DIFFERENCES BETWEEN RECENT AND HISTORICAL RECORDS OF UPPER SPECIES LIMITS IN THE NORTHERN EUROPEAN ALPS

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With 4 figures

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Summary: Are there differences in historical and recent upper range limits of vascular plants and are such differences more pronounced in individual species groups? The current limits of 1103 plants of the Northern Alps are compared to range limits in the mid-19th century. The comparison is based on two surveys. The first survey was conducted by Otto Sendtner in 1848–1853, the second in 1991–2008 during a habitat inventory. To our knowledge this is the first comparative studies reaching back to the end of the "Little Ice Age" and comprising an almost entire regional flora covering the complete range of habitats. During the recent survey, most species were found at higher elevations. Even though the differences fit well with the expected shifts due to climate warming we cannot exclude effects of sampling bias. However, we assume that the relative differences between species groups can be safely interpreted. The differences in upper limits between both surveys were significantly larger among forest species. The most important reason is probably discontinued pasture and mowing, which may have amplified possible warming effects. Nitrogen deposits may have contributed to this effect by placing competitive species in a more advantageous position.

Zusammenfassung: Unterscheiden sich historische und aktuelle Beobachtungen von Höhengrenzen der Pflanzen? Betreffen solche Unterschiede Artengruppen in unterschiedlichem Maße? Hier werden aktuelle und historische Beobachtungen der oberen Höhengrenzen von 1103 Gefäßpflanzen der Nördlichen Alpen verglichen. Der Vergleich beruht auf zwei Erhebungen: Die Studie von Otto Sendtner entstand zwischen 1848 und 1853; die zweite beruht auf Daten der Bayerischen Alpenbiotopkartierung (1991–2008). Dies ist unseres Wissens der erste Vergleich zwischen den aktuellen Höhengrenzen einer fast kompletten Gebietsflora mit denen am Ende der „Kleinen Eiszeit". Die meisten Arten wurden bei der jüngeren Kartierung an wesentlich höher gelegenen Orten gefunden. Auch wenn diese Unterschiede den zu erwartenden, klimabedingten Verschiebungen entsprechen, kann ein Einfluss des Erhebungsverfahrens auf die Ergebnisse nicht ausgeschlossen werden. Relative Unterschiede zwischen Artengruppen sind hingegen kaum als methodische Artefakte zu interpretieren. So gewannen Waldarten signifikant stärker an Höhe als andere. Ein Grund ist vermutlich die Aufgabe landwirtschaftlicher Nutzung von Hochlagen, deren Folgen für die Artenzusammensetzung mögliche Erwärmungseffekte verstärkte. Auch atmosphärische Einträge von Nährstoffen können zur schnelleren Aufwärtswanderung von Waldarten beigetragen haben, indem sie konkurrenzstarken Arten bessere Etablierungschancen verschafften.

Keywords: Bavarian Alps, biogeography, climatic change, land use change, species shifts

1 Introduction

Species respond to climatic warming by shifting their distributions in latitude and altitude (Parmesan and Yohe 2003; Walther 2003; Hickling et al. 2006; Thomas 2010). A substantiated consensus indicates that most current shifts of mountain species point upwards (Lenoir et al. 2010). In temperate mountain areas, prevailing upward shifts have been reported in numerous studies (Hofer 1992; Grabherr et al. 1994; Keller et al. 2000; Walther et al. 2005; Baker and Moseley 2007; Pauli et al. 2007; Beckage et al. 2008; Lenoir et al. 2008; Parolo and Rossi 2008; Vittoz et al. 2008; Frei et al. 2010). These findings do not preclude inverse shifts of certain species, as described by Frei et al. (2010) and Lenoir et al. (2010).

