the analysis: while the topographical niches of some species were strongly characterized by microrelief properties (on a spatial scale of 1–100 m²), the distributions of other species were correlated with macro-relief properties (on a scale of 10 000–50 000 m²). These topographical data accounted for 30% of the species variation in the sampled plots; taking into account the randomness of the scattered high alpine vegetation patterns, this value is quite high. Nevertheless, some gradients in the species data obviously remained unexplained.

In a second step, the topographical niches defined

by the CCA were used to calculate species distribution patterns for the entire model area. Figure 4 shows the conceptual scheme of the method. In a CCA ordination diagram three important types of information can be graphed: the position of species (for clarity not shown in Fig. 4); the position of samples [referred to as sampled plots (sp) and predicted plots (pp) in Fig. 4]; and the direction of environmental gradients that structure the distribution of the species (eg 1–3 in Fig. 4). On the one hand, the position of each plot in such an ordination diagram depends on the species collection of that plot. On the other hand, its position approximates its relations to the involved environmental gradients. These positions are calculated using the environmental variables of the plots (derived from the DEM), weighted by the canonical coefficients. The positions of both types of plots – those which were sampled in the field (sampled plots) and those whose species collection should be predicted (predicted plots) – are calculated in this manner, but the weighting factors used are based only on the information derived from sampled plots. Next, for each predicted plot the nearest neighbouring sampled plot in the ecological space is searched. The species collection of this sampled plot is assigned to the predicted plot. By predicting the species collection of all pixels in the model area in this way, spatially explicit species distribution patterns can be derived; then they can be visualized in GIS maps.

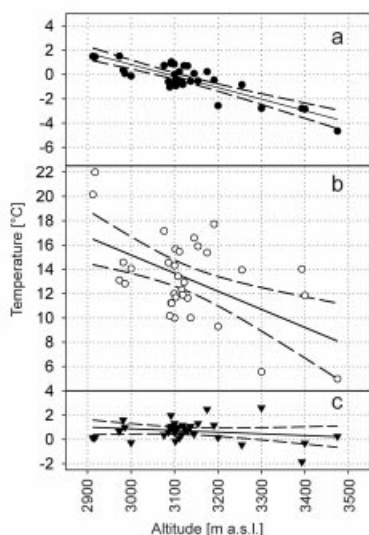


Fig. 3. Three typical patterns of temperature decrease as a function of altitude, measured by 33 instruments at different time intervals. The slopes of the regression lines (solid lines) denote the lapse rates (see Fig. 2 for the numeric values). The 95%-confidence interval of the regressions is plotted in dashed lines. a) annual 24 h mean; b) monthly daytime mean of September 1997; c) monthly night-time mean of September 1997. Further explanations are given in the text.

For methodological details of CCA see ter Braak (1987–1992, 1995), further information about the extrapolation procedure can be found in Gottfried *et al.* (1998).

The results of such predictions, which form the basis of the present study, are shown in the diagrams at the bottoms of Figs 5,6,7. They reflect the modelled current situations on a 1-m² scale (the resolution of the underlying DEM) and are referred to as +0°-scenarios hereafter. Kappa values (Cohen, 1960; Monserud & Leemans, 1992) of 0.41 (*Androsace alpina*), 0.45 (*Oreochloa disticha*), 0.3 (*Erigeron uniflorus*), 0.52 (*Sedum alpestre*), 0.23 (*Saxifraga exarata*), and 0.28 (*Saxifraga oppositifolia*) are a measure of the accuracy of the model; Gottfried *et al.* (1998).

