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FORUM

Increasing species richness on mountain summits: Upward migration due to anthropogenic climate change or re-colonisation?

Kammer, Peter M.[1*]; Schöb, Christian[2] & Choler, Philippe[3]

[1]*University of Teacher Education, Biology Department, Gertrud-Wokerstr. 5, CH-3012 Bern, Switzerland;*
[2]*Institute of Geography, University of Bern, Hallerstr. 12, CH-3012 Bern, Switzerland; christian.schoeb@phbern.ch;*
[3]*Station Alpine J. Fourier and Laboratoire d'Ecologie Alpine UMR 5553 UJF-CNRS, Université J. Fourier-Grenoble I, FR-38041 Grenoble, France; philippe.choler@ujf-grenoble.fr;* [*]*Corresponding author; peter.kammer@phbern.ch*

Abstract. Over the last 20 years, several studies comparing recent survey data with historical data from the early 20th century documented an increase in species numbers on high mountain summits of the European Alps. This increase has more or less explicitly been attributed to an upward migration of plant species due to anthropogenic climate warming. However, a reconsideration of the historical and recent data has revealed that more than 90% of the recent species occurrences on mountain summits concern species that were already present at the same or even at higher altitudes within the study region at the time of the historical surveys. This finding suggests that suitable habitats already occurred on these summits under the mesoclimatic conditions prevailing at the beginning of the 20th century and that these habitats were, at least in part, occupied by these plant species. Consequently, the observed increase in species number during the last century does not require the additional temperature increase due to anthropogenic climate change. We therefore consider the phenomenon of increasing species number on high mountain summits to be primarily the result of a natural dispersal process that was triggered by the temperature increase at the end of the Little Ice Age and that is still in progress mostly due to the dispersal limitation of the species involved. Since both the natural dispersal process and a potential upward migration due to anthropogenic climate warming would take place at the same time, we suggest seeding and transplanting experiments in order to assess their respective roles in the increase in species number on mountain summits.

Keywords: Alpine flora; Dispersal limitation; European Alps; Long-term monitoring; Species diversity; Vegetation shift.

Nomenclature: Aeschimann & Heitz (1996).

Abbreviation: LIA = Little Ice Age.

Introduction

Climate warming is expected to influence the distribution ranges of plant species along latitudinal and altitudinal gradients (Hughes 2000; Walther 2003). In order to verify this prediction, inventories have been compiled of the recent plant species occurrences on various summits in the European Alps of which historic censuses were available. The comparison of the historical and the recent data revealed more or less distinct increases in species number on almost all summits under study; e.g. Hofer 1992; Grabherr et al. 1995; Camenisch 2002; Burga et al. 2004, and most recently Walther et al. 2005b. This finding was generally attributed to an upward migration of plant species due to climate warming (e.g. Gottfried et al. 1994; Grabherr et al. 1994; Pauli et al. 1996; Burga et al. 2004; Walther et al. 2005a) and, more or less explicitly, to the anthropogenic warming resulting from increasing emissions of greenhouse gases as observed over the last 50 years (Anon. 2001).

However, the underlying ecological mechanisms were hardly specified in these studies. Most probably, the authors imply that during the period of observation new suitable habitats occurred progressively on the summits due to climate warming, and that these new habitats were more or less directly colonised by species usually occurring on lower altitudes. Subsequently, we will refer to this hypothesis as the 'upward migration process'. According to this explanation, the number of species on a summit would be determined by the rate of occurrence of new suitable habitats. However, these studies do not represent controlled experiments and thus, different possible causes may have led to the results observed (Hughes 2000). As shown in the following, the data also allow for an alternative explanation for the increase in species number on mountain summits.

Re-colonisation process

Piz Linard (3410 m a.s.l.), a nival summit in the Engadine Valley (SE Switzerland), is the mountain with the longest tradition in summit flora survey. The first census was carried out by O. Heer as early as 1835 (Heer 1866 cited in Pauli et al. 2003). He recorded just one species, *Androsace alpina*, on the uppermost 30 m of this peak. This finding suggests that the nival summits of this region were mostly bare of vegetation at the end of the Little Ice Age (LIA), i.e. about 1850. Suitable habitats most probably occurred on these summits before the period of the LIA, i.e. before 1600, and they were occupied by plant species. During the LIA, however, these habitats became temporarily unsuitable for these species due to the unfavourable climatic conditions. Consequently, the species became extinct from the summits, even though their habitats still existed in terms of their pedological features. At the end of the LIA, the summit habitats again became suitable due to the increase in temperature, which was, much like the large scale temperature anomaly of the LIA, particularly a consequence of naturally-forced climate variability (Anon. 2001; Crowley 2000). The suitable habitats could be colonised more or less immediately, thereby leading to the increase in species number as observed. We refer to this development as a 're-colonisation process', since the plant species re-occupy sites at which they occurred before.

