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# Tree line shifts in the Swiss Alps: Climate change or land abandonment?

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## Abstract

**Questions:** Did the forest area in the Swiss Alps increase between 1985 and 1997? Does the forest expansion near the tree line represent an invasion into abandoned grasslands (ingrowth) or a true upward shift of the local tree line? What land cover / land use classes did primarily regenerate to forest, and what forest structural types did primarily regenerate? And, what are possible drivers of forest regeneration in the tree line ecotone, climate and/or land use change?

**Location:** Swiss Alps.

**Methods**: Forest expansion was quantified using data from the repeated Swiss land use statistics GEOSTAT. A moving window algorithm was developed to distinguish between forest ingrowth and upward shift. To test a possible climate change influence, the resulting upward shifts were compared to a potential regional tree line.

**Results**: A significant increase of forest cover was found between 1650 m and 2450 m. Above 1650 m, 10% of the new forest areas were identified as true upward shifts whereas 90% represented ingrowth, and we identified both land use and climate change as likely drivers. Most upward shift activities were found to occur within a band of 300 m below the potential regional tree line, indicating land use as the most likely driver. Only 4% of the upward shifts were identified to rise above the potential regional tree line, thus indicating climate change.

**Conclusions:** Land abandonment was the most dominant driver for the establishment of new forest areas, even at the tree line ecotone. However, a small fraction of upwards shift can be attributed to the recent climate warming, a fraction that is likely to increase further if climate continues to warm, and with a longer time-span between warming and measurement of forest cover.

**Keywords:** Climatic tree line; Forest cover change; Forest ingrowth; Land use change; Moving window analysis; Upward shift.

**Nomenclature**: Aeschimann & Heitz (1996).

## Introduction

The higher elevation habitats of the Alps and other mountain regions are changing. Tree line species show dramatically increased grow rates (Paulsen et al. 2000; Motta & Nola 2001), alpine plant communities and species compositions are changing (Keller et al. 2000; Pauli et al. 2001; Walther et al. 2005) and increased young tree establishment in forest gaps near the tree line can be observed in many locations (Körner 2003). But what are the driving forces behind these changes in the alpine ecosystem?

A first possible explanation of these changes is a major shift in climate. As alpine tree lines are climatically-determined ecotones (Körner 1998; Körner & Paulsen 2004), they are considered particularly sensitive to altered temperature regimes (Theurillat & Guisan 2001). Thus, the predicted climate warming (McCarthy et al. 2001) is expected to result in structural changes of tree composition as well as in a rise of the alpine tree line (Albrecht et al. 2002). The actual change in temperature is apparent already. Beniston et al. (1997) analysed the annual minimum temperatures during the last century for the European Alps and found a temperature increase of 2 °C, which is clearly above the observed global increase in temperatures of 0.7 °C (Jones & Moberg 2003). Newer results confirm these findings and report that, in particular, a strong warming has been detected in the Swiss Alps since the 1980s (Beniston 2001; Rebetez & Reinhard in press). Correspondingly, data from climate stations at the tree line ecotone in the Swiss Alps, between 1650 m and 2450 m, show a 2.5 °C mean air temperature increase during the twentieth century, with a marked increase of 1 °C since 1980 (Fig. 1). Compared to the altitudinal lapse rate showing a linear decrease of 0.55 °C on average per 100 m elevation, we would expect to find a potential tree line shift in the Swiss Alps of nearly 200 m as a result of these recent climate changes since 1980. Walther et al. (2005) found that vegetation change in the southeastern Swiss Alps has indeed accelerated since 1985, which was consistent with increased temperature regime observed at the same sites.

A second possible explanation for tree line changes

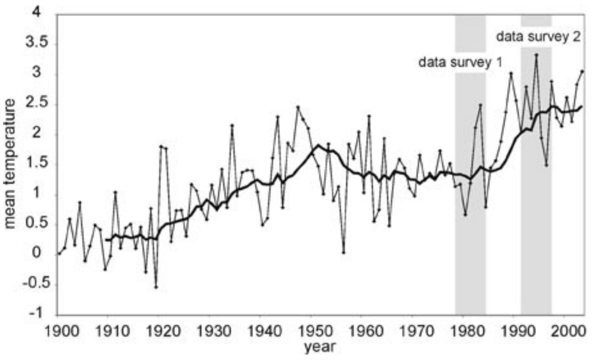

**Fig. 1.** Annual mean air temperatures for the period 1900 - 2003 in the Swiss Alps. For this analysis, 24 meteoswiss temperature stations located between 1650 and 2450 m were used. The bold line represents a 10-year mean. Grey bars represent the time-span of the two Swiss Areal Statistics data surveys AS85 and AS97.

**Fig. 2.** Study area: Dark grey area represents the study area covering the Swiss Alps.

is a change in land use intensity. Besides temperature effects, the tree line ecotone in the Alps is assumed to have been largely determined by agricultural management (Dirnböck et al. 2003). Agricultural land use is currently changing rapidly in the Alps and is considered to be one of the major driving forces behind changes in ecosystem functioning and dynamics (Cernusca 1999). In the Swiss Alps, natural undisturbed tree lines are rare, often concentrated on steep, convex and rocky slopes. For centuries the alpine farming and forest pasturing have forced the tree line downslope and prevented rejuvenation (Holtmeier 2003). However, since the mid-19th century alpine farming in the tree line ecotone has declined considerably (Surber et al. 1973; Mather & Fairbairn 2000). Simultaneously, the forest area in Switzerland has increased by roughly 30% in the last 150 years (Brändli 2000) with a large proportion of this increase having occurred on abandoned agricultural land. This close relationship between land abandonment and forest re-growth in the Swiss mountains was already shown by Gellrich et al. (2007) and Gellrich & Zimmermann (2007).

In summary, two anthropogenic disturbances – rapid climate and land use changes – appear to be closely related to changes in the tree line ecotone. Except where settlements and recreational activities will continue to develop, reduced land use intensity above the tree line and increasing temperatures are expected to act jointly to accelerate the recolonization of the potentially forested habitats (Theurillat & Guisan 2001). Yet, disentangling the respective effects of climate and land use changes in defining these already observed tree line responses to global change is a necessary step to understand, predict and eventually anticipate future changes.

Here, we present a new empirical approach that uses spatial land use data to calculate forest cover change within tree line habitats across Switzerland, and then allows dissociating the respective effects of climate and land use on observed forest cover changes near tree lines. It is based on the assumption - hereafter called 'potential regional tree line model' – that climate change, as a driver of forest regeneration, would primarily be responsible for tree line upward shifts that reach above the natural, climatically-determined tree line, whereas land abandonment would predominate below this line. Thus, if tree line upward shifts primarily occur near the climatic tree line, we argue that climate change is the primary driver, whereas if tree line upward shifts are more frequent farther away (downward) from the climatic tree line, we conclude that reduced land use pressure is responsible. In this paper, we test the plausibility of using the 'potential regional tree line model' concept as a reference to identify the likely drivers of tree line change.

