

Upward shift of alpine plants increases floristic similarity of mountain summits

Jurasinski, Gerald^{1*} & Kreyling, Jürgen²

¹*Biogeography, University of Bayreuth, DE-95440 Bayreuth, Germany;*

²*UFZ - Centre for Environmental Research Leipzig-Halle, Permoserstr. 15, DE-04318 Leipzig, Germany;*

**Corresponding author; Tel. +49 921552299; Fax +49 921552315;*

E-mail gerald.jurasinski@uni-bayreuth.de; Url www.uni-bayreuth.de/departments/biogeo

Abstract

Question: Does the upward shift of species and accompanied increase in species richness, induced by climate change, lead to homogenization of Alpine summit vegetation?

Location: Bernina region of the Swiss Alps.

Methods: Based on a data set from previous literature we expand the analysis from species richness to beta-diversity and spatial heterogeneity. Species compositions of mountain summits are compared using a two-component heterogeneity concept including the mean and the variance of Sørensen similarities calculated between the summits. Non-metric multidimensional scaling is applied to explore developments of single summits in detail.

Results: Both heterogeneity components (mean dissimilarity and variance) decrease over time, indicating a trend towards more homogeneous vegetation among Alpine summits. However, the development on single summits is not strictly unidirectional.

Conclusions: The upward shift of plant species leads to homogenization of alpine summit regions. Thus, increasing alpha-diversity is accompanied by decreasing beta-diversity. Beta-diversity demands higher recognition by scientists as well as nature conservationists as it detects changes which cannot be described using species richness alone.

Keywords: Bernina; Beta-diversity; Climate change; Heterogeneity; Long-term monitoring; Non-metric Multidimensional Scaling; Similarity; Species composition; Swiss Alps.

Abbreviations: NMDS = Non-metric Multidimensional Scaling; Rmse = root mean square error.

Introduction

Shifts in species distributions have been linked increasingly to climate change (e.g. Grabherr et al. 1994; Hughes 2000; Walther et al. 2001; Parmesan & Yohe 2003; Root et al. 2003). Experiments have proven a causal link between warming and species responses: modified competitive power or changes in reproductive success lead to changes in species composition (Chapin et al. 1995; Harte & Shaw 1995; Arft et al. 1999). However, with such experiments neither broad-scale nor long-term range shifts can be detected. Long-term data sets are needed to estimate and predict range shifts due to climate change (Grabherr et al. 2001).

Alpine regions show strong gradients in abiotic conditions and contain highly specialized biota (Grabherr 1997). Therefore they are especially suited for long-term observational studies of range shifts related to climate change. High-alpine plant species are thought to be temperature-limited and thus changes in their distributions can be directly interpreted as changes in temperature (Grabherr et al. 2001). Furthermore, alpine regions appear to be subject to more rapid response to climate warming than other regions (Beniston 2003). Numerous studies show that there is an upward shift of plant species (Hofer 1992; Grabherr et al. 1994; Walther et al. 2001; Kullman 2002; Parmesan & Yohe 2003; Walther et al. 2005). All these studies indicate an increase in species number without loss of species. However, Klanderud & Birks (2003) find reduced occurrence of less competitive species native to the highest altitudes in a long-term comparative study in Norway.

Up to now, most studies on climate change and diversity focused on species richness, but conservation and management decisions, as well as scientific investigations regarding the influence of global change on ecosystems, should be based on a comprehensive measurement of biodiversity (Anon. 2005a). Beta-diversity or heterogeneity is an additional important factor in this regard (Vellend 2001; Su et al. 2004). It is a key concept

for understanding ecosystem function, conservation of biodiversity, and ecosystem management (Legendre et al. 2005; Balvanera et al. 2002; Condit et al. 2002; Kluth & Bruelheide 2004). However, up to now none of the studies focusing on the impact of climate change incorporates the question of homogenization which is intensively debated in the research area of invasive species (e.g. McKinney 2004; Kühn & Klotz 2006; Olden et al. 2006; see special issue of *Biological Conservation* Vol. 127). In general, biodiversity can decrease for two reasons: First, species may go extinct. Second, beta-diversity might decrease as specialized species are replaced by ubiquitous species. The resulting homogenization can lead to a reduction of spatial biotic diversity (McKinney 2005).