However, as the further surveys of Piz Linard revealed, this re-colonisation process takes time. The number of species on Piz Linard increased continuously to three in 1864, four (1895), eight (1911) and reached a maximum of ten species in 1937 (Braun-Blanquet 1957). This number has not been exceeded so far (Pauli et al. 2003). Therefore, the question is why this re-colonisation process has not proceeded faster, given the availability of suitable habitats on the summits and the favourable mesoclimatic conditions.

In addition to the availability of suitable habitats, several other conditions have to be fulfilled in order to facilitate the quick re-colonisation of a specific summit by a specific species: (1) safe sites for germination on the summit (Urbanska & Schütz 1986; Stöcklin & Bäumler 1996; Grabherr 2003); (2) the existence of a nearby source area of the species; (3) a migration route (Pauli et al. 1996; Grabherr 2003; Klanderud & Birks 2003), i.e. the availability of suitable habitats between the source area and the summit; (4) a high dispersal potential of the species. Conditions two and three refer to the importance of the geographic traits of a summit for colonisation. Isolated summits and/or summits with unfavourable geomorphologic characteristics, e.g. high erosion rates, may be colonised later or not at all by a specific species, in contrast to less isolated summits and/or summits with more stable substrate (Gottfried et al. 1994; Pauli et al. 1996; Camenisch 2002; Burga et al. 2004). Especially the fourth condition is often not fulfilled, since most alpine species have relatively low dispersal capacities (Stöcklin & Bäumler 1996). Even characteristic species from early successional communities ('alpine ruderals') show slow population dynamics (Diemer 2002). This leads to a situation where suitable habitats on mountain summits may remain empty for a long time due to a dispersal limitation of species (Pulliam 2000). The eminent relevance of dispersal limitation to the distribution of a species was explicitly shown by Primack & Miao (1992). However, rare cases of long distance dispersal may account for the establishment of populations far beyond their primary distribution (Petit et al. 1997; Clark 1998). This phenomenon, as well as the existence of a proximate source area, may be responsible for the early occurrence of a specific species on a summit as it was observed in the historical surveys at the beginning of the 20th century.

The probability for species, which occurred on a summit once, to remain there is relatively high, provided that the average mesoclimatic conditions do not become less favourable. Firstly, the majority of these nival species are long-living (Grabherr et al. 2001); once established in a place, they may remain there for several decades. Secondly, these species may flower and seed even at this altitude, as observed by Braun (1913) and Braun-Blanquet (1955), forming a local seed bank from which they may recruit in case of local extinctions. This means that these extreme habitats may represent source habitats (Pulliam 1988; Dias 1996) for some species. In cases where the summits represent sink habitats (Pulliam 1988; Dias 1996), local extinctions may be compensated by conspecific immigrants from proximate, but marginally lower lying source areas ('rescue effect' *sensu* Brown & Kodric-Brown 1977; Stevens 1992). Additionally, the presence of one species may facilitate the occurrence of other species; non-cushion species, for example, may establish inside cushions (Olofsson et al. 1999).

Thus, the re-colonisation process suggests that the increase of species numbers on summits is primarily the result of two phenomena: 1. The natural dispersal process which was triggered by the temperature increase at the very end of the LIA and which is still in progress due to the dispersal limitation of the species involved. 2. The high persistence of the species on the summits. This process will theoretically go on for as long as there are species in the regional species pool which are not yet present on the mountain summits and which are capable of colonising the suitable habitats.

Evidence for the re-colonisation process

Both processes, upward migration and re-colonisation, lead to the same result: an increase in species number on mountain summits. Most probably, they will take place at the same time and the difficulty consists in differentiating between them. The problem is that no censuses were made around 1950, i.e. before the beginning of anthropogenic climate warming (Anon. 2001). This makes rigorous tests to discern between the two processes impossible. However, the historical and recent data allow performing simple statistics in order to find support for the upward migration or the re-colonisation hypothesis.

1. Braun (1913) compiled data of species occurrences from 84 summits (median 3104 m) in the nival zone of the Engadine Valley (surface area of about 2500 km^2). Although this data set does not provide complete inventories of every summit, it is apparent that several summits harboured a high number of species already at the beginning of the 20th century: 30 summits contain more than ten species within the uppermost 30 m (altitudinal); a maximum of 53 species was found on Las Sours (2979 m). This suggests high rates of increase in species number for these summits in the second half of the 19th century, assuming that the nival summits were more or less bare of vegetation at the end of the LIA (around 1850). Furthermore, the Braun data set also reveals that many species were widely distributed within the nival zone in the 1900s in this region: We separated a group of 29 species, which occur regularly in the nival zone, from the remaining 147 species that were found only sporadically at this altitude (Table 1). Subsequently, we name the first group the 'nival' species and the latter the 'alpine' species. These data suggest that suitable habitats already occurred on nival summits under the mesoclimatic conditions prevailing at the beginning of the 20th century and that these habitats were, at least in part, occupied by plant species. In fact, there is no need for a further increase in temperature for plant species to be able to colonise these altitudes.