The rectangular structures seen in Figs 5, 6 and 7 are methodological artefacts: some of the fine-scaled topographical descriptors computed in the GIS could not be smoothed continuously to coarser resolution

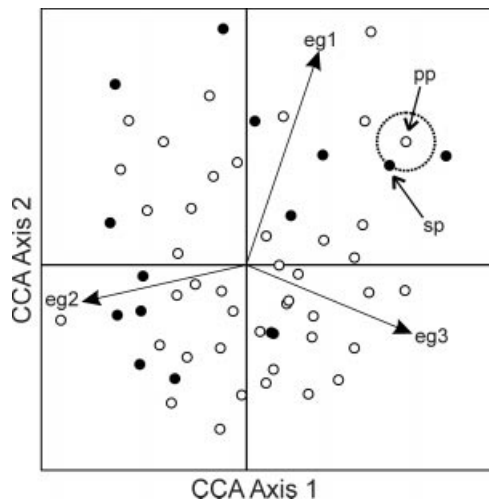


Fig. 4. Conceptual scheme of the extrapolation method. The CCA ordination diagram shows two types of information in a multidimensional ecological space (two dimensions – CCA Axis 1 and 2 – are shown here): the direction of environmental gradients (arrows eg 1–3) which structure the distribution of the species (species' positions are not shown here for clarity), and the position of the samples, denoted as sampled plots (i.e. plots whose species collection were sampled in the field; sp; black dots) and predicted plots (i.e. plots whose species collections are to be predicted; pp; open dots). Dotted circle: nearest neighbour search around pp for sp. Once the nearest neighbouring sp for a pp is found, the species collection of sp is assigned to pp.

levels; instead, they had to be resampled in steps for larger cell sizes. These macro-relief factors have varying influences on the prediction outputs in different parts of the model area (see Gottfried 1998; for more details).

In this work, which represents the third step, we used the altitude factor of the described model to perform extrapolations for two warming scenarios. Assuming that the altitudinal ranges of species are determined by temperature and knowing the temperature lapse rate, future species distribution patterns for a temperature increase of +1 and +2 °C (referred to as +1°-scenarios and +2°-scenarios, respectively) were predicted. This was achieved by increasing the values of the altitude factor in the environmental data set of the sampled plots corresponding to the temperature lapse rate; then the extrapolation for the predicted plots was rerun. The approach used in these predictions implies that species collections growing today at lower and, hence, warmer situations will occur in a warmer climate at similar

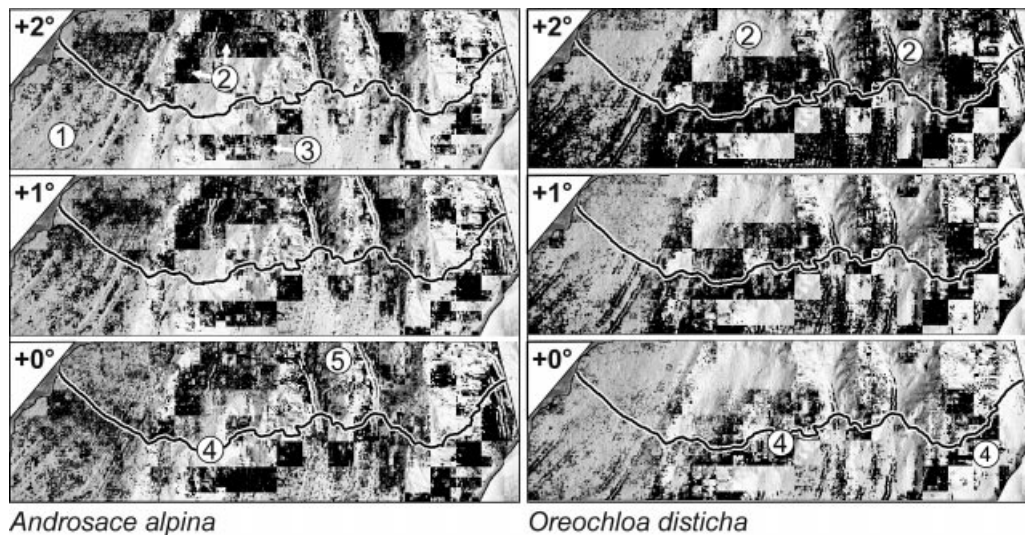


Fig. 5. Predicted distribution patterns of *Androsace alpina* and *Oreochloa disticha*. Bottom: current situation, i.e. +0°-scenario; centre: +1°-scenario; top: +2°-scenario. Black and white line = 3000 m contour line.