We ask the following questions: 1. Did the forested area in the Swiss Alps increase between 1985 and 1997? 2. To what degree does observed forest regeneration near the alpine tree line represent a recolonization of trees into abandoned grassland (ingrowth) or a true upward shift of the local tree line? 3. Which land cover / land use classes did primarily regenerate to forest, and which forest structural types were primarily developed in the regeneration process? 4. To what degree can we attribute locally observed tree line upward shifts to their potential drivers, changes in climate and/or land use?

## Data and Methods

### *Study area*

The study was carried out in the Swiss Alps, featuring a complex topography and a highly fragmented landscape (Fig. 2). The Swiss Alps are orientated WSW to ENE, thereby creating a topographic barrier to precipitations. Along a north-south gradient of 220 km, three main climate types can be identified. The northern Alps have an oceanic climate (generally humid, with cool summers, and moderately cold winters), the central Alps are characterized by a continental climate (hot and dry summers with intensive radiation, cold winters), while the climate of the Southern Alps is more of a Mediterranean type (hot and partly dry summers intermitted with heavy rainfalls, moderately cold and humid winters). This small-scale climate diversity leads to remarkable differences of vegetation over short distances. In the northern Swiss Alps, *Picea abies* is the dominant tree line species associated with *Sorbus aucuparia* and *Alnus viridis*. In the dry interior valleys the dominant tree line species are *Larix decidua* and *Pinus cembra*, locally replaced by *Pinus mugo* ssp. *mugo* in some regions in the East. In most of the southern parts of the Swiss Alps, *Larix decidua* and *Picea abies* dominate the uppermost forests, but *Fagus sylvatica* can reach the tree line in the southernmost parts.

### *Data sets used*

For our analysis of tree line change, we used data from the repeated Swiss land use statistics GEOSTAT (Anon. 2001a), which sampled and stored land use types on a 100 m point lattice for the whole area of Switzerland (41 300 km$^2$) in two surveys (1979-1985 and 1992-1997). To generate this data set, aerial photographs were overlaid with transparent sheets featuring a 100 m × 100 m lattice of regularly spaced sampled points. A combined land use/land cover classification was attributed to each intersection of the 100-m coordinate network (Anon. 2001a). We used the data from the 1979/1985 (hereafter AS85 data set) and the 1992/1997 (hereafter AS97 data set) surveys representing an average time span of 12 years, with few points spanning 13 years. While the majority of the classes (72 and 74 respectively) were derived by interpreting simply the intersection points of the 100 m lattice, the classes relevant to trees and forests were derived from a more complex approach and in the same manner as done by the Swiss national forest inventory (Anon. 1992; Brassel & Lischke 2001). A 50 × 50 m sub-grid of 25 points (10 m distance between points) is analysed around each lattice point, and tree height as well as tree cover fraction within this sub-grid area is assessed and used to distinguish individual classes of woody vegetation. For the current study, a forest definition combining the four classes closed forest, open forest, shrub forest and grove was used (Table 1). All other classes were set to 'no forest' even if they contained some low woody vegetation like dwarf-shrubs or scrub. Shrub forest and grove were thereby included into the forest class to account for the open and often small-scale structure of Swiss mountain forest and to detect even minor shifts in forest cover change.

In addition, with this aggregation we only identified areas as newly forested areas which changed from unforested areas to one of the forest classes. For subsequent analyses we used the official 100-m grid data set (converted from the point lattice data set by the Swiss Federal Statistical Office), which allows for easier analysis of neighbourhood metrics. Lattice and grid are thus used interchangeably.

### *Derivation of forest cover change*

To calculate the forest cover change between 1985 and 1997, the data from the two surveys was reclassified into forest/non forest binary information. By adding the two grids, newly forested areas, deforested areas as well as areas with no change in forests were identified. The resulting grid was combined with a digital elevation model to add altitude information. We used the Wilcoxon rank sum test to see if the net effect of the new establishment and removal of forest areas was different from zero in three elevation bands.

**Table 1.** Criteria of forest definitions according to the Swiss land use statistics GEOSTAT.

| Criteria | Closed forest | Open forest | Shrub forest | Grove |
|---|---|---|---|---|
| Stand height | ≥ 3 m | = 3 m | any | >= 3 m |
| Stand width | ≥ 25 m | ≥ 50 m | >= 25 m | any |
| Canopy cover | ≥ 60 % | > 20-60 % | >= 60 % | any |
| Original classes | 10,11,14 | 12,13 | 15 | 17,18,19 |

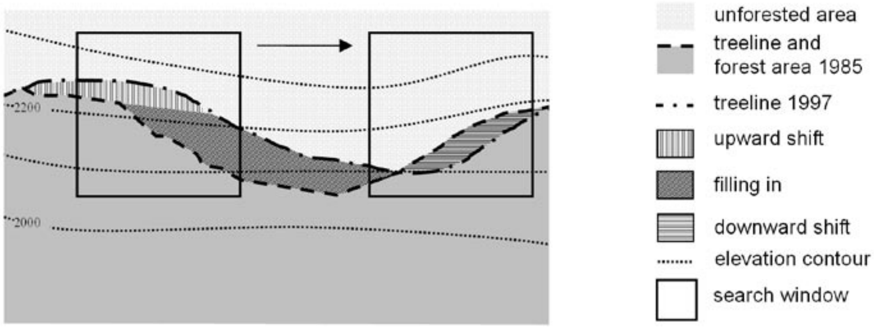

**Fig. 3.** Conceptual model for discriminating between upward shifts, filling in (ingrowth), and downward shifts. The search window to the left identifies an upward shift, while the window to the right identifies a downward shift of the highest forest pixels within the window when comparing AS85 with AS97.

*Separating upward shift from ingrowth*

The methods described above allow us to quantify the forest cover change but not to detect its nature. Specifically, it does not allow the distinction between filling in of a suppressed tree line (ingrowth) from upward shifts. In order to separate these two types of forest regeneration and to quantify the maximum ascent of the upward shifts, we developed a moving window algorithm based on the following principle: within a search neighbourhood, we compared the elevations of the highest forest areas between the two surveys, and we linked this analysis to the newly established forests as seen in AS97 (Fig. 3). To do this, we had recourse to focal analyses (Tomlin 1990), which statistically summarize the values of all cells contained in a moving window of defined size and assigns the resulting summary statistic (e.g. min, mean or max) to the central (focal) cell. The window is moved across the whole study area and each cell obtains, as its new value, the statistics calculated on all neighbouring cells.