At global to continental scales biotic heterogeneity is expected to increase with climate warming because of asymmetries in warming trends (Walther et al. 2002). However, homogenization due to invasions and range shifts might contradict this pattern. The pool of species which benefit from warming by expanding their ranges upward in a specific alpine region is largely the same for all summits of that region. That is why we hypothesize that the increase in species richness (alpha-diversity) on mountain summits – which is driven by climate change – is accompanied by homogenization, expressed as a decrease in differentiation (beta-diversity or heterogeneity) between summits. We use a long-term data set from the literature which covers three points in time to test this hypothesis.

Material and Methods

Data set

The data used for the analysis were assembled by Walther et al. (2005) during a resurvey of mountain summits which had been studied prior to 1907 (Rübel 1912) and in 1985 (Hofer 1992). This analysis included ten summits of the Bernina Group in the Swiss Alps. Eight summits consist of siliceous rock, two of calcareous rock (Piz Alv and Piz Tschüffer, Table 1). In all three surveys, the

uppermost 10 m of each summit was searched in detail and the presence of vascular plant species was recorded. One exception was Piz Languard where 30 m was studied (for details see Walther et al. 2005).

The calcareous summits differ substantially from the summits underlain by siliceous rock regarding their abiotic features, as well as their species inventory (Walther et al. 2005). As there were not enough replicates to overcome such a high initial noise, we omitted the calcareous summits from the analysis. For the same reason we excluded Piz Trovat, as the top of this summit is 'completely composed of loose scree' (Hofer 1992). It showed the lowest species numbers at all sampling dates (8, 8, and 7 species respectively) and strong, trendless differences between the surveys. The main difference was that two species were absent in the second sampling but were found in the first and third sampling. Therefore we assumed that the highly dynamic substrate dominates the species composition of this summit and conceals all other trends.

We used the recorded presence data and applied the following procedures to describe and analyse heterogeneity of the data set based on dissimilarity between the summits.

Assessing spatial heterogeneity

We use the dissimilarity between summits as a descriptor of spatial patterns of biodiversity or more specifically as a measure of differentiation, or heterogeneity, among landscape patches of a similar habitat type. In this way it is a measure of beta-diversity (Whittaker 1972), i.e. the dissimilarity in species composition measured as the complement of the Sørensen similarity coefficient ($1 - \beta_{sim}$) (Sørensen 1948; for a broad discussion of binary similarity indices see Koleff et al. 2003).

Two components of heterogeneity are distinguished. The *mean dissimilarity component* which can be compared to attempts by Williams (1996) or Lennon et al. (2001) was calculated as the mean of all dissimilarities between a focal mountain summit and all other summits

Table 1. Description of investigated mountain summits located at UTM WGS84. The last three (in italics) were not included in the analysis due to their differences in bedrock and morphology.

Summit	Altitude[m asl]	Rock	Morphology	UTM WGS84	Easting	Northing
Munt Pers	3207	gneiss	compact, little scree		3207	793302
Las Sours	2979	gneiss	compact		2979	790891
Piz Languard	3262	gneiss	compact		3262	793294
Piz Chatscheders	2986	gneiss	compact, little scree		2986	797950
Piz Minor	3049	gneiss, mica slate	compact, fine scree		3049	798946
Piz dals Lejs	3041	gneiss, mica slate	compact, fine scree		3041	799680
Piz Lagalb	2959	gneiss	compact, blocks, fine scree		2959	798642
(Piz Trovat)	3146	gneiss	coarse scree		3146	794660
(Piz Tschüffer)	3123	dolomite	compact, fine scree		3123	796814
(Piz Alv)	2975	dolomite	blocks, fine scree		2975	796744