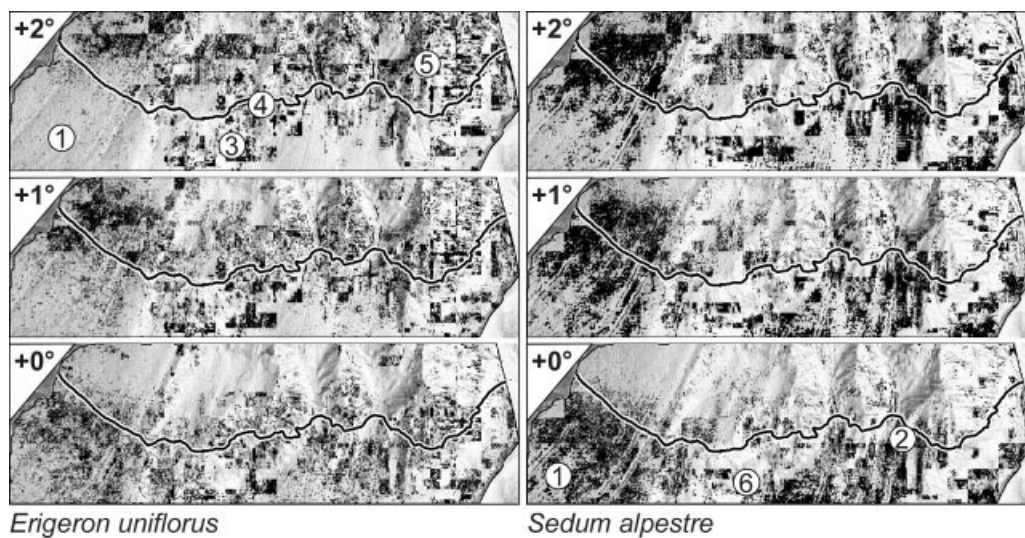


Fig. 6. Predicted distribution patterns of *Erigeron uniflorus* and *Sedum alpestre*. Bottom: current situation, i.e. +0°-scenario; centre: +1°-scenario; top: +2°-scenario. Black and white line = 3000 m contour line.

topographical situations, but at higher altitudes. A combination of GIS and BASIC programs was used for the calculations.

The nomenclature used follows Ehrendorfer (1973) for species, and Grabherr & Mucina (1993) for plant communities.

RESULTS

Altitudinal temperature gradients

The annual mean temperature lapse rate at Schrankogel near the relief surface (indicated as annual 24 h mean

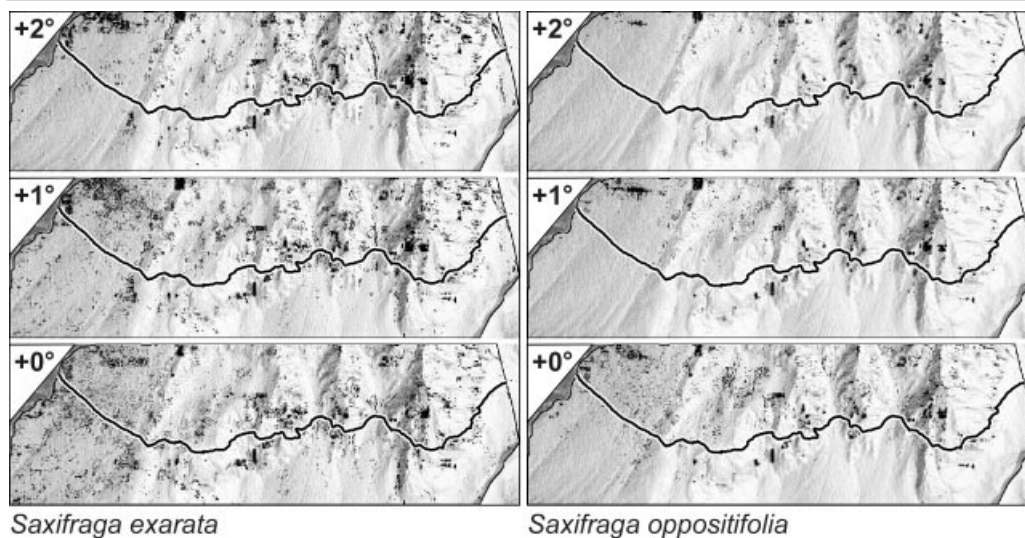


Fig. 7. Predicted distribution patterns of *Saxifraga exarata* and *S. oppositifolia*. Bottom: current situation, i.e. +0°-scenario; centre: +1°-scenario; top: +2°-scenario. Black and white line = 3000 m contour line.