2. Grabherr et al. (2001) and Walther et al. (2005b) showed impressive numbers of new occurrences of species on summits where they had not been observed in the historical surveys (Table 2). They considered this finding to be a sign of the upward shift of plant species due to the increase in temperature and, more or less explicitly, to anthropogenic climate warming. However, more than 90% of the occurrences concern species that had already been observed on the same or even on higher altitudes in the historical surveys, albeit in part on other mountains in the same region. *Saxifraga bryoides*, for example, occurred on 39 summits between 2973 m and 3418 m at the beginning of the 20th century (Braun 1913). Eighty years later, the same species was found on one more summit (P. Chatscheders, 2986 m; Hofer 1992; Walther et al. 2005b).

Table 1. Set of species that regularly occurred in the nival zone (at least on 18 different summits) and within the summit area (uppermost 30 m) in the early 20th century. The list is based on the observations provided by Braun (1913) for the Engadine Valley region (Central Alps, Switzerland) including the Bernina, Err, Kesch, Puschlav, Silvretta, and Vadret mountains (surface area of about 2500 km^2). In the text, we refer to this set of species by the term 'nival'.

Species	Number of occurrences	
	Nival zone	Summit area
Ranunculus glacialis	49	40
Saxifraga bryoides	47	39
Saxifraga oppositifolia	46	37
Androsace alpina	45	38
Poa laxa	44	40
Leucanthemopsis alpina	43	32
Saxifraga exarata	41	31
Cerastium uniflorum	40	28
Minuartia sedoides	38	30
Gentiana bavarica	38	28
Geum reptans	35	20
Luzula spicata	34	23
Phyteuma globulariifolium	32	23
Carex curvula	30	19
Silene exscapa	30	19
Oreochloa disticha	28	19
Draba fladnizensis	27	19
Festuca halleri	27	16
Eritrichium nanum	25	16
Erigeron uniflorus	25	15
Potentilla frigida	25	13
Saxifraga seguieri	23	12
Senecio incanus ssp. *carniolicus*	22	12
Poa alpina	22	10
Cardamine resedifolia	21	11
Linaria alpina	20	11
Artemisia genipi	19	8
Draba dubia	19	8
Doronicum clusii	18	11

Naturally, identical elevations are not necessarily climatically identical on different mountains. For example, the climate in the summit area may be harsher than the climate met at the same altitude on a higher mountain. Furthermore, local differences in elevational lapse rates of temperature and/or precipitation, as well as differences in slope and aspect may also be responsible for climatically differing growing conditions at the same altitude. However, the data do not allow to take these points into consideration, as the required information is not available, with the exception of the indications of aspect in the Grabherr data set (Grabherr et al. 2001).

According to the upward migration process, one could assume that a species will first colonise the climatically favourable exposition and later, after a further mitigation of the climate, establish itself on less favourable expositions as well. Considering the exposition pattern at a specific time, one would expect that the species occurring on high summits primarily grow on favourably exposed slopes, while less favourable expositions on lower summits may also be colonised. In the Engadine Valley region, south exposed slopes offer the best growing conditions; not only with respect to irradiation and temperature, but also regarding wind shelter and snow accumulation, since north is the prevailing wind direction on the summits of this region (data from P. Corvatsch, 3451 m; www.meteoswiss.ch).

However, a verification of this prediction revealed that the mean altitude of the new occurrences of 'alpine' species exposed southward (ESE-S-WSW; 3073 ± 59 m, $n = 67$) is not significantly higher (Mann-Whitney-Test) than the one in a northward exposition (WNW-N-ENE; 3067 ± 39 m, $n = 14$). The corresponding values for the 'nival' species are 3114 ± 115 m (south; $n = 31$) and 3064 ± 61 m (north; $n = 14$), respectively. Hence, both the 'nival' and the 'alpine' species preferably grow on southward exposed slopes, but independent of altitude. However, further investigations should aim at elucidating the possible climatic differences between the summits under study and their relevance for the altitudinal distribution of plant species.

Thus, we conclude that the major part of the new occurrences of species on summits, where they were not observed in the historical surveys, are not the result of an upward migration of species, plant communities, or even vegetation zones in this region. They rather reflect the filling of empty habitats by slow, late coming species within the framework of the re-colonisation process, or, in other words, the filling of gaps in the distribution area of the species involved.