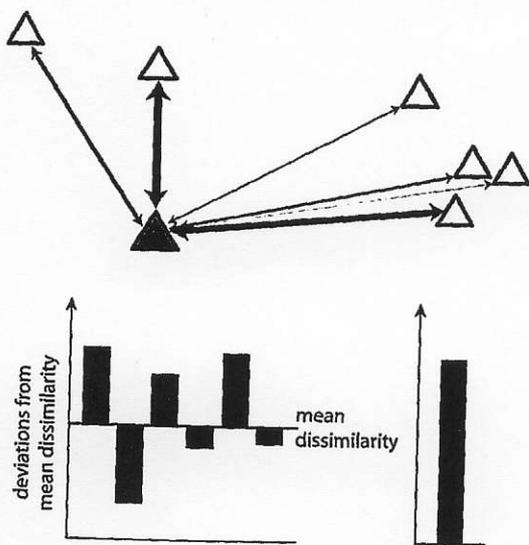


Fig. 1. Heterogeneity measurement. The arrangement approximates the actual geographic position of the summits. Width of arrows represents the similarity between the focal summit (grey triangle) and the other summits (white triangles). To incorporate the spread or variability of the similarities, the deviation of each single similarity value from the mean is taken into account (the grey line represents the mean similarity and light grey bars represent the deviation). The stacked bar represents the aggregated measure, with standard deviation of the deviations from the mean in light grey, and mean of mean dissimilarity values in black. Dissimilarity is measured as $(1 - \beta_{sim})$ where β_{sim} is the Sørensen dissimilarity index.

in the data set (see Fig. 1).

To incorporate the variance of the dissimilarities calculated for a focal summit, we accounted for the deviation of each dissimilarity value from the mean. We call it the *variance component*. The higher it is for a given summit, the more variable (heterogeneous) the calculated dissimilarities are between this summit and the other summits in the data set. Furthermore, the variance of the variance components can be seen as a measure of spatial heterogeneity itself. Thus, decreasing variance indicates increasing homogeneity. For a proper representation of the spread around the mean we use the standard deviation of the dissimilarity values calculated for a focal summit. See Fig. 1 for a graphical representation of the concept.

As we investigated the changes of the dissimilarity structure over time in a constant spatial configuration, we are not affected by the inherent problems of distance decay due to unevenly spaced objects (Tobler 1970; Legendre 1993; Nekola & White 1999). It is likely, that there is a variability in the dissimilarity values which is based on spatial configuration, but it is not responsible for changes in time. Therefore we did not account for spatial auto-correlation in our analysis.

Comparison between groups

Data points of dissimilarity matrices are not independent. Furthermore, our sample size is rather small – for each sampling period, n equals the number of summits (7). Therefore mean dissimilarity of the summits was compared between the different time steps using a permutation procedure. The mean dissimilarity values for all summits of each sampling date are compiled and the difference in mean between two sampling dates is calculated (Δ). Then the values of these two sampling dates are put into a combined set from which two random sets of the same size as the original sets are drawn. The difference in mean between these random sets is calculated and stored (permuted Δ s). Repeating the last step 1000 times provides a potential significance level of $p < 0.001$ by testing the original Δ against the distribution of the permuted Δ s. Because of the small sample size and as we are testing against 1000 permutations all differences in mean with $p \geq 0.01$ are understood to be not significant.

Non-metric multidimensional scaling (NMDS)

For illustration and interpretation of the heterogeneity analysis results, we applied a non-metric multidimensional scaling (Kruskal 1964) with the species data of all included summits and time steps. Here, NMDS was conducted according to the procedure recommended by Minchin (1987), which is based on the algorithm described by Kruskal (1964) and Mather (1976) with several random starts to find the best global solution. An important factor describing the quality of the solution is the stress. It is a measure of the mismatch between distance measures and the distance in ordination space. Stress values smaller than 20 generally lead to usable pictures and interpretations (Kruskal 1964; Clarke 1993). Again, the Sørensen-based coefficient ($1 - \beta_{sim}$) was used to quantify the dissimilarity in species composition between summits. The NMDS was calculated with the function *metaMDS* in the package *vegan* (Oksanen et al. 2005) for the R statistics system (Anon. 2005b). It was conducted with the presence/absence data and *metaMDS* was used with defaults (two-dimensional solution, maximum number of random starts = 50).

Results

The two heterogeneity components

The mean dissimilarity components decrease over time (Fig. 2a). The decrease is significant on the $p < 0.001$ level from 1907 to 1985 and from 1907 to 2003. However, it is not significant for the last time step (1985 to 2003, for details see Fig. 2a). The values of the variance component are also dropping significantly from 1907 to 2003. Analogously to the mean dissimilarity component the decrease is less pronounced for the variance component between 1985 and 2003, but it is still significant ($p < 0.01$). However, from 1907 to 1985 there is no significant decrease in the variance component (see Fig. 2a). From the boxplot in Fig. 2b a change in spread of the values is apparent. An increase from 1907 to 1985 is followed by a decrease from 1985 to 2003. The variance of these values is itself a measure of heterogeneity. To test whether the change in variance is significant we