The following steps were conducted in a GIS: 1. So-called *focalmax* analyses using a quadratic window of varying size (see below) were applied to two spatial layers originating from both surveys (AS85 and AS97) that contained an elevation grid each with all non-forest areas masked out, thus revealing per pixel the highest forest area within the search neighbourhood. 2. A difference grid was calculated between the two processed land use layers, indicating local upward or downward shifts relative to the search window. 3. Pixels in the AS97 map were identified that (a) represented new forest areas (compared to AS85), and (b) had elevations that coincided with the elevation of the identified upward shifted highest forest pixels (step 1). The final result of this moving window algorithm was a layer containing only the uppermost pixels of true local upward shifts of forests with the amount of upward shift attached in metres. All forested pixels representing a filling in of open forest gaps (zero elevation difference to AS85 highest forest within moving window) were removed by this analysis. Samples of the resulting layer were visually screened to verify that identified pixels with true upward shifts did not represent forest ingrowth. Finally, the true upward shifts and their source pixels were overlaid with the AS85 data set and the AS97 data set, respectively, to identify the former and new land use classes of the upward shifted forests.

As our aim was to analyse the tree line dynamic on a regional scale we presumed an intermediate moving window of a size around 1000 m to be best suited. With small windows (< 500 m), slopes are not covered sufficiently and small scale changes tamper the ingrowth versus upward shift ratios. On the other hand, very large window sizes (> 1500 m) often include over-regional effects, resulting in large-area combination of opposite slopes of different valleys, thus potentially overestimating climate-driven forest increase. Following, results are presented on a 900 m resolution. However, to test for potential scaling biases, the above analyses were calculated with additional window sizes of 500, 600, 700, 800, 1000, 1100, 1200, 1500, and 3000 m. We present the full range of these results in App. 1. In this paper, however, we only report the findings from the 900 m window, since we found the results to be clearly stable around a window size of 800-1200 m.

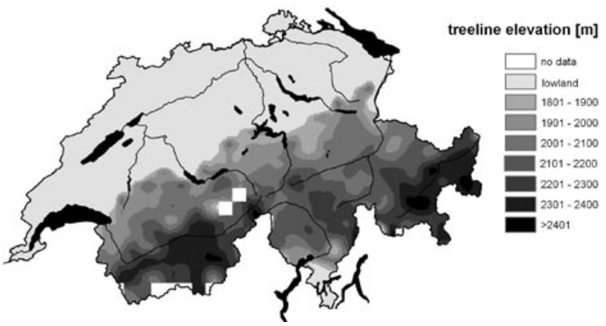

**Fig. 4.** Calculated potential regional treeline elevations in Switzerland. Data source: Swiss land use statistics 85 GEOSTAT.

**Table 2.** Number of areas with forest cover change per altitude range according to the Swiss land use statistics 85 and 97. One area equals one ha in size. The lowest forested area is located at 192 m, the highest at 2414 m.

| Altitude range (m) | New forests (ha) | % of total forests | Deforestation (ha) | % of total forests | *p*-value[1] |
|---|---|---|---|---|---|
| 192-800 | 5864 | 1.3 | 5984 | 1.3 | 0.31 |
| 801-1650 | 14 880 | 3.1 | 5461 | 1.2 | < 0.0001 |
| 1651-2414 | 10 651 | 4.8 | 1079 | 0.5 | < 0.0001 |

[1] Wilcoxon signed rank sum test.

### *Evaluating likely drivers of tree line upward shifts*

To determine the drivers of the forest regeneration according to our potential regional tree line model, we analysed those forests that were identified above to shift upward, and we related these shifts to the potential regional tree line. The potential regional tree line was calculated following an approach developed by Paulsen & Körner (2001), where the regional tree line was derived from highest forest patches identified by a moving window algorithm. Based on the AS85 data set we derived the regionally highest forest patches in a rectangular 10 km × 10 km moving search window using the *focalmax* function to derive the potential climatic tree line. A spatial resolution of 10 km is small enough to capture regional differences in climatic tree line elevation but large enough to remove information reflecting small scale fluctuations of local growth conditions on trees (Paulsen & Körner 2001). The extracted highest forested pixels were then spatially interpolated using regression splines in order to get a regional smoothed tree line with a resolution of 10 km (Fig. 4). Prior to the spatial interpolation, a GIS-filter was applied removing all tree line pixels which were not lower than the actual highest land surface elevation within the respective window, therefore removing pixels representing forest-covered mountain tops (Paulsen & Körner 2001).

To test a possible climate change influence, the identified upward shifts were compared to the potential regional tree line by calculating the difference in elevation of the respective pixels. The altitude of the potential regional tree line was thereby considered as a reference. Upward shifts above the potential regional tree line were considered to be influenced primarily by climate change, while upward shifts below the potential regional tree line were interpreted as primarily influenced by land abandonment.

## Results

### *Forest cover change*

The nation-wide analysis of the land use statistics AS85 and AS97 showed that forest cover had considerably changed in this 12-year time period (Fig. 5). At elevations above 800 m – including the tree line range between 1650 m and 2450 m – we observed a significant net forest regrowth (Table 2). This net increase in forest area was particularly strong between 1400 m and 2100 m.

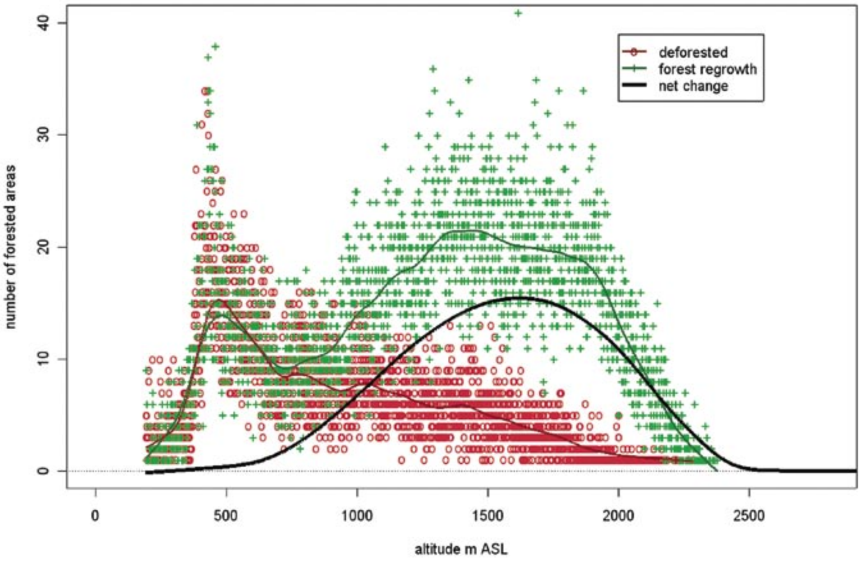

**Fig. 5.** Changes in forested areas between 1985 and 1997. Data source: Swiss land use statistics GEOSTAT. One symbol represents the area of 1 ha. Red and green symbols stand for areas where forest disappeared and was newly established, respectively. See text for forest and non-forest definitions.