Land use is probably the most controversially discussed factor blurring the climate signal: land abandonment or change in farming practices may cause a retreat of former beneficiaries and cause upwards shifts of previously suppressed species (i.e. forest species; Dirnböck et al. 2003; Penuelas and Boada 2003; Gehrig-Fasel et al. 2007; Gellrich et al. 2007; Van Bogaert et al. 2011). Land-use change may also lead to downhill range expansions by providing suitable habitats at lower altitudes (e.g. for non-forest species; Halloy and Mark 2003;

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Lenoir et al. 2010). Vice versa, it may also lower the chance of species to shift further up (Cairns and Moen 2004; see also Tape et al. 2010). Pasture farming plays a crucial role in these processes, as do human-caused fires. Dispersal abilities may cause different speeds of range expansions (Parolo and Rossi 2008).

Many of the above mentioned empirical studies are based on sample plots and therefore limited in terms of sampled species. None comprises an entire regional flora with a broad range of habitat types. The data used in the current study provides such an opportunity. In the current study, we present a comparison of upper species limits in the Northern European Alps as observed in the mid-19th century and today. Apart from reaching further back in time than other comparative studies (down to the end of the "Little Ice Age"), the data comprise an almost entire regional flora of 1103 plant species including thermophilous species of the valley bottoms and nival species of the summits. To our knowledge, this broad coverage of ecosystem types is unprecedented.

The research questions addressed in this paper are whether historical and recent observations of upper limits of vascular plants differ in altitude and if such shifts are more pronounced in individual species groups. A critical drawback of using historical, empirical data is uncertainty about biases caused by sampling. We mitigate this problem by interpreting relative differences in the behaviour of species-subsets. This opens up perspectives for assessing factors such as land-use change that tend to blur the response of vegetation to warming (Walther 2003).

2 Materials and methods

We compared maximum altitudes reached by 1103 vascular plant species as observed in the mid-19th century and today. The two underlying surveys, 150 years apart, cover the Bavarian Alps in Germany (Fig. 1), a narrow 245 km stretch of mountains ranging from 430 to 2962 m above sea level (a.s.l.). The natural vegetation of these predominantly calcareous mountains consists mainly of mixed beech forests reaching up to ≈1500 m a.s.l. followed by coniferous forests with an upper limit at ≈1900 m a.s.l. Since medieval times, parts of these forests have been replaced by mountain summer pastures (Ringler 2009).

2.1 Climate change

In the mid-19th century, a 300 year period of decreased temperatures in Europe, the Little Ice Age, was coming to an end (Bradley and Jonest 1993). In the ensuing 150 years the area has experienced an increase in annual mean temperature of 1.7 K (western part) to 2 K (eastern part; rates referring to differences between the periods of 1848–1853 and 1991–2008). The records were taken from the most current release of the homogenised HISTALP time series (Fig. 2), which are based on long-term observational data (www.zamg.ac.at/histalp; Auer et al. 2007; Brunetti et al. 2009; Böhm et al. 2010). The Bavarian Alps fall into the north-eastern and north-western HISTALP subregions with 32 (8) and 35 (10) stations, respectively (the values in parentheses refer to stations with temperature records starting earlier

Fig. 1: Area of investigation (red)

than 1850). Figure 2 shows two temperature minima in the 19th century (in the 1850s and around 1890). The subsequent increase reaches a first peak in the 1940s and new heights in recent decades. Increases in temperature have been found for all seasons and at all altitudes and correspond to a marked retreat of glaciers (Hagg et al. 2012). Mountain stations did not show a weaker or stronger warming signal than stations at low elevations (Auer et al. 2007). Based on data from 23 stations in the Bavarian Alps, Ewald (1997) found a mean annual temperature lapse rate of -0.48 K (100 m)$^{-1}$. A local meteorological station network run by the Berchtesgaden National Park (Konnert 2004) suggests lapse rates of -0.47 K (100 m)$^{-1}$. With these rates, a temperature increase of 1.7–2 K corresponds to an upward shift in climate of 358–418 m between both surveys (increasing from east to west). While changes in temperature were strong and uniform across seasons, changes in precipitation were low and variable. Changes were more notable in the western region (for 1901–2000 summer precipitation decreased from 119 to 96% as compared to the mean for this period, and winter precipitation increased from 71 to 100%).