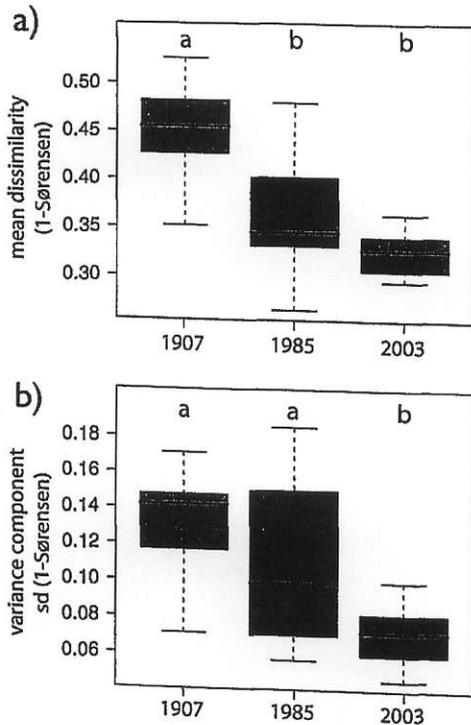


Fig. 2. Development of heterogeneity through time: a. Mean dissimilarity component. The decrease is significant (tested with a permutation procedure) from 1907 to 1985 and from 1907 to 2003 ($p < 0.001$ for both), though less pronounced, between 1985 and 2003 ($p = 0.027$). b. Variance component. The decrease is significant from 1907 to 2003 ($p < 0.001$) and from 1985 to 2003 ($p = 0.008$). For 1907 to 1985 $p = 0.134$. (Box legend: thick black line: median, lower box end: 1st quartile, upper box end: 3rd quartile, whiskers: extremes).

employed Levene's test for the inequality of variances. Although Fig. 2b depicts changing variances, they do not differ significantly between the three sampling dates (F -ratio = 3.56 with $p = 0.05$).

Summit specific developments

Increasing species richness is accompanied by decreasing dissimilarity among summits (Fig. 3). Nevertheless, this general pattern of increasing homogeneity and decreasing spatial variability is not uniform for all summits. The development on Piz Lagalb and Munt Pers was not uni-directional and less obvious as seen on the barplots in Fig. 3. The summit specific developments are best reflected in the NMDS plot shown in Fig. 4a which depicts the dissimilarity situation in the data sets. The final stress value of 10.77 is very low, and the low rmse implies that the probability is very high that the chosen solution is the global solution.

It is evident from Fig. 4 that the different peaks do not evolve linearly and in the same direction. On the contrary a 'back and forth' development can be seen in Piz Languard, whereas most of the other summits exhibit a somewhat 'hooked' development. 'Hooked' means that a displacement in one direction for time step 1 is roughly orthogonal to the direction for the second time step. Only Piz Minor and Piz dals Lejs develop largely unidirectional (broadly along axis 1). Munt Pers, Piz Chatscheders, Piz dals Lejs and Piz Minor show the strongest changes.

The direction of change in species composition

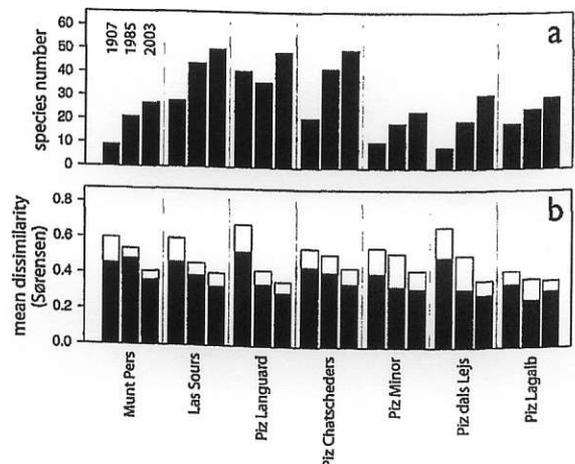


Fig. 3. Development on single summits, for each from left to right: 1903-1909 (Rübel 1912); 1983-1985 (Hofer 1987); 2003 (Walther 2005). a. Species numbers generally increase (for details see Walther et al. 2005). b. Mean dissimilarity (black) generally decreases, development is not always uni-directional (see Piz Lagalb, Munt Pers); the variance component (white) generally decreases and development is again not always uni-directional (Piz Lagalb and Piz Minor deviate).