in Fig. 2) amounted to 0.95 °C per 100 m altitudinal increase. The annual daytime and night-time lapse rates were 1.31 and 0.7 °C, respectively. These three gradients change with the seasons, which is shown by the monthly 24 h means, the monthly daytime means, and the monthly night-time means. Both their absolute values, and their relative magnitude varied. They were identical only in the early and late winter season, and were remarkably different through the summer and the mid-winter (see Discussion for possible reasons).

The correlations between the measured means of the 33 instruments and their altitudes, indicated in Fig. 2 as R of lapse rate, are negative because T generally decreases with increasing altitude. In absolute values the correlations are mostly well above 0.5, thus denoting convincing gradients. Only a few R -values, mainly those of night-time gradients in summer and mid-winter, are low. The R -values of the annual mean lapse rates were -0.85 for the 24 h mean, -0.82 for the daytime mean, and -0.6 for the night-time mean.

Figure 3 shows three typical gradient patterns, the annual 24 h mean (a), as well as the monthly daytime mean (b) and the monthly night-time mean (c) of September 1997 measured at 33 positions in different altitudes. The linear shape of the relationship between temperature and altitude demonstrated by the three plots is typical for all monthly periods studied. But the slopes of these gradients vary remarkably: e.g. the daytime mean lapse rate in September 1997 (b) was

almost twice as steep as the annual 24 h mean lapse rate (a); by contrast, the altitudinal night-time gradient in this month (c) did not deviate significantly from zero. The latter finding explains why correlation indices for some night-time lapse rates are so low (compare Fig. 2).

The overall annual mean (i.e. the annual 24 h mean) lapse rate of 0.95 °C per 100 m was used for the subsequent modelling runs.

Warming scenarios for species distribution patterns

Androsace alpina, a character species of the alliance *Androsacion alpinae*, i.e. the alpine-nival cushion plant communities at siliceous screes of the Alps, is one of the common species of the subnival and nival scree habitats of the slope system. Today (Fig. 5, bottom left) it is well distributed over the model area, avoiding only the most pronounced stable areas around ridges (4, 5; these and other numbers in Figs 5, 6 and 7, as well as in the text, were introduced in Fig. 1b; for references to altitudes see Fig. 1b as well). With warming, *A. alpina* is predicted to disappear from many places and to concentrate in areas near the summit, mostly in hollows and gorges (2). According to the scenario, the migration is most pronounced on the wide south-west-facing slope (1), where the species will be almost completely wiped out at lower altitudes. In

more complicated terrain situations below major ridges (3), it seems to be more resistant. Other specialists for high altitudes such as *Poa laxa*, *Ranunculus glacialis*, or *Saxifraga bryoides* showed similar behaviour in our models.

The pressure on *A. alpina* will be caused mainly by the invasion of pioneer swards, represented by *Oreochloa disticha* (Fig. 5, right). The species is frequent in alpine swards of *Caricetum curvulae*, but dominant in pioneer swards which reach the subnival zone. Starting from favourable habitats of today at south-east-facing slopes (4), it is predicted to expand its area significantly, avoiding only conditions of pronounced instability and snow pressure in hollows and gorges (2). These habitats will therefore act as refugia for *A. alpina*. Note that the distribution pattern changes of *O. disticha* will occur mainly through a filling process rather than by upward movement alone (see Grabherr *et al.*, 1995). Outpost populations of this species can already be found today in the higher parts of the model area, but its occurrence is scattered and restricted to spatially narrow habitats. These are likely starting points for the expansion of their area by filling the nival habitats in between.