2.2 Land-use change

During the same period land use underwent changes. A high rate of summer pasturing on moun-

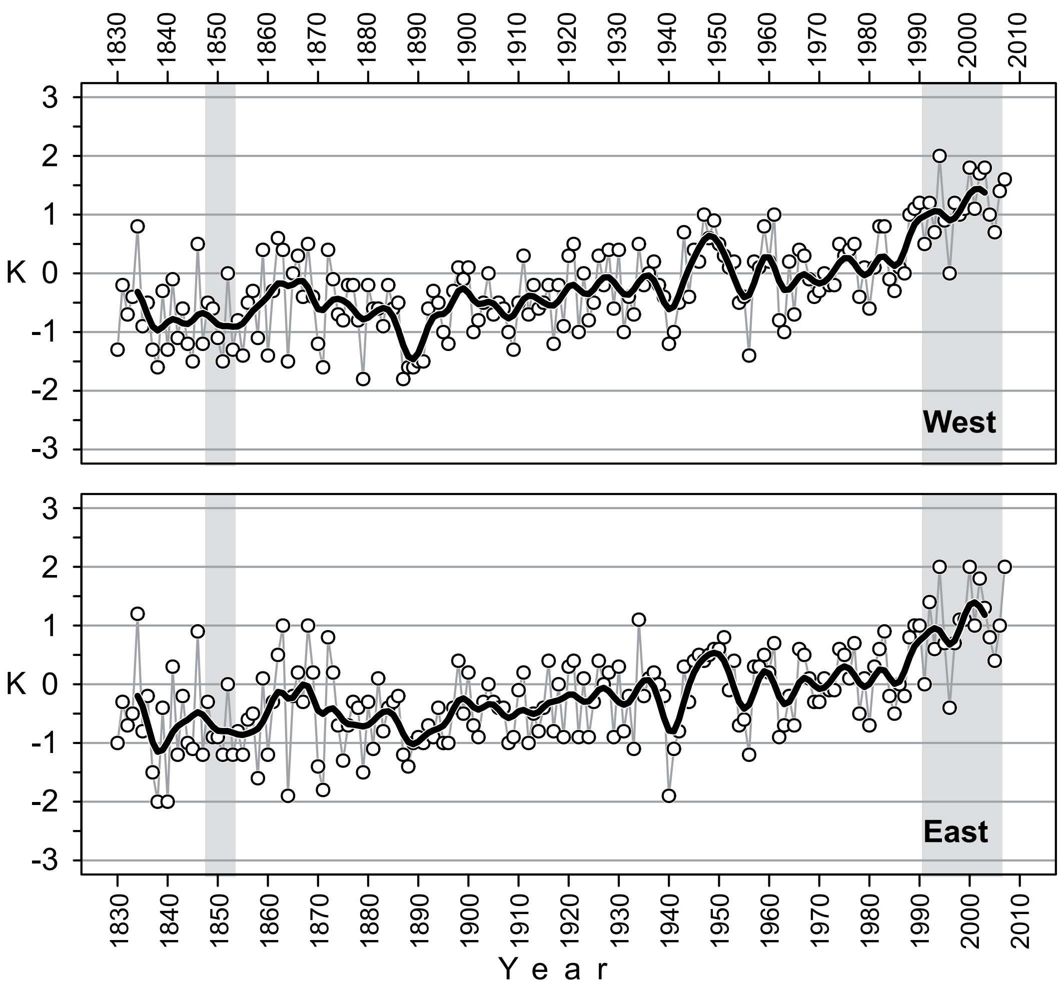

Fig. 2: Change in mean annual temperatures in the Northern Alps (western and eastern parts). Underlying data are taken from the homogenised series developed in the HISTALP project. The bold lines are the results from 10 year Gaussian low-pass filters (nine weights). White circles represent anomalies from 1901–2000 temperature means. The grey shaded zones indicate the recording periods of the two surveys compared in this study

tain slopes at the end of the 18th century was followed by a stepwise decline (with setbacks) that is still ongoing today (Ringler 2009). In Bavaria, 6540 ha of mountain pastures and hay meadows were abandoned between 1954 and 1972 (Ringler 2009). Both succession and reforestation brought about an increase in forests at the cost of open habitats (Sachteleben 1995; Ringler 2009). The process is typical for many parts of the European Alps (Carcaillet and Brun 2000; Didier 2001; Motta and Nola 2001; Dirnböck et al. 2003; Löffler et al. 2011). In Switzerland, succession following land abandonment seems to account for most of the recent increases in forest area while 4% of the gain could be attributed to climate change (Gehrig-Fasel et al. 2007; Gellrich et al. 2007).