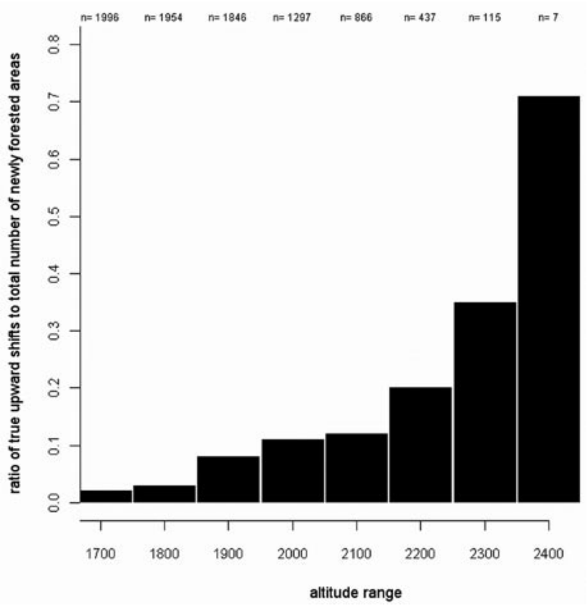

**Fig. 6.** Fraction of pixels identified to be true local upward shifts relative to the total number of newly established forest per altitude band. *n* indicates the total number of newly forested areas per 100 m altitude band.

### *Upwards shift versus ingrowth*

The newly regenerated forests were separated through our algorithm into areas with forest ingrowth and areas with true local upward shifts. A visual inspection of the sample areas confirmed the functioning of the algorithm, i.e. no overestimated shifts or relevant missed patches were found. Results showed that in the Swiss tree line range the ratio of true upward shifts to total forest expansion is positively correlated with elevation, i.e. the higher the elevation the greater the portion of actually upward shifting forest as compared to simple ingrowth (Fig. 6). The proportion of upward shifts rises from only 3% in the 1650-1750 altitudinal band to 19% in the 2050-2150 band, and to 49% in the 2250-2350 band. The uppermost band located between 2350 m and 2450 m revealed a proportion of 86% upward shifts, though it contains only seven newly forested areas. When analysing the sum of all new forest pixels above 1650 m, we found 10% (893 ha) to be true upward shifts whereas 90% (7,729 ha) were considered forest ingrowth. When restricting the analysis to elevations above 2250 m, however, 51% (62 ha) were found to be true upward shifts.

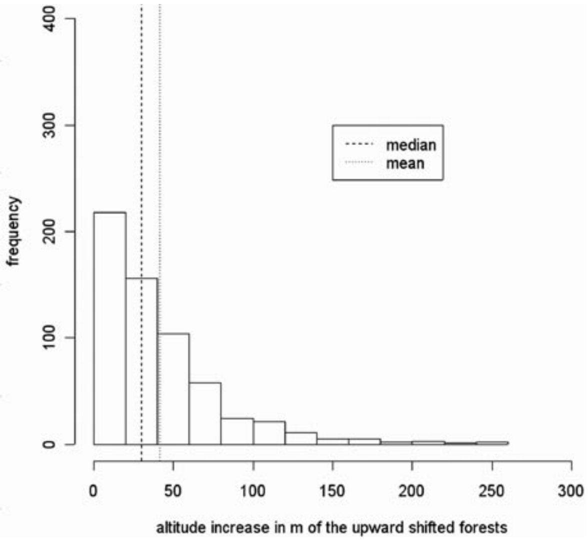

**Fig. 7.** Histogram of locally highest upward shifts of forests at the Swiss treeline with median (dotted line) and mean (solid line) values of upward shifts.

The developed algorithm also quantified the altitude increase of the upward shifted forests. It is important to notice that this is the highest upward shift per 900 m window as identified by our algorithm. It thus represents the average of the upward shifting moving front, not the mean of all newly established shifting forest pixels. In the Swiss tree line range, between 1650 m and 2450 m, the distribution of the altitude increases showed an exponential decline (Fig. 7). Most forest shifted upwards between 1 and 50 m. On the average an upward shifted forest rose by 37.9 m with a median of 28.0 m.

When analysing the distribution of upward shifts in 100 m altitude bands, ranging from 1650 m to 2450 m (Fig. 8), we found similar patterns as in Fig. 7. Each altitude band showed a skew distribution with a median around 28 m and single outliners above 100 m altitude increase. The exception to this distribution was found in the very highest class, which showed a more symmetric and increased mean upward shift, yet it was observed in few cases only (*n* = 6) and thus may not represent a trend.

### *Scaling bias of the algorithm*

To test for potential scaling biases, the above moving window algorithm was calculated using different window sizes. All results are provided in the electronic App. 1. No strong scaling effects concerning the distribution of the upward shifted forest pixels were found. The distributions and therefore also the median and mean values of the upward shifts were robust. Equally robust towards changing window sizes was the count of the identified upward shifted forest pixels in the highest altitude bands, indicating that the highest forests are generally selected independent of the window size. However, the bigger the size of the moving window, the smaller was the overall count of identified upward shifted forests. This results directly form the focalmax function which selects only the highest forest pixel within the moving window. As a

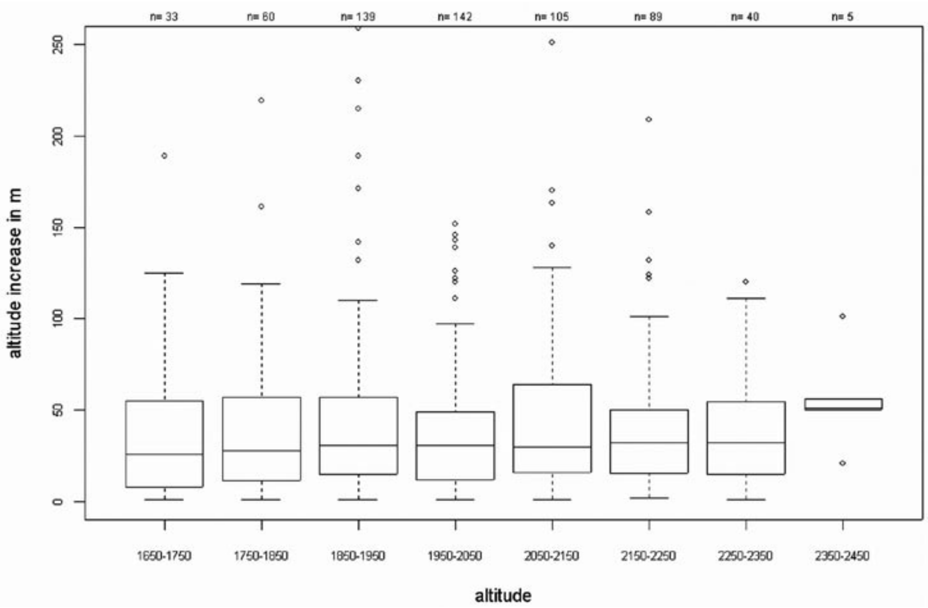

**Fig. 8.** Range and variation of upward shifted forests in bands of 100 m along the altitude gradient. *n* indicates the total number of upward shifted forest pixels per altitude band.

consequence, the ratio of upward shifts reaching above the climatic tree line to the upward shifts reaching only elevations below the climatic tree line rises with growing window size (from 2% for window size 500 m to 16% for window size 3000 m, see Table A1 in App. 1). However, at intermediate window sizes (800–1200 m), the ratio of primarily climate-driven versus total number upward shifts varies only slightly between 4% and 6%, and is thus still fairly stable.