Carex curvula (not shown here) matches essentially the current distribution pattern of *O. disticha*, but it is restricted to somewhat lower altitudes; furthermore, it does not extend beyond the core areas of *O. disticha*. Early successional stages of closed alpine swards of *Caricetum curvulae* are currently present at these core areas and are predicted to start their expansion from there.

Erigeron uniflorus (Fig. 6, left) plays an intermediate role between *A. alpina* and *O. disticha* at Schrankogel. It is a frequent member of the subnival pioneer swards, but extends today widely into the lower Androsacion habitats. During upward migration, it is likely to compete with *A. alpina* by using similar migration paths. Again, its movement will be pronounced on the homogeneous south-west slope (1) and will be more reserved in complicated situations (3, 4, 5). While presently more or less restricted to the subnival zone, this species is predicted to leave this lower part of the model area during warming.

Another species which clearly does not extend beyond the subnival belt of today is *Sedum alpestre* (Fig. 6, right). This scree specialist avoids rocks more or less completely and plays an important role in the community *Sieversio-Oxyrietum digynae* (Pauli *et al.* 1999). This Androsacion community is typical for cold and moist habitats with a lot of scree and a long lasting

snow cover. Such situations are found today not only in gorges and hollows (2), but also on debris cones (6) and on the south-west slope (1) due to the varying microtopography that is found there. With warming, *S. alpestre* will find suitable habitats at higher altitudes, but such habitats occur less extensively than in lower zones.

Two *Saxifraga* species – *S. exarata* (Fig. 7, left) and *S. oppositifolia* (Fig. 7, right) – serve as examples of species which are not widespread on Schrankogel in terms of surface cover, but whose role lies more in their contribution to biodiversity. They show the same general migration patterns during the warming scenarios, with *S. oppositifolia* being even more threatened by habitat loss and being concentrated at smaller refugia than *S. exarata*.

DISCUSSION AND CONCLUSIONS

Altitudinal temperature gradients

The most remarkable feature of the measured temperature gradients is their tendency to be steeper in winter than in summer. This is in clear contrast to the literature. Ozenda & Borel (1991) report 0.7 °C/100 m as summer lapse rate and 0.4 °C/100 m as winter lapse rate relevant for the Alps, with an annual mean of 0.55 °C/100 m. In the Austrian Alps, Hann (1906; cited in Barry, 1992) found the following lapse rates between Kolm Saigurn, 1600 m, and the summit of Sonnblick, 3106 m: winter 0.49 °C/100 m at 2 am, 0.66 °C/100 m at midday; summer: 0.6 °C/100 m at 2 am, 0.89 °C/100 m at midday. However, our measurements do fit Hann's data in that night-time gradients are less pronounced than daytime gradients.

The correlations between the elevations of the measurement locations and temperature (i.e. *R* of lapse rate; Fig. 2) tend to be slightly higher in summer, at least for the 24 h mean and the daytime mean. This is in accordance with Pielke & Mehling (1977), who also found correlations to be highest in summer (with an *R* of -0.95), using linear regression analysis to determine lapse rates for an area in north-western Virginia. The weakest (in terms of *R*) and flattest gradients in our data were measured at night-time, especially in late summer (Figs 2 and 3c). Local temperature inversions which occur commonly in that season are the most likely explanation. However, most of the correlations are sufficiently high to confirm the calculated *T* gradients.

Two important factors clearly contribute to the differences between our measurements and the literature. Firstly, we measured a comparably short elevation section of about 600 m; this makes it difficult to draw comparisons with lapse rates determined from altitudinal differences of 1500 m or more. Secondly and more important, we measured temperatures a few centimetres above the surface. Many of the counts refer in fact to snow temperatures rather than to air temperatures. This may lead to the generally steep temperature gradients at this slope system, which is characterized by snowy precipitation and melting processes throughout most of the year. Temperature gradients on slopes are generally known to be steeper during snow melting (Barry, 1992).