2.3 Sendtner's survey from 1848 to 1853

Otto Sendtner conducted his survey on the vegetation ecology of Southern Bavaria in the years 1848–1853 (Sendtner 1854). In his work he reported the individual upper limits of most vascular plant species occurring in this area and supported these observations by barometric measurements. In a very early example of numerical biogeography, his investigation identified altitudes with high species turnover and he made subsequent numerical definitions of altitudinal belts, which "could not be defined in any other way than through the numerical values resulting from the sum of all species occurrences" (Sendtner 1854, 374). Sendtner sampled plants along his paths and recorded the first and last occurrences along the altitudinal gradient. We do not know the exact coverage of his investigations, which took place during five major trips (Wunschmann 1892), but thousands of geo-located records published in Sendtner (1854) document a very dense coverage reaching from the valley bottoms up to the highest summits.

2.4 The new survey from 1991 to 2008

The Alpine Habitat Survey (German acronym: ABK) was carried out in 1991–1994 and 1997–2008 during a habitat inventory by the Bavarian Environment Agency (Urban and Mayer 1996). This survey aimed at a complete inventory of habitats with relevance to nature conservation (usually protected habitats according to Bavarian or European regulations). These habitats cover, with few exceptions, the entire area above treeline but only parts of the lower areas. The final coverage was 28% of the total area. The mapping resulted in sampling units of differing size, shape and altitudinal extent, each consisting of one or multiple habitat types. A complete inventory of vascular plant species was carried out in each sampling unit.

For every spatial sampling unit, a corresponding list of species observations is given. The exact position of species occurrences within these units is unknown. However, a minimum and a maximum possible position of a species' upper limit can be derived (Fig. 3). Based on a 10 m-resolution digital elevation model obtained from the Bavarian Land Survey Authority, lowest and highest altitude of each sampling unit were extracted. For the highest possible position of a species (m_h) we identified the highest point of the highest reaching sampling unit containing this species. To derive the lowest possible position of upper limits m_l, the highest among all individual lower limits of sampling units containing the species was extracted (Fig. 3).

The two measures represent extremes. In most cases, species limits should not be expected to cluster near to the highest or lowest possible positions. Instead, it can be assumed that species limits scatter around intermediate values. Exceptions are sampling units in the summit regions where topographical limitations may inhibit the formation of a climate-driven upper limit of plants. We compared the measures shown in figure 3 with the upper limits reported by Sendtner (1854).

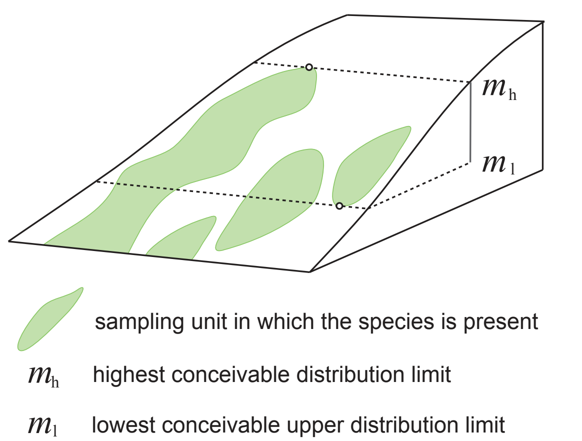

Fig. 3: Schematic representation of four ABK sampling units occupied by the same species. The exact position of occurrences within these sampling units and, as a consequence, the exact absolute upper limit, are unknown. Two measures are used to describe the possible position of a species' upper distribution limit