*Former and new classes of tree line upward shifts*

Overall, 26% of the identified upward shifts originated from areas without any woody vegetation in the AS85, whereas 74% started from low-growing woody vegetation (scrub) (Fig. 9). We did not find a clear elevational trend towards the potential regional tree line. 42% of the upward shifted forest grew after 12 years to grove, 40% to shrub forest, 10% to open forest, and 8% to closed forest (Fig. 10). In summary, more than 80%

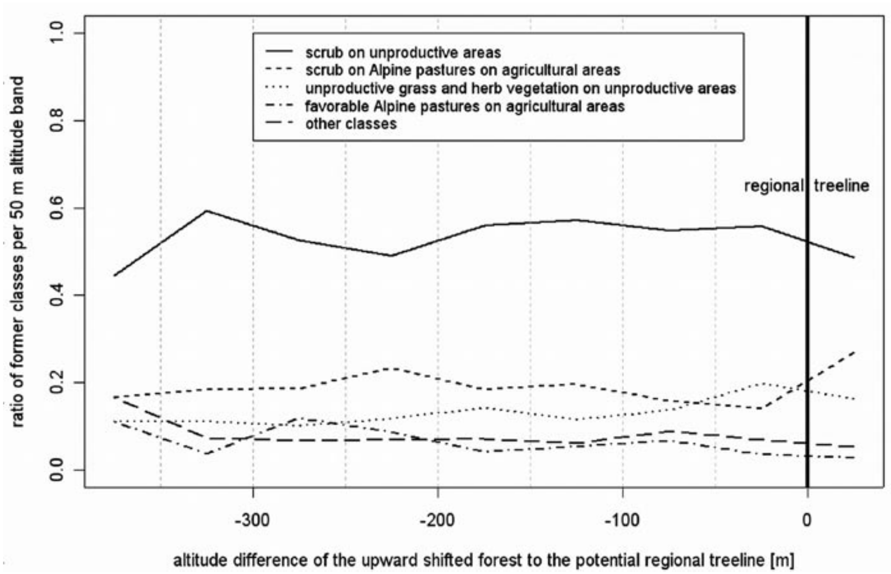

**Fig. 9.** Ratio of the original AS85 classes contributing to the identified upward shifts per 50 m altitude band in reference to the potential regional treeline. The line 'other classes' represents the sum of all classes with a ratio of less than 5 % per altitude band.

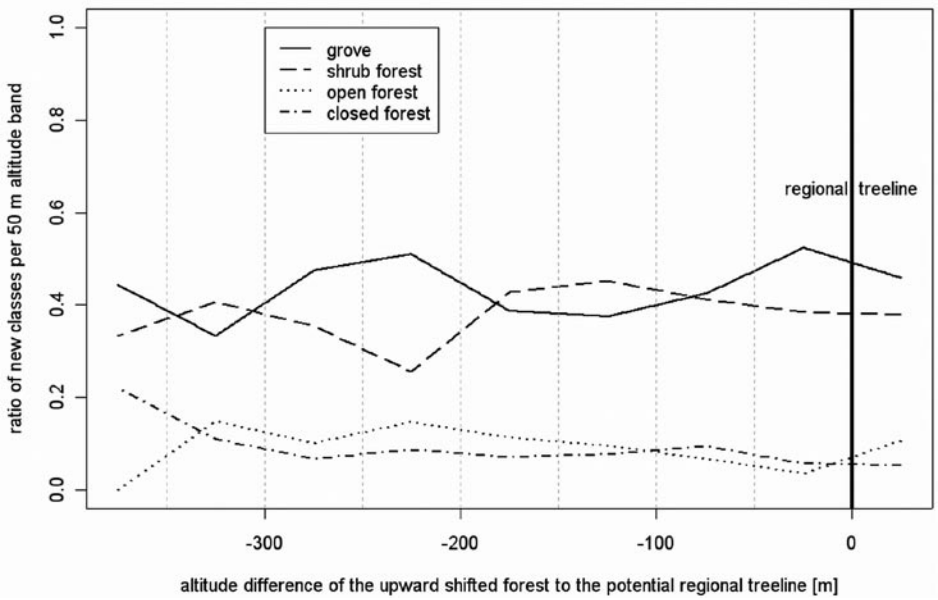

**Fig. 10.** Ratio of new AS97 forest classes per 50 m altitude band in reference to the potential regional treeline. New classes consist primarily of low height (< 3 m; grove and shrub forests).

of the newly forest patches were shrub forests or open tree populations of low canopy height (<3 m), distinctly separated as the dominant group from the established tree stands (open and closed forests with canopy heights >3 m). In addition, an altitudinal trend was evident in that the low canopy height types became more frequent towards the potential regional tree line at the cost of the established tree classes.

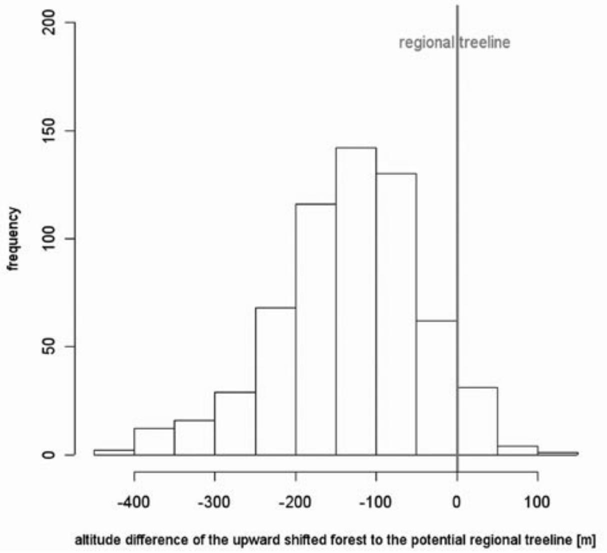

**Fig. 11.** Number of identified upward shifted forest pixels relative to the altitude of the potential regional treeline (vertical line).

### *Drivers of tree line upward shifts*

To identify the likely drivers for the found upward shifts, we analysed how close the upward shifted forest pixels were with respect to the potential regional tree line (Fig. 11). Results showed that only 4% of the upward shifted forests reached above the potential regional tree line (vertical line in Fig. 11), while 96% of all identified upward shifts were located below this line. The frequency of upward shifts with respect to the regional tree line showed a Gaussian distribution. The majority (78%) of all upward shifts was located within a band of 300 m below the potential regional tree line, and with a peak around 125 m below the potential regional tree line.