over time seems to be similar for Las Sours and Munt Pers whereas the development on Piz Chatscheders was different. Even though the direction of development is different for the summits, a clear trend can be seen: in Fig. 4c the positions of the summits at the three time steps are outlined (shortest boundary) showing that the summits are clumping closer together over time, indicating a homogenization of species composition. This holds

even true for summits not belonging to the same massif although there are apparent differences between summits of different ridges. Especially when the development over time of the single summits is taken into account, three groups according to the different massifs can be relatively clearly distinguished in the NMDS plot (compare Fig. 4a, b). The most obvious is the dissimilarity of Munt Pers which is clearly separated from the other summits on axis 2. In real geographical space the large Bernina valley disconnects this summit (together with the summit of Piz Trovat which is on the same ridge) from the others. Piz Lagalb, Piz dals Lejs, and Piz Minor belong to another group distinguishable from the group of Las Sours, Piz Languard, and Piz Chatscheders mainly along NMDS axis 1. In reality these groups are separated by the da Fain valley.

Discussion

Homogenization

In the time period covered (1907-2003) mean dissimilarity of the investigated Alpine summits is decreasing, indicating ongoing homogenization. However, initial species composition, geographical position, and geographical context of individual summits have resulted in the general trend not being reflected equally on all summits. Another important issue might be the accessibility and popularity to humans as vectors – carrying and spreading diaspores – but we have no data on this. Nevertheless, we found an increase in the spread of the variance component for 1985 (although it was not significant). This might be due to the non-linear developments on the different summits. Piz dals Lejs and Piz Minor exhibited comparatively high variance components in 1985 (Fig. 3b) leading to the large spread of the values. These were amongst the summits with most dramatic changes in species number and identity which started from a rather low level. The increase of the spread of the variance component in the 1980s might be due to delayed developments on other summits. Future investigations of the summits might help answer this question.

When the position of the summits in ordination space is compared to the position in geographical space, a clear congruence can be seen. This might have various reasons. A simple one could be that the summits share different geographical distances. Summits which are geographically closer are most likely to have more species in common than remote summits. This distance decay of similarity is a well known characteristic of geographical systems (Condit et al. 2002; Nekola & White 1999) and is often explained by the dispersal capacities of the species.

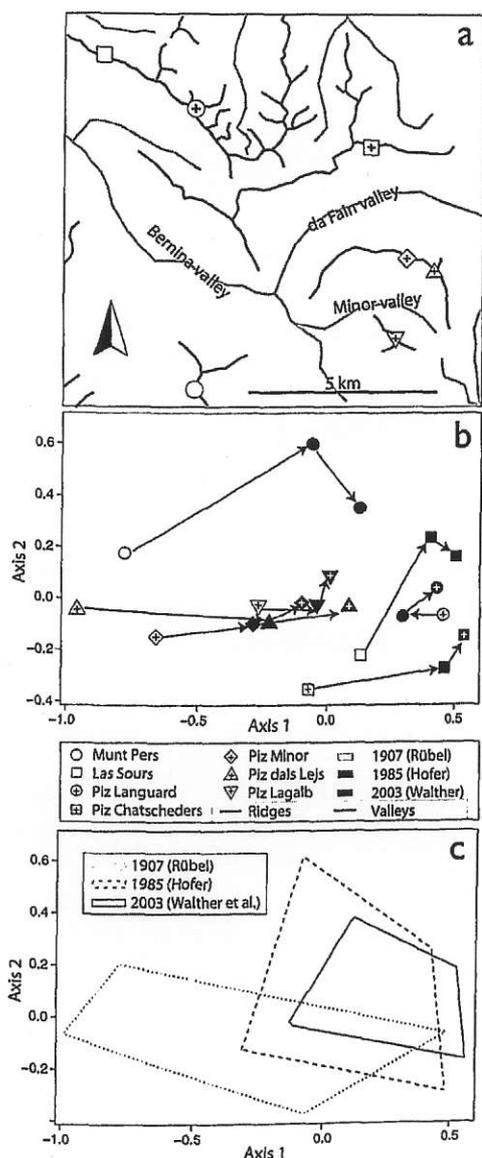


Fig. 4. a. Map sketch of the investigation area showing ridges, valleys (see legend below b) and position of the summits. b. NMDS-ordination of species compositions of seven mountain peaks (symbols) at three time steps (grey scale). Shown is the output after 19 random starts (final stress = 10.77, rmse = 0.0000377, max residual = 0.000103) as then a global solution was found (see text for details). c. Outlines of the positions of the summits in ordination space (shortest distance) show that homogenization occurs.