2.5 Taxonomic concepts and selection of species for comparison

Sendtner's taxonomic concepts were carefully interpreted in relation to the recent survey and all interpretations were archived. Many taxa considered as individual species today were not differentiated in the 19th century. Also, the new survey made pragmatic use of species aggregates. In order to avoid uncertainties several genera (*Alchemilla*, *Callitriche*, *Festuca*, *Hieracium* and *Taraxacum*) were excluded from the analysis. For the sake of simplicity we use the term species throughout the paper, even if we are partly dealing with aggregated taxa. From the remaining set of plants we removed all ruderal, euhemerobic and polyhemerobic species (Hill et al. 2002) according to the BIOLFLOR database (Klotz and Kühn 2002a, b; Kühn et al. 2004). The reason was that their habitats (mostly heavily used places around farms) were systematically neglected during the ABK survey.

2.6 Comparison of species groups

The data were split into two groups of species. The first group consists of forest species (n = 102); the second group consists of light-demanding species bound to managed and unmanaged grassland, alpine meadows, rocks, scree, bogs and swamps (n = 379). Both groups were defined according to a comprehensive list of plant species growing inside and outside of German forests (Schmidt et al. 2011).

Differences in shifts observed between both groups were tested for significance using Wilcoxon rank sum tests (also known as Mann-Whitney tests). Differences in terms of seed weight and type of reproduction were taken from the BIOLFLOR database (Klotz and Kühn 2002a, b; Kühn et al. 2004). Seed weights were available for 60 (65) forest species and for 188 (186) species of open habitats. In each group, one outlier was removed before testing for significant differences using again a Wilcoxon rank sum test. All analyses and graphics have been realized using R (R Development Core Team 2011. R: A Language and Environment for Statistical Computing. Vienna, AT).

Figure 4 (A) illustrates the altitudinal differences between recent and historic records of upper limits of 1103 species. For this figure, species were grouped according to their upper limits observed in the 19th century; each group stretches across 200 m of altitude (with an overlap of 100 m for smoother representation). The species were divided into the two subsets of species occurring in forests and species of open habitats. The vertical extension of bars in figure 4 (A) is an expression of variation between species of the respective group but it is also an outcome of vertical ranges within polygons in the ABK survey. Due to the latter reason, the upper and lower tips of the bars will rarely represent true upper limits. In most cases, true upper limits are most likely centred between the extremes. This is well illustrated by the fact that many forest species, which should not be expected above treeline, reach their – from a data view – highest possible occurrences well above treeline. Since this point cannot be clarified we decided to represent the uncertainties rather than intermediate values.

3 Results

Figure 4 (A) shows that during the recent survey, most species were found at higher elevations. Both subsets of species followed the general trend of higher upper limits in the recent survey. However, we found significant differences in magnitude. Species of the forest-group showed more differences between both surveys while differences in species of open habitats were less accentuated. At high altitudes, no clear upward shifts were observed. As shown in figure 4 (B), above approximately 2600 m a.s.l. there was not much area left at higher elevations. Accordingly, the chance to reach a habitat situated at higher elevations decreased rapidly with increasing elevation.

Average seed weights were higher among forest species ($P < 0.001$ according to a Wilcoxon rank sum test). This corresponds to the observation that plants with heavier diaspores (average > 0.5 mg) do not show fewer shifts than plants with light diaspores. Seed dispersal was found in 20% of the forest plants as compared to 43% of the control group. Switching between seeds and vegetative dispersal was frequent in both groups (68% of forest plants and 52% in the control).

4 Discussion

The prevalence of upward shift in upper species limits is in line with results from previous studies in the European Alps. However, we refrain from interpreting absolute shift rates because it is not possible to estimate the influence of different sampling intensities in retrospective. While Sendtner did