## Discussion

### *New forest area – ingrowth vs. upward shift*

Considerable changes in the forested area were detected although our data only covered a time span of 12 years. This is a relatively short time period compared to the growth and life cycle of trees. Certainly, the wide definition and aggregation of 'forest' including trees of low canopy height (shrub forest and grove) used in this study may have prevented the detection of some forest conversions from smaller to taller trees. In general, the results of the forest change analysis confirmed the long-term trend of forest area increase in Switzerland (Brändli 2000; Mather & Fairbairn 2000). In the Swiss tree line range between 1650 m and 2450 m, our results show a significant increase of newly established forests, which clearly exceeds the area increase observed at lower altitudes. This corresponds well to the results of the analysis of the recent Swiss national forest inventory (Brassel & Brändli 1999), where the natural forest regeneration was found to be especially high towards today's tree line. The Swiss Statistical Office also states that between the 1980s and 1990s new forest established mainly in steep and isolated areas and on mountainous and alpine areas below the natural tree line (Hotz & Weibel 2005).

By separating the forest expansion at the Swiss tree line into forest ingrowth and upward shifts, we found a large portion of new forest resulting from ingrowth rather than from true upward shifts. Similar results were found in North America. Szeicz & MacDonald (1995) analysed white spruce dynamics at the alpine tree line in northwestern Canada over 100-150 years and found only minor changes in the upper limits of trees, but an increasing population density within the forest stands. Klasner (1998, 2002), who analysed changes in alpine tree line vegetation patterns in Glacier National Park, also observed changes in the spatial composition while tree line location was even found to remain the same. Shiyatov et al. (2005) found a marked increase in forest density and filling in of open patches below the tree line and only minor upward shifts in the polar Ural Mountains in Russia in an analysis of forest structural changes covering 90 years. However, in other regions, such as the northern European mountains, a recent advance of the tree limit has been reported (Kullman 2001, 2002). In the Swedish Scandes several species have advanced rapidly since the 1950s. While such clear trends could not be supported by our analyses, which concurs with the 'conservative behaviour' of the tree line in the Alps as described by (Grace et al. 2002), we have found evidence that upward shifts indeed transcend the local tree lines. We discuss possible reasons thereof below.

### *Quantifying upward shifts*

Within the upward shifts identified, some remarkable absolute changes in elevation were found. A maximum of more than 100 m elevation increase of the local tree line within only 12 year appears unrealistically high and even the median of 28 m is surprising. Even more so if our findings are compared to historical tree line fluctuations. The widely accepted palaeoecological hypothesis that the upper tree line in the alpine region oscillated by no more than ± 100 m throughout the Holocene (e.g. Burga & Perret 1998; Haas et al. 1998) was lately confirmed by pollen and macrofossil studies (Tinner & Theurillat 2003) as well as a model-based reconstruction of Holocene tree line dynamics (Heiri et al. 2006). Even though charcoal analysis suggests a tree line that is at least 200 m higher than the one proposed by palynologists (Carcaillet & Brun 2000), an actual shift of 28 m (median value) within 12 years seams highly unlikely.

However, all of our findings represent maximum upward shifts within search windows and do not quantify mean upward shift. Thus, these numbers represent the upward shift of the moving tree line front, not the average forest area upward shift. Also, it is important to note, that our classification of 'forest' does not necessarily mean that full grown trees have established within 12 years. They represent both small woody structures (<3 m tall) and larger trees. And often , trees had already been there before, but within 12 years they reached sufficient stand height and stand width to be classified as forest. This effect can be seen in the fact that the vast majority of new forests has developed from scrub vegetation. The results thus also represent altitude increases that had indeed started earlier.

### *Land use changes as major driver for ingrowth and upward shifts*

Land abandonment has been identified as the main driver for forest re-growth in alpine areas by several authors (Surber et al. 1973; Walther 1986; Mather & Fairbairn 2000; Anon. 2001a). The large amount of 90% ingrowth near the alpine tree line we have found suggests that limitations to forest expansion have considerably changed recently, with the trees reacting immediately by filling in the open forest gaps. Land abandonment may explain such behaviour. In the last decades alpine farming has declined in the Swiss tree line ecotone; agriculture retreated from the peripheral regions and from the steep mountain regions where machines are of limited use (cf. introduction). Less intensive sheep, goat and cattle grazing has additionally allowed the forests re-invade to their potential habitat from patches in the vicinity. Such factors were identified to explain forest regeneration on abandoned agricultural land primarily in the montane belt (Gellrich et al. 2007).

Besides ingrowth, land abandonment may also have led to some of the 10% identified upward shifts. According to our regional tree line model, upward shifts of forests located below the potential regional tree line (= climatic tree line) are most likely human driven because climatically, they should have risen to a higher elevation already earlier. This hypothesis is partly confirmed by the fact that we found 25% of the upward shifts to regenerate from agricultural areas where land use change was obviously taking place. These upward shifts follow the same drivers as we have discussed for the forest ingrowth above. However, 75% of the upward shifts regenerated from unproductive areas. These areas were possibly abandoned already by alpine farmers several decades ago, as is documented for example for the southern part of Switzerland (Surber et al. 1973). Therefore, they may also be assigned to land use change. Yet, these upward shifts could also indicate a climate change effect, as they occur on steep and isolated areas which were hardly managed by mountain farmers and therefore could have regenerated already much earlier.

### *Climate change and likely reasons for a possible underestimation*

Although our results and research cited above describe land abandonment as the major driver for spatial changes of forests near tree line, it is unlikely that observed climatic changes had no effect at all. In many other ecosystems the effect of global warming on distribution of biota has been demonstrated (Parmesan & Yohe 2003). As the warming in the Alps has been reported by many authors (Beniston et al. 1997; Anon. 2001c; Begert et al. 2005; Beniston 2005), a potential tree line upward shift of almost 200 m can be expected from the recent warming. Although we did not detect such a strong overall tree line shift, we clearly found local changes in the elevational tree distribution. Yet, the marginal evidence for the role of climate change as the likely driver for the few upward shifts detected by our analysis may have different causes.

Firstly, local effects such as microclimate, herbivore pressure (Cairns & Moen 2004), and frequent stochastic processes such as avalanches, snow creeping, or discontinuous permafrost may have forced the local tree line below the average potential regional tree line. As a consequence, also areas close to, but below the potential limit may be reacting to recent changes in climate. These areas were not interpreted as climatically influenced by our potential regional tree line model approach.

Secondly and related to the first, responses to land abandonment may partly also be influenced by changes in climates. The sensitivity of anthropogenic tree lines to climate has been described by Holtmeier & Broll (2005). They state that after the removal of former forests, site conditions can change radically and prevent trees from invading former pastures. Subalpine pasture grassland in particular can be very resistant against invasion of tree species and may thus slow down tree line upward shifts considerably (Dullinger et al. 2004). If these limiting conditions improve due to changing climate, the subsequent forest advance could be considered as climate-driven even though it actually occurs below the climatic tree line. However, with our approach we only detect these upwards shifts as climate-driven once they reach at least the 1985 potential regional climatic tree line. Thus, we may underestimate the climate effect with our potential regional tree line approach.