We did not account for spatial auto-correlation because the spatial configurations of the summits do not change over time. For that reason we are not able to tell which part of the variance is due to the spatial configuration alone. It is possible to partial out the space component (e.g. Borcard & Legendre 1992; Wagner 2005), but one needs to test against the variation caused by environmental variables which we do not have. To obtain an idea about the influence of geographical distance on compositional similarity we conducted a Mantel test (Legendre 1998). The results hint to a generally high importance of spatial configuration on the observed pattern although there is much change between the time steps (Mantel correlations between compositional similarity (Sørensen) and geographical distance between summits (Euclidean distance): 1907 = -0.64 ($p < 0.001$), 1985 = -0.33 (ns), 2003 = -0.82 ($p < 0.001$)).

Especially in mountain regions the situation is even more complicated as the pool of available species for colonization might differ – at least partially – on different massifs due to barriers (e.g. deep mountain valleys or ridges) which certain species cannot overcome or which prolong the possible dispersal way. In Fig. 4a, b the combined effect of geographical distance and belonging to massifs or ridges is apparent although we cannot tell which is more important. However, we rather want to focus on another point: even summits on different massifs become more similar. In 1907 the grouping was much less apparent and the summits were more distinct in species composition than they are in 2003. Today the summits of the Minor group are not only much more similar to each other but also more similar to the summits of the Languard group (which also have more species in common now) from which they are separated by the da Fain valley. This clearly illustrates the ongoing homogenization. Such relations might also be the reason for the hooked developments of Piz Languard or Piz Minor because warming possibly changes dispersal ways. However these questions cannot be answered with the presented data and more research in this regard is desirable.

Meeting at the top

When plant species ranges are shifting, it is to be expected that those traveling upwards will meet species already present. Walther et al. (2005) show that there are currently more species than there have been recorded before on the investigated summits. They also find that in general up to 2003 no species was lost from the summits. Although the pattern is not as evident as the upward shifting, our results show that there is a homogenization of Alpine summits. Alpine regions are very special concerning the spatial organization of their

biota and ecosystems. Because of the tremendous small-scale variation of environmental parameters, particularly at mountain tops, no peak is like another regarding its environmental conditions. An ongoing homogenization leads to a decrease in beta-diversity in Alpine summit regions even though alpha-diversity is increasing on the summits. Different aspects of biodiversity develop in different directions. If only one of the aspects is taken into account, wrong conclusions might be drawn. This special example could be taken as a model for ecosystems in general although it must be tested if our results can be replicated for other alpine regions as well.

Biodiversity is more than just species richness. Therefore the assessment and analysis of ecosystems has to include heterogeneity (which can be expressed by beta-diversity) and possibly functional diversity as well (Beierkuhnlein 2001). Otherwise unreliable conclusions might be drawn. Increasing alpha-diversity means increasing biodiversity and is thus positive from a conservationist view. However, as this might be accompanied by a decrease in beta-diversity it is not so simple. See Gering et al. (2003), Sax & Gaines (2003), Legendre et al. (2005), and Olden et al. (2006) for the importance of beta-diversity in science and conservation.

Data set

If all ten summits of the original data set would be included in the analysis, the observed tendencies are generally the same, but less obvious and not significant (neither for the mean dissimilarity nor for the variance component). This implies that either the results are not valid generally or that the sample size of the original data set is too small relative to the noise level. The significant results for the reduced data set of similar abiotic conditions support the second conclusion and indicate that comparable environments which differed historically in species composition are currently becoming more similar. Nevertheless, the insignificant homogenization effect for the whole data set implies that the effect is still weaker than the variance in species composition due to abiotic differences. This is not surprising regarding the considerable differences in environmental conditions between siliceous and calcareous rocks. At large there is the same species pool of possible colonizers for all of the summits in the region. More information on environmental variables would be needed to clarify the reasons for the actual species composition but this is not the scope of this contribution.

Conclusions

Our results indicate that the upward shift of plant species might lead to a homogenization of alpine summit regions, i.e. a decreasing dissimilarity between summits. Thus, increasing alpha-diversity is accompanied by decreasing beta-diversity. This shows that species richness alone cannot be used as an indicator for the impact of changing climate on biodiversity. One option might be to study the reaction of single species to climate warming. However, the reactions will presumably be ambivalent and results may not be easily generalized. A possibility to incorporate single species reactions into the analysis and thus widen our understanding regarding the impacts of climate change on mountain biota is demonstrated in the presented paper.