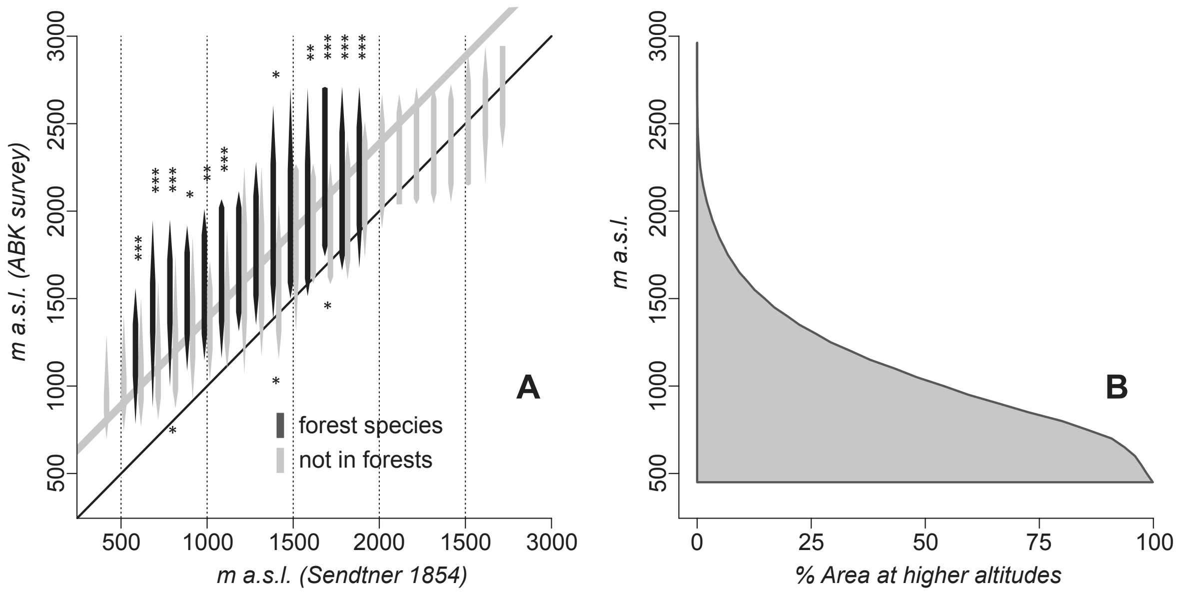

Fig. 4: (A) Upper limits of plant species as observed by Sendtner 1848–1853 (1854) and during the recent ABK survey (Urban and Mayer 1996). The pairs of vertical bars relate to groups of plants reaching their 19th century upper limit within an altitudinal range of 300 to 500 m a.s.l., 400–600 m a.s.l. and so forth up to 2700–2900 m a.s.l. The vertical extensions of the bars are defined by summarizing m_l and m_h (Fig. 3) for each group: The lower ends of the wide parts of the bars correspond to the medians of the lowest possible upper limits (m_l, Fig. 3). The upper ends of the wide parts correspond to the medians of the highest possible upper limits (m_h, Fig. 3). At the upper and lower tips, 75% of the species have reached their highest or lowest conceivable upper limit, respectively. The grey diagonal marks a shift corresponding to an observed warming of 1.7–2 K between both inventories, assuming a lapse rate of −0.47 K to −0.48 K $(100\ m)^{-1}$. The asterisks indicate if advances measured at m_h (symbols above bars) or m_l (symbols below bars) were significantly greater for forest species (* P< 0.001; ** P< 0.01; * P< 0.05). (B) At 2200 m a.s.l. only 1% of the total area is left for colonization at higher altitudes (Bavarian Alps)**

most of the survey on its own, the ABK project has been conducted by several persons working in parallel. Sendtner accomplished the survey within six years while the recent survey took 18 years. Higher sampling intensity in the second survey may have increased the chances for finding outlying occurrences of plant species at high altitudes. Both surveys were patchy. The recent survey covers 28% of the area and, even if thousands of published records document a very dense sampling, Sendtner's sampling was preferential.

Given these limitations we do not recommend giving too much weight to absolute shifts and based this study on relative differences between species groups. We assume that the relative differences between species groups can be safely interpreted. Bias in terms of relative differences between species groups could have been introduced by the sampling scheme of the ABK survey where certain forest types were excluded. The partial exclusion of forests from the ABK survey may have led to lower estimates of shifts for forest species. Nevertheless, forest species were found higher above their 19th century range than species avoiding forests indicating a low influence of this bias or larger differences between both groups than suggested by the data.