Thirdly, the short time frame of only 12 year between the two surveys may be another reason for the marginal climate effect found in our analyses as it does not allow the trees to fully react to recent changes in climate. This could explain why over 80% of our upward shifted forests were smaller than 3 m in height. There is evidence for a 'lagged response' of tree lines to a changing climate and tree recruitment peaks (Zackrisson et al. 1995; Camarero & Gutierrez 2004). Trees are restricted in their migration pace as seed dispersal and regeneration ecology inhibit this process (Dullinger et al. 2004). In the region of the climatic tree line, trees are conditional upon exceptionally good years of regeneration in order to shift upwards. Depending on the tree species, a good seed crop year occurs only once every 7-10 year (Holtmeier 2000), which leads to fewer upward shift opportunities than expected from the 12-year span. Additionally, not only seed quantity but also seed quality and favourable growing conditions after seedling establishment are essential for a successful forest advance. The resulting 'regeneration pulses' (Zackrisson et al. 1995) may lead to considerable time lags in the re-adjustment of the tree line to climate change. To reliably capture such key events, monitoring the dynamics over a longer time span is imperative. The importance of longer time frames when analysing tree migration is also confirmed by Holtmeier & Broll (2005) who found tree line sensitivity to be different for various time-scales: the medium-term response (some years to a few decades) is mirrored by increasing tree coverage in contrast to forest and tree limit advance or retreat in the long term response (several decades to hundreds of years). According to their classification, our analysis lies in medium-term response which would explain the few found responses to a changing climate. In the future, it is therefore important to capture long-term changes by extending the analysis of tree line and forest dynamics in time.

### *Effectiveness of the algorithm and the potential tree line model*

As the algorithm has successfully separated elevational upward shifts from forest ingrowth with no strong sensitivity to changing window size for most characteristics analysed, it appears suitable for analysis of spatial patterns of the observed forest expansion near high elevation tree lines. However, the variation of moving window size resulted in different forest increase ratios. Thus, statements addressing likely drivers for forest changes (climate and land use change) always have to refer to the moving window sizes used. Overall, we believe that the results using medium-sized moving windows

(800-1200 m) are robust and allow realistic estimates of climate effects near the regional climatic tree line. For areas below the potential regional tree line, our model may not have accurately identified or quantified climate effects as likely driver.

## Conclusion

Our results have revealed extensive changes near the Swiss tree lines. Not only has there been widespread ingrowth but we also found a considerable occurrence of upward shifts which is remarkable for a heavily human dominated tree line landscape. Our results suggest that land abandonment is the most dominant driver for both forest ingrowth and a majority of the upward shifts in the Swiss Alps near the tree line. The relatively small effect of climate change is attributed to anthropogenic suppression of the current tree line and the short time frame of only 12 year between the two surveys. It is therefore assumed that in the long run, climatic effects will become more obvious as forests rise towards their climatic potential. Future work should focus on long-term and area-wide monitoring of regeneration and tree development to capture the full dynamics in the tree line ecotone and better identify the underlying drivers.

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### References

Anon. (Swiss Federal Statistical Office) 1992. *Die Bodennutzung der Schweiz: Arealstatistik 1979/85 Kategorienkatalog*. pp. 189. Bundesamt für Statistik, Bern, CH.

Anon. (Swiss Federal Statistical Office) 2001. *The changing face of land use: Land use statistics of Switzerland*. Swiss Federal Statistical Office, Neuchâtel, CH.

Aeschimann, D. & Heitz, C. 1996. *Index synonymique de la Flore de Suisse*. Centre du Réseau Suisse de Floristique (CRSF), Genève, CH.

Albrecht, C., Baccini, P., Branzini, A., Beniston, M., Bugmann, H., Bürki, T. Fankhauser, S., Fischlin, A., Fuhrer, J., Gonseth, Y., Güsewell, S., Hohmann, R., Janssen, J., Joos, J., Kägi, W., Keuerleber-Burk, D.K., Künzli, N., Oglesby, L., Previdoli, P., Schädler, B., Stocker, T. 2002. *Das Klima ändert - auch in der Schweiz: die wichtigsten Ergebnisse des dritten Wissensstandsberichts des IPCC aus der Sicht der Schweiz*. Beratendes Organ für Fragen der Klimaänderung, Bern, CH.

Begert, M., Schlegel, T. & Kirchhofer, W. 2005. Homogeneous temperature and precipitation series of Switzerland from 1864 to 2000. *Int. J. Climatol*. 25: 65-80.

Beniston, M. 2001. The effect of global warming on mountain regions: a summary of the 1995 report of the Intergovernmental Panel on Climate Change. In: Visconti, G., Beniston, M., Iannovelli, E.D. & Barba, D. (eds.) *Global change and protected areas*, pp. 155-185. Kluwer Academic Publishers, Dordrecht, NL.

Beniston, M. 2005. Mountain climates and climatic change: An overview of processes focusing on the European Alps. *Pure Appl. Geophys*. 162: 1587-1606.

Beniston, M., Diaz, H.F. & Bradley, R.S. 1997. Climatic change at high elevation sites: An overview. *Clim. Change* 36: 233-251.

Brändli, U.-B. 2000. Waldzunahme in der Schweiz – gestern und morgen. —*Informationsbl. Forsch.bereich Landschaft* 45: 1-4.

Brassel, P. & Brändli, U.B. 1999. *Schweizerisches Landesforstinventar Ergebnisse der Zweitaufnahme 1993 - 1995*. Eidgenössische Forschungsanstalt für Wald, Schnee und Landschaft (WSL), Birmensdorf and Bundesamt für Umwelt, Wald und Landschaft (BUWAL), Bern, CH.

Brassel, P. & Lischke, H. 2001. *Swiss National Forest Inventory: Methods and Models of the Second Assessment*. Swiss Federal Research Institute WSL, Birmensdorf, CH.

Burga, C.A. & Perret, R. 1998. *Vegetation und Klima der Schweiz seit dem jüngerem Eiszeitalter*. Ott Verlag, Thun, CH.

Cairns, D.M. & Moen, J. 2004. Herbivory influences tree lines. *J. Ecol*. 92: 1019-1024.

Camarero, J.J. & Gutierrez, E. 2004. Pace and pattern of recent tree line dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. *Clim. Change* 63: 181-200.

Carcaillet, C. & Brun, J.J. 2000. Changes in landscape structure in the northwestern Alps over the last 7000 years: lessons from soil charcoal. *J. Veg. Sci*. 11: 705-714.

Cernusca, A. 1999. Aims and Tasks of ECOMONT. In: Cernusca, A., Tappeiner, U. & Bayfield, N. (eds.) *Land-use changes in European Mountain Ecosystems. ECOMONT – concepts and results*, pp. 13-35. Blackwell, Berlin, DE.