Not surprisingly, measuring temperature on surfaces with or without snow has strong effects on the differences between daytime and night-time gradients. While these values differed significantly from each other during most of the year, they were identical in December and from March to May, presumably because snow buffered the temperature fluctuations occurring from night to day. The situation of each instrument (i.e. covered by snow or not) can be determined by autoregression analysis of counts neighbouring in time. An initial examination of the data revealed that the slope was completely snow-covered in these months, while snow seemed to be blown away at many locations during mid-winter. The transition from May to June, when the gap between daytime and night-time gradients widens again, marks the start of the melting process.

Which parts of the temperature regime determine the distribution patterns of high mountain plants is currently not fully understood. Although much information is available about timberline patterns (Tranquillini, 1979), less is known about which factors affect high alpine and nival species. Körner (1995b) argued that summer night-time temperatures overrule daytime temperatures as a determinant of high mountain plant growth. However, the weakly pronounced lapse rates we found for night-time temperatures may indicate that night-time temperature gradients are of minor importance in explaining the altitudinal zonation of species distributions. Clearly, more detailed examinations of the data and additional annual series are necessary to answer this question. Moreover, factors other than the altitudinal T gradients, such as temperature accumulation, snow-melting patterns, or frost regimes, are important. We are currently working on such analyses, and expect

results to improve when more measurement series will have been accumulated.

The model

The considerations discussed so far led to the decision to use the annual mean lapse rate of $0.95\text{ }^{\circ}\text{C}/100\text{ m}$ for the present study. Although this value exceeds by far the average annual mean given in the literature, it is the true lapse rate measured on Schrankogel, at least for 1997–98. It represents a compromise between night-time and daytime gradients, and between seasonal fluctuations. Moreover, the exact value of the lapse rate is not critical for the presented type of model. Flatter lapse rates, e.g. the $0.6\text{ }^{\circ}\text{C}$ summer night rate of Hann (1906), would lead to similar results even earlier (the $+1^{\circ}$ -scenario would be reached after an increase in temperature of $0.63\text{ }^{\circ}\text{C}$ and the $+2^{\circ}$ -scenario after an increase of $1.26\text{ }^{\circ}\text{C}$, respectively). This supports the idea that vegetation pattern changes will be related not solely to T lapse rates, but also to the rate of increase of the atmospheric temperature itself.

The presented model is 'predictive' in two ways: First, it predicts the current vegetation patterns of the model area based on a certain number of sampled plots. These results have already been evaluated (see above). Second, it predicts future distribution patterns. These predictions can be evaluated when the results of the monitoring effort accompanying this study become available. Until then, they should be viewed – and are referred to – as scenarios rather than as exact forecasts.

The advantages and drawbacks of treating all species with the same basic response model (i.e. the Gaussian model of CCA) were discussed in Gottfried *et al.* (1998). Another criticism is that such static models do not take into account the transient nature of vegetation shifts. This concerns rates of change in time and space, with plants developing tillers and seeds from year to year while migrating stepwise over short distances, and questions of the niche concept, with species having the potential to change their niche during environmental changes. Clearly, the term 'migration', as used in the result section above, does not address questions of seed dispersal and successful establishment. It only reflects the stepwise manner in which species will potentially follow the changing locations of their favoured habitats.

These limitations can only be overcome by the use of mechanistic modelling, which treats species and even single plants and their life histories separately and which takes into account their relationships to climate

and topography in a causal manner. Such models should be applied to high mountain environments as soon as possible, but they will intrinsically require the input from monitoring of both microclimatic changes and changes in vegetation patterns. The precondition for the development of such models, however, is a detailed understanding of the ecophysiological key processes which determine the life histories of the species under consideration. For most alpine and nival plants, this knowledge is still missing.