The differences between both surveys are reduced near to the summits (Fig. 4). One explanation is a reduced chance to disperse due to a lack of available area. This could be amplified by an increasing area of bare rock and screes at higher altitudes and by dispersal limitations between isolated mountain summits that inhibit plants to make use of the entire area available for colonization (Kammer et al. 2007). Another explanation is a reduced chance to introduce sampling bias due to a lack of available area.

As outlined before, land-use change in the region is mainly a matter of land abandonment causing open habitats to shrink. This suggests benefits for forest species and disadvantages for species of open habitats. According to our knowledge and according to the rich literature on vegetation succession in abandoned mountain pastures of the Alps (review by Ringler 2009), there is no evidence for processes that could have led to an upward shift of species of open habitats after cessation of land use. These plants were therefore used as a control for accelerated upward migration caused by land abandonments.

The re-establishment of forests in former pasture land increased the chances of forest species to find suitable habitats at higher altitudes (Dirnböck et al. 2003; Penuelas and Boada 2003; Gehrig-Fasel et al. 2007; Van Bogaert et al. 2011). To the contrary, species of open habitats could have had a higher chance of downslope contractions. This is a rather convincing explanation for the observed differences between forest species and species of open habitats. Moreover, the number of generalist species tends to be lower among plants of open habitats (a fact that is difficult to prove though), which means fewer chances to disperse and higher risk of extinction if growing conditions change. This would add to the fact that these species could not profit from land use change but it could also lead to an alternative explanation for the observed differences: slower reactions to warming.

In the western part of the area, summer precipitation during the times of Sendtner was about 20% higher than in the 1901–2000 period while winter precipitation was about 30% lower. However, the absolute sums have always been high so that for most plants limitation by water shortage is probably not an issue. Furthermore, drought effects can be mainly expected for the lower limits of mountain plants (Lloyd and Bunn 2007; Normand et al. 2009), which are not considered in the current study. Even if changes at the lower limits of species may change the competitive situation for others it seems to be unlikely that a general upward shift in entire groups of species could be caused by decreased summer precipitation.

Instead, severely increased nitrogen depositions of 35–45 kg a^{-1} ha^{-1} (Wochele and Kiese 2010) in the area of investigation are likely to affect the competitive situation of many species (Klanderud and Birks 2003; Bobbink et al. 2010; Löffler et al. 2011). Higher nutrient supply may compensate for reduced decomposition at higher altitudes (Schappi and Körner 1996; Körner 2003). This may have contributed to upward shifts, especially of competitive species. This requires further examination. Experiments are needed to understand how different species react to the interplay of warming and nutrient deposition (Schappi and Körner 1996; Bassin et al. 2009).

Another potential reason for the observed differences between species shifts are differences in the ability to disperse. Forest species tend to have lower abilities to disperse (Bierzychudek 1982). We show indeed, that seed weight is higher among forest species (Fig. 4). In our case, possible effects seem to be ruled out by other processes. In the Bavarian Alps temperatures shifted at a speed of 2–3 vertical meters per year. Even heavy-seeded plants have a good chance to keep pace at that rate (Cain et al. 1998); long-distance skills are not necessary. Instead, disadvantages and advantages due to abandonment of pastures and meadows or a generalist strategy seem to be more important. This underlines that interactions between dispersal and habitat availability are crucial for our understanding of vegetation changes (Higgins and Richardson 1999).

5 Conclusions

For the first time to our knowledge, the present paper addresses differences between recent upper limits of an almost entire flora of vascular plant species and corresponding upper limits recorded at the end of the Little Ice Age. The use of historical data comes at a price: The interpretation of differences between both data sets is hampered by possible sampling bias. This prevents us from interpreting an observed, accentuated difference between historical and recent observations of upper limits in the Bavarian Alps, which would nicely fit the observed warming. However, we can safely state that upper limits of forest plants advance faster than upper limits of other plants. The most likely reason for these differences is the abandonment of pastures and meadows, eventually amplified by nitrogen deposition, a more generalist strategy of many forest species and finally: warming. Dispersal ability seems to be less relevant.

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Nomenclature: Wisskirchen & Haeupler (1998)

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