3. The upward migration of species or of entire vegetation zones as a result of climate warming could lead to the loss of species of the higher zone (Ozenda & Borel 1995). Therefore, a high proportion of 'nival' species which occurred in the historic censuses but were no longer found during the recent investigations would represent strong evidence in favour of the upward migration process. In the historical data, the proportion of 'nival' species accounts for 75 % of all species occurrences on the 28 mountain summits investigated in recent surveys. However, among the species occurrences that were not confirmed in recent surveys (38 occurrences), the 'nival' species are underrepresented (42 %). The small number of unconfirmed occurrences (38) compared to the number of new occurrences (388), as well as the relatively high proportion of disappeared 'alpine' species, indicate that a replacement of 'nival' species by 'alpine' species is not taking place, thereby supporting the re-colonisation process.

Evidence for the upward migration process

As outlined above, the increase in species richness on mountain summits does not require human-induced climate warming. However, this does not mean that anthropogenic climate change has had no impact on the altitudinal distribution of plant species so far. Two findings may be considered as the first signs of species upward migration due to human-induced climate warming: Firstly, Walther et al. (2005b) observed that the rate of increase in species number became significantly higher in the period from 1985 to 2003, compared to the previous observation period (1905 to 1985). Secondly, in recent surveys (Grabherr et al. 2001; Walther et al. 2005b), several species which are characteristic of alpine heaths and grasslands (namely *Arnica montana*, *Avenella flexuosa*, *Nardus*

Table 2. Key data of the studies reconsidered in this article. In general, not definitely determined species (labelled with cf. in the original references) were excluded from the analysis, as well as species of unclear taxonomic status. Historical data originate from Rübel (1912), Braun (1913), and Braun-Blanquet (1957). *Three summits were surveyed by both investigators: Munt Pers, Piz dals Lejs, Piz Trovat.

	Grabherr et al. (2001)	Walther et al. (2005b)
Year of survey	1992 / 1993	2003
Region	Engadine mountains, Central Alps, Switzerland	Bernina mountains, Central Alps, Switzerland
Number of summits surveyed*	21	10
Mean altitude of summits (median)	3124 m a.s.l.	3014 m a.s.l.
Total number of species sampled	97	101
Total number of species occurrences	444 (100 %)	336 (100 %)
Number of new occurrences of species on summits where they were not observed in the historical surveys	156 (35.1 %)	182 (54.2 %)
Number of first time observations of species above the altitude of the highest historical record	35 (7.9 %)	19 (5.7 %)
Number of species reaching for the first time the nival zone (>3000 m a.s.l.)	6	3

stricta, and *Vaccinium myrtillus*) were discovered for the first time in the nival zone in this region, which may be considered as the first signs of an upward migration of species to altitudes at which they were never found before.

Conclusions

It is important to stress that we do not question the existence of human-induced climate change and that we do not negate that anthropogenic climate warming will influence the distribution areas of species. Furthermore, we fully appreciate the significance of the studies carried out on this subject. However, further analyses should take into consideration the traits of the species involved, especially their temperature sensitivity, dispersal ability, as well as their recent and historic distribution, i.e. their arrival probability (Zobel et al. 2006). For example, if the species are currently migrating upward due to climate warming, they should exhibit similar temperature sensitivity. On the other hand, they may show great interspecies variability in dispersal capacity and in distance to their source area. If the opposite holds, then this would be in favour of the re-colonisation process.

However, only experiments may provide reliable information on the underlying mechanisms of the increase in species number on high mountain summits. Here, we outline three possible approaches.

1. *Androsace alpina* is widely distributed on the nival summits of the study region (Table 1) and occurs on 27 of the 28 summits surveyed in the recent investigations. Seeding or planting of these kinds of species on a summit on which they did not occur so far could clarify whether their absence was due to dispersal limitation or to (climatically) unsuitable habitats.

2. *Oxyria digyna* and *Artemisia umbelliformis* are species which are widely distributed in the alpine zone within the study region, but they rarely occur on nival summits. Thus, these species represent potential colonisers of these summits. Seeding or transplanting such species along an altitudinal gradient would allow to determine their recent climatic limit. The further observation of their performance would provide information on the upward migration due to recent climate warming.

3. Population investigations of transplanted species (or of species recently arrived on nival summits) would permit to verify whether they exhibit the attributes of source or of sink populations. Source populations would be evidence of an altitudinal enlargement of their distribution area.

As long as we do not understand the underlying mechanisms, we should be cautious about the interpretation of the increase of species richness on high mountain summits. A statement such as "The upwards shift on high mountain summits suggests that plants already respond to climate warming." (Pauli et al. 2001) is confusing. It implies that human-induced climate warming has allowed numerous plant species to migrate upwards on altitudes at which they could not survive before. But, to this day, no assured observation of this phenomenon is available.

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