Warming scenarios

'Winners' and 'losers' of the upward migration effect will emerge. In some studies, the alpine timberline was observed not to move as rapidly as climate change would imply. This may be due to a general conservative behaviour of this ecotone as a result of grazing effects and of shelter effects due to parent trees (e.g. Crawford, 1989; Holtmeier, 1994; Hättenschwiler & Körner, 1995). At the nival-alpine ecotone, on the other hand, grazing is virtually absent and shelter effects should be less pronounced in a single-layered vegetation. Although the moving rates of some high mountain species lagged behind the ongoing warming (Grabherr *et al.*, 1995), this ecotone is likely to react more sensitively to climate change than the timberline. Thus, the alpine belt may enhance its area and alpine and high alpine species like *Carex curvula* or *Oreochloa disticha* may 'win'. Species centred in or restricted to today's subnival and nival areas will therefore lose' and become concentrated to specific topographical situations not easily accessible for grassland species.

In the medium term (decadal scale), depending on the speed of global warming, biodiversity is not likely to decrease markedly in terms of numbers of species. High altitude specialist species, if widespread (like *Androsace alpina*), will reach refugium habitats without severe problems. Nevertheless, species of local rarity, exemplified here by *Saxifraga exarata* and *S. oppositifolia*, will probably become extinct on some mountains. Caution must be exercised in extrapolating such examples of local effects to a wider region: e.g. while *S. oppositifolia* is rare at Schrankogel, it was observed to be widespread on other high summits of the Alps.

In special situations, however, true genetic losses are possible, even in the medium term. For instance *Draba ladina*, an endemic Brassicaceae, restricted to a few summit areas within a small region of Eastern Switzerland (Braun-Blanquet, 1958; Grabherr *et al.*

1999), is severely threatened with extinction. A number of other similar examples can be found throughout the Alps.

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REFERENCES

- Auer, I., Böhm, R. & Mohnl, H. (1993) Die hochalpinen Klimaschwankungen der letzten 105 Jahre beschrieben durch Zeitreihenanalysen der auf dem Sonnblick gemessenen Klimaelemente. *Jahresbericht des Sonnblickvereins*, **88-89**, 3-36.
- Barry, R.G. (1992) *Mountain weather and climate*. 2nd edn, p. 402. Routledge, London.
- Braun-Blanquet, J. (1957) Ein Jahrhundert Florenwandel am Piz Linard (3414 m). Extrait du *Bulletin Jardin Botanique Etat Bruxelles*, volumes jubilaire Walter Robyns. Station Internationale de Geobotanique Mediterraneenne et Alpine, Montpelier, 221-232.
- Braun-Blanquet, J. (1958) Über die obersten Grenzen pflanzlichen Lebens im Gipfelbereich des Schweizerischen Nationalparks. *Kommission der Schweizerischen Naturforschenden Gesellschaft zu Wissenschaftlichen Erforschung des Nationalparks*, Bd. **6**, 119-142.
- Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurement*, **20**, 37-46.
- Crawford, R.M. (1989). *Studies in plant survival*, p. 296. Blackwell, Oxford.
- Ehrendorfer, F., ed. (1973). *Liste der Gefäßpflanzen Mitteleuropas*. 2nd edn, p. 318. Fischer, Stuttgart.
- ESRI (1995) *ARC/INFO*. Environmental Systems Research Institute, Inc. 1982-1995, Version 7.0.3.
- Gottfried, M., Pauli, H. & Grabherr, G. (1994) Die Alpen im 'Treibhaus': Nachweise für das erwärmungsbedingte Höhersteigen der alpinen und nivalen Vegetation. *Jahrbuch des Vereins zum Schutz Bergwelt*, **59**, 13-27.
- Gottfried, M., Pauli, H. & Grabherr, G. (1998) Prediction of Vegetation Patterns at the Limits of Plant Life: a New View of the Alpine-Nival Ecotone. *Arctic and Alpine Research*, **30**, 207-221.