Studies not incorporating a comprehensive view on diversity – adding at least differentiation (beta-) diversity – should be evaluated with care. Our findings add to the recent debate about the importance of beta-diversity: beta-diversity demands greater recognition by scientists and nature conservationists as it detects changes which cannot be described by species richness (Balvanera et al. 2002; Condit et al. 2002; Legendre et al. 2002) and is able to widen our understanding of ecosystem processes (Legendre et al. 2005).

Even though the trend of homogenization can clearly be shown with this data set, it becomes apparent that the effect is much weaker for the time step between 1985 and 2003. The reason might be that 15 years is not a long time for mountain-summit species. We still do not know much about the life spans of plants smaller than trees or bushes, but available results suggest that these can be quite long (e.g. Steinger et al. 1996). This highlights the importance of long-term data sets for an understanding of the effects of global change. Without such data sets findings will often be weak and statistical evidence hard to obtain. Data on more summits would have been desirable in the presented study but long-term and large data sets are quite rare. As we can see by the problem of different bedrock, such long-term monitoring sites have to be chosen very carefully, with statistical requirements and ecological theory in mind for being useful to future analyses. To gain further insight in the homogenizing effect of climate change induced range shifts, more research with larger data sets should be done.

Acknowledgements. We thank Gian-Reto Walther for kindly providing the data sets and for giving substantial comments on an earlier version of the manuscript. Further comments of two anonymous reviewers and Beverly Collins are thankfully acknowledged. Kerry D. Woods and two anonymous reviewers made helpful comments on another earlier version of this manuscript. Thanks as well to Vroni Retzer for constructive comments and fruitful discussions and to Katherine Owen for revising the English.

References

- Anon. 2005a. *Ecosystems and human well-being: Biodiversity synthesis*. Millennium Ecosystem Assessment, World Resources Institute, Washington, DC, US.
- Anon. (R Development Core Team) 2005b. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL: <http://www.R-project.org>
- Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F. et al. 1999. Responses of tundra plants to experimental warming: Meta-analysis of the international tundra experiment. *Ecol. Monogr.* 69: 491-511.
- Balvanera, P., Lott, E., Segura, G., Siebe, C. & Islas, A. 2002. Patterns of beta-diversity in a Mexican tropical dry forest. *J. Veg. Sci.* 13: 145-158.
- Beierkuhnlein, C. 2001. Die Vielfalt der Vielfalt – Ein Vorschlag zur konzeptionellen Klärung der Biodiversität. *Ber. Reinhold-Tüxen-Ges.* 13: 103-118.
- Beniston, M. 2003. Climatic change in mountain regions: A review of possible impacts. *Climate Change* 59: 5-31.
- Chapin, F.S., Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J. & Laundre, J.A. 1995. Responses of arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694-711.
- Clarke, K.R. 1993. Nonparametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18: 117-143.
- Condit, R., Pitman, N., Leigh, E.G., Jr., Chave, J., Terborgh, J., Foster, R.B., Nunez, P., Aguilar, S., Valencia, R., Villa, G., Muller-Landau, H.C., Losos, E. & Hubbell, S.P. 2002. Beta-diversity in tropical forest trees. *Science* 295: 666-669.
- Gering, J.C., Crist, T.O. & Veech, J.A. 2003. Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. *Conserv. Biol.* 17: 488-499.
- Grabherr, G. 1997. The high-mountain ecosystems of the Alps. In: Wielgolaski, F.E. (ed.) *Polar and alpine tundra*. Ecosystems of the World 3, pp. 97-12, Elsevier, Amsterdam, NL.
- Grabherr, G., Gottfried, M. & Pauli, H. 1994. Climate effects on mountain plants. *Nature* 369: 448.
- Grabherr, G., Gottfried, M. & Pauli, H. 2001. Long-term monitoring of mountain peaks in the Alps. In: Burga, C.A. & Kratochwil, A. (eds.) *Biomonitoring: General and applied aspects on regional and global scales*, pp. 153-177, Kluwer, Amsterdam, NL.