Dirnböck, T., Dullinger, S. & Grabherr, G. 2003. A regional impact assessment of climate and land-use change on alpine vegetation. *J. Biogeogr*. 30: 401-417.

Dullinger, S., Dirnböck, T. & Grabherr, G. 2004. Modelling climate change-driven tree line shifts: relative effects of temperature increase, dispersal and invasibility. *J. Ecol*. 92: 241-252.

Gellrich, M. & Zimmermann, N.E. 2007. Land abandonment in the Swiss mountains: A spatial statistical analysis at the regional scale. *Landscape Urban Planning* 79: 65-76.

Gellrich, M., Bauer, P., Zimmermann, N.E. & Koch, B. 2007. Agricultural land abandonment and natural forest re-growth in the Swiss mountains: A spatially explicit economic analysis. *Agricult. Ecosyst. Environ*. 118: 93-108.

Grace, J., Berninger, F. & Nagy, L. 2002. Impacts of climate change on the tree line. *Ann. Bot.* 90: 537-544.

Haas, J.N., Rischoz, I., Tinner, W. & Wick, L. 1998. Synchronous Holocene climatic oscillations recorded on the Swiss Plateau and at timberline in the Alps. *Holocene* 8: 301-309.

Heiri, C., Bugmann, H., Tinner, W., Heiri, O. & Lischke, H. 2006. A model-based reconstruction of Holocene tree line dynamics in the Central Swiss Alps. *J. Ecol.* 94: 206-216.

Holtmeier, F.-K. 2000. *Die Höhengrenze der Gebirgswälder*. Natur & Wissenschaft, Münster, DE.

Holtmeier, F.-K. 2003. *Mountain timberlines: Ecology, patchiness, and dynamics*. Kluwer Academic Publishers, Dordrecht, NL.

Holtmeier, F.-K. & Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar tree lines to environmental change at landscape and local scales. *Glob. Ecol. Biogeogr.* 14: 395-410.

Hotz, M.C. & Weibel, F. 2005. *Arealstatistik Schweiz: Zahlen - Fakten – Analysen*. Swiss Federal Statistical Office, Neuchâtel, CH.

Houghton J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J. & Xiaosu, D. 2001. *Climate Change 2001: The Scientific Basis*. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), pp 944. Cambridge University Press, Cambridge,UK.

Jones, P.D. & Moberg, A. 2003. Hemispheric and large-scale surface air temperature variations: An extensive revision and an update to 2001. *J. Climate* 16: 206-223.

Keller, F., Kienast, F. & Beniston, M. 2000. Evidence of response of vegetation to environmental change on high-elevation sites in the Swiss Alps. *Reg. Environ. Change* 1: 70-77.

Klasner, F.L. 1998. *Spatial changes in alpine tree line vegetation patterns in Glacier National Park, Montana*. Department of Geography, Oregon State University, Corvallis, OR, US.

Klasner, F.L. 2002. A half century of change in Alpine patterns at Glacier National Park, Montana, U.S.A. *Arct. Alp. Res.* 34: 49-56.

Körner, C. 1998. A re-assessment of high elevation tree line positions and their explanation. *Oecologia* 115: 445-459.

Körner, C. 2003. *Alpine plant life – Functional plant ecology of High Mountain ecosystems*. 2nd. ed. Springer, Berlin - Heidelberg, DE.

Körner, C. & Paulsen, J. 2004. A world-wide study of high altitude tree line temperatures. *J. Biogeogr.* 31: 713-732.

Kullman, L. 2001. 20th centure climate warming and tree-limit rise in the southern Scands of Sweden. *Ambio*. 30: 72-80.

Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *J. Ecol.* 90: 68-77.

Mather, A.S. & Fairbairn, J. 2000. From floods to reforestation: The Forest Transition in Switzerland. *Environ. History* 6: 399-421.

McCarthy, J.J., Canziani, O.F., Leary, N.A., Dokken, D.J. & White, K.S. 2001. *Climate Change 2001: Impacts, Adaptation & Vulnerability.* Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), pp 1000. Cambridge University Press, Cambridge,UK.

Motta, R. & Nola, P. 2001. Growth trends and dynamics in subalpine forest stands in the Varaita Valley (Piedmont, Italy) and their relationships with human activities and global change. *J. Veg. Sci.* 12: 219-230.

Parmesan, C. & Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37-42.

Pauli, H., Gottfried, M. & Grabherr, G. 2001. High summits of the Alps in a changing climate. The oldest observation series on high mountain plant diversity in Europe. In: Walther, G.R., Burga, C.A. & Edwards, P.J. (eds.) *Fingerprints of climate change. Adapted behaviour and shifting species ranges*, pp. 139-149. Kluwer Academic/Plenum Publishers, NY, US.

Paulsen, J. & Körner, C. 2001. GIS-analysis of tree-line elevation in the Swiss Alps suggests no exposure effect. *J. Veg. Sci.* 12: 817-824.

Paulsen, J., Weber, U.M. & Körner, C. 2000. Tree growth near tree line: Abrupt or gradual reduction with altitude? *Arct. Antarct. Alp. Res.* 32: 14-20.

Rebetez, M. & Reinhard, M. In press. Monthly air temperature trends in Switzerland 1901-2000 and 1975-2004. *Theor. Appl. Climatol.*

Shiyatov, S.G., Terent'ev, M.M. & Fomin, V.V. 2005. Spatiotemporal dynamics of forest-tundra communities in the polar urals. *Russian J. Ecol.* 36: 69-75.

Surber, E., Amiet, R. & Kobert, H. 1973. *Das Brachlandproblem in der Schweiz.* EAFV (Eidgenössische Anstalt für das Forstliche Versuchswesen), Birmensdorf, CH.

Szeicz, J.M. & MacDonald, G.M. 1995. Recent white spruce dynamics at the subarctic alpine tree line of north-western Canada. *J. Ecol.* 83: 873-885.

Theurillat, J.P. & Guisan, A. 2001. Potential impact of climate change on vegetation in the European Alps: A review. *Clim. Change* 50: 77-109.

Tinner, W. & Theurillat, J.P. 2003. Uppermost limit, extent, and fluctuations of the timberline and tree line ecotone in the Swiss Central Alps during the past 11 500 years. *Arct. Alp. Res.* 35: 158-169.

Tomlin, C.D. 1990. *Geographic Information Systems and Cartographic Modelling*. Prentice-Hall, Englewood Cliffs, NJ, US.

Walther, G.-R., Beissner, S. & Burga, C.A. 2005. Trends in the upward shift of alpine plants. *J. Veg. Sci.* 16: 541-548.

Walther, P. 1986. Land abandonment in the Swiss Alps a new understanding of a land-use problem. *Mountain Res. Develop.* 6: 305-314.

Zackrisson, O., Nilsson, M.C., Steijlen, I. & Hörnberg, G. 1995. Regeneration pulses and climate-vegetation interactions in nonpyrogenic boreal Scots pine stands. *J. Ecol.* 83: 469-483.

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