- Grabherr, G. (1997) The high-mountain ecosystems of the Alps. *Ecosystems of the world 3. Polar and alpine tundra* (ed. by F. Wielgolaski), Elsevier, Amsterdam, pp. 97–121.
- Grabherr, G., Gottfried, M., Gruber, A. & Pauli, H. (1995) Patterns and current changes in alpine plant diversity. *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences* (ed. by F.S. Chapin III & C. Körner), Springer, Berlin, pp. 167–181.
- Grabherr, G., Gottfried, M. & Pauli, H. (1994) Climate effects on mountain plants. *Nature*, **369**, 448.
- Grabherr, G., Gottfried, M. & Pauli, H. (2000) Long term monitoring of mountain peaks in the Alps. *Vegetation monitoring/global change. Tasks for vegetation science* (ed. by C. Burga & A. Kratochwil), Kluwer, Dordrecht, in press.
- Grabherr, G. & Mucina, L., eds. (1993). *Die Pflanzengesellschaften österreicher. Teil 2: Natürliche Waldfreie Vegetation*, p. 523. Fischer, Jena.
- Hann, J. von, Hättenschwiler, S. & Körner, C. (1995) Responses to recent climate warming of *Pinus sylvestris* and *Pinus cembra* within their montane transition zone in the Swiss Alps. *Journal of Vegetation Science*, **6**, 357–368.
- Holtmeier, F.K. (1994) Ecological aspects of climatically timberline fluctuations: review and outlook. *Mountain environments in changing climates* (ed. by M. Beniston), Routledge, London, pp. 220–233.
- Körner, C. (1995a) Alpine plant diversity: A global survey and functional interpretations. *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences* (ed. by F.S. Chapin III & C. Körner), Springer, Berlin, pp. 45–62.
- Körner, C. (1995b) Impact of atmospheric changes on alpine vegetation: the ecophysiological perspective. *Potential ecological impacts of climate change in the Alps and Fennoscandian mountains* (ed. by A. Guisan *et al.*) Conserv. Jard. Bot. Genève, pp. 113–120.
- Monserud, R.A. & Leemans, R. (1992) Comparing global vegetation maps with the Kappa Statistic. *Ecological Modelling*, **62**, 275–293.
- Nilsson, S. & Pitt, D. (1991). *Mountain world in danger – climate change in the forests and mountains of Europe*, p. 196. Earthscan Publications, London.
- Ozenda, P. & Borel, J.-L. (1991) Mögliche Auswirkungen von Klimaveränderungen in den Alpen, pp. 71. *Internationale Alpenschutz-Kommission CIPRA, Kleine Schriften 8/91*.
- Pauli, H., Gottfried, M. & Grabherr, G. (1996) Effects of climate change on mountain ecosystems – upward shifting of alpine plants. *World Resource Review*, **8**, 382–390.
- Pauli, H., Gottfried, M. & Grabherr, G. (1999) Vascular plant distribution patterns at the low-temperature limits of plant life – the alpine-nival ecotone of Mount Schrankogel (Tyrol, Austria). *Phytocoenologia*, **29**, 297–325.
- Pauli, H., Gottfried, M., Reiter, K. & Grabherr, G. (1998) Monitoring der floristischen Zusammensetzung hochalpin/nivaler Pflanzengesellschaften. *Handbuch Des Vegetationsökologischen Monitorings* (ed. by A. Traxler), Umweltbundesamt, Wien, pp. 320–343.
- Pielke, R.A. & Mehring, P. (1977) Use of mesoscale climatology in mountainous terrain to improve the spatial representation of mean monthly temperatures. *Monthly Weather Review*, **105**, 108–112.
- ter Braak, C.J.F. (1986) Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**, 1167–1179.
- ter Braak, C.J.F. (1987–92) CANOCO – a FORTRAN program for Canonical Community Ordination. Microcomputer Power, Ithaca, New York, USA.
- ter Braak, C.J.F. (1995) Ordination. *Data analysis in community and landscape ecology* (ed. by R.H.G. Jongman, C.J.F. ter Braak, & O.F.R. van Tongeren), Cambridge University Press, Cambridge, pp. 91–169.
- TINYTAG – Gemini Data Loggers (UK) Ltd, Scientific House, Terminus Road, Chichester, West Sussex, UK.
- Tranquillini, W. (1979) *Physiological ecology of the alpine timberline*, p. 137. Springer, Berlin.
- Wagner, A. (1930) Über die Feinstruktur des Temperaturgradienten längs Berghängen. *Zeitschrift für Geophysik*, **6**, 310–318.