- Harte, J. & Shaw, R. 1995. Shifting dominance within a montane vegetation community – results of a climate-warming experiment. *Science* 267: 876-880.
- Hofer, H.R. 1992. Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. *Ber. Geobot. Inst. Eidg. Tech. Hochsch. Stift. Rübel Zür.* 58: 39-54.
- Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends Ecol. Evol.* 15: 56-61.
- Klanderud, K. 2005. Climate change effects on species interactions in an alpine plant community. *J. Ecol.* 93: 127-137.
- Klanderud, K. & Birks, H.J.B. 2003. Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *Holocene* 13: 1-6.
- Kluth, C. & Bruehlheide, H. 2004. Using standardized sampling designs from population ecology to assess biodiversity patterns of therophyte vegetation across scales. *J. Biogeogr.* 31: 363-377.
- Koleff, P., Gaston, K.J. & Lennon, J.J. 2003. Measuring beta diversity for presence-absence data. *J. Anim. Ecol.* 72: 367-382.
- Kruskal, J.B. 1964. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29: 115-129.
- Kühn, I. & Klotz, S. 2006. Urbanization and homogenization – Comparing the floras of urban and rural areas in Germany. *Biol. Conserv.* 127: 292-300.
- Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. Ecol.* 90: 68-77.
- Lauber, K. & Wagner, G. 1998. *Flora Helvetica*. 3rd. ed. Haupt, Stuttgart, DE.
- Legendre, P. 1993. Spatial autocorrelation – trouble or new paradigm. *Ecology* 74: 1659-1673.
- Legendre, P., Borcard, D. & Peres-Neto, P.R. 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecol. Monogr.* 75: 435-450.
- Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. *J. Anim. Ecol.* 70: 966-979.
- Mather, P.M. 1976. *Computational methods of multivariate analysis in physical geography*. J. Wiley & Sons, London, UK.
- McKinney, M.L. 2004. Measuring floristic homogenization by non-native plants in North America. *Global Ecol. Biogeogr.* 13: 47-53.
- McKinney, M.L. 2005. Species introduced from nearby sources have a more homogenizing effect than species from distant sources: evidence from plants and fishes in the USA. *Divers. Distrib.* 11: 367-374.
- Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89-107.
- Nekola, J.C. & White, P.S. 1999. The distance decay of similarity in biogeography and ecology. *J. Biogeogr.* 26: 867-878.
- Oksanen, J., Kindt, R. & O'Hara, R.B. 2005. *Vegan: Community Ecology Package version 1.6-10*. URL <http://cran.r-project.org/>
- Olden, J.D., Poff, N.L. & McKinney, M.L. 2006. Forecasting faunal and floral homogenization associated with human population geography in North America. *Biol. Conserv.* 127: 261-271.
- Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.
- Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.
- Rübel, E. 1912. *Pflanzengeographische Monographie des Bernina-Gebietes*. Engelmann, Leipzig, DE.
- Saetersdal, M. & Birks, H.J.B. 1997. A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. *J. Biogeogr.* 24: 127-152.
- Sax, D.F. & Gaines, S.D. 2003. Species diversity: from global decreases to local increases. *Trends Ecol. Evol.* 18: 561-566.
- Sørensen, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content. *Biol. Skrift.* 5: 1-34.
- 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: 307-324.
- Su, J.C., Debinski, D.M., Jakubauskas, M.E. & Kindscher, K. 2004. Beyond species richness: Community similarity as a measure of cross-taxon congruence for coarse-filter conservation. *Conserv. Biol.* 18: 167-173.
- Tobler, W.R. 1970. A computer movie simulating urban growth in the Detroit region. *Econ. Geogr.* 46: 234-240.
- Vellend, M. 2001. Do commonly used indices of beta-diversity measure species turnover? *J. Veg. Sci.* 12: 545-552.
- Walther, G.-R., Beißner, S. & Burga, C.A. 2005. Trends in the upward shift of alpine plants. *J. Veg. Sci.* 16: 541-548.
- Walther, G.-R., Burga, C.A. & Edwards, P.J. (eds.) 2001. *'Fingerprints' of climate change – Adapted behaviour and shifting species ranges*. Kluwer Academic/Plenum Publishers, New York, NY, US.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.
- Whittaker, R.H. 1972. Evolution and measurement of species diversity. *Taxon* 12: 213-251.
- Williams, P.H. 1996. Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proc. R. Soc. Lond. Ser. B Biol. Sci.* 263: 579-588.

Received 9 October 2006;

Accepted 9 February 2007;

Co-ordinating Editor: B.S. Collins.