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Risks of global warming on montane and subalpine forests in Switzerland – a modeling study

J. Bolliger · F. Kienast · N. E. Zimmermann

Abstract In this study, we assess the risks of global warming on distributions of individual tree species in Switzerland. Applying a spatially explicit model, tree occurrence is predicted as a function of high resolution and physiologically relevant biophysical variables. The study shows that warming only slightly alters the overall abundance of tree species. However, the preferred temperature regimes are unevenly distributed along an elevational gradient, and the sensitivity to temperature varies considerably between the species. As a result, major reorganizations of forests in montane and subalpine belts are expected, i.e., a segregation of the core distributions of *Fagus sylvatica* and *Picea abies* is observed. Tree distribution potentials near timberlines, however, remain roughly the same.

Key words Spatially explicit model · Individual tree species · Global change · Switzerland

Introduction

Risk assessments of changes of the global climatic pattern have generated numerous ecological models that deal with potential vegetation shifts caused by measured or anticipated systematic changes in temperature, precipitation, and other climatic schemes. The fundamental role of macroclimate (e.g., thermal energy, relief energy, water

availability, radiation, etc.) to determine the distribution pattern of vegetation units has been investigated at various hierarchical biotic levels: biomes (Holdridge 1947; Prentice et al. 1992; Kirilenko and Solomon 1998), ecosystems (Beerling et al. 1997), functional types (Box 1981; Henderson-Sellers and McGuiffie 1995), vegetation types (Brzeziecki et al. 1993; Brown 1994; Zimmermann and Kienast 1999), and individual species (Lenihan 1993; Austin and Gaywood 1994; Huntley et al. 1995; Rutherford et al. 1995; Leathwick et al. 1996; Iverson and Prasad 1998). Although the approaches differ in detail, they can be attributed to contrasting concepts in vegetation ecology, e.g., the concepts of the static equilibrium and the dynamic-transient character of the vegetation (e.g., Korzukhin et al. 1996). These concepts provide an important theoretical framework for vegetation models. Static equilibrium models claim that vegetation is simulated as a function of its environment, suggesting that vegetation and environment are in equilibrium. Therefore this type of model does not account for changes of the vegetation through time. Rather, risk assessments that are based on static equilibrium models perform time-independent scenarios. The dynamic-transient type of vegetation model emerges from the fact that vegetation can be viewed as a changing mosaic over time. Such individual-based process-oriented models usually require detailed data of driving forces that oftentimes are not available over large spatial scales, or, if available, are not detailed enough (e.g., Box 1981; Prentice et al. 1992; Tchebakova et al. 1993; Kienast et al. 1998). Thus, individual-based dynamic models are primarily computed for specific localities and spatial extrapolation often becomes a delicate matter (e.g., Bugmann and Fischlin 1996; but see also Roberts 1996; Steffen et al. 1996; He and Mladenoff 1999). Hence, large-scale spatial predictions primarily rely upon static equilibrium approaches. The static equilibrium approach is therefore often seen as a necessary simplification on the cost of a temporal assessment in order to deal with large spatial scales rather than striving for an overall valid concept in ecology. In this paper we use a large-scale risk assessment that relies on the static equilibrium approach. We identify, quantify, and evaluate the risk of global warming on the distributions of six tree species on a regional scale (Switzerland) by means of a spatially explicit model. By this, we focus on tree distributions of the entire study area, as well as along altitudinal belts. The model includes the following properties: (1) use of high-resolution biophysical data on the basis of a 25-m digital terrain model (DTM); (2) variable calculation

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based on long-term standardized meteorological recordings; (3) biophysical variables which include frequencies of extreme events which are interpretable on the basis of up-to-date physiological concepts; and (4) estimation of individual tree-species occurrence using a database (National Forest Inventory) containing basal area data measured on a 1×1 -km grid throughout the study area. Results of many global change assessments identify the risk of global change causing major shifts of the vegetation due to altered environmental conditions on a variety of spatial scales (e.g., Box 1981; Lenihan 1993; Brown 1994; Henderson-Sellers and McGuiffie 1995; Leathwick et al. 1996; Beerling et al. 1997; Iverson and Prasad 1998). According to these findings, tree abundance on a regional spatial scale is expected to behave comparably. We therefore challenge the following question: Are there any changes in tree abundance due to an increase in temperature?

Working in a mountainous region whose vegetation is primarily driven by strong altitudinal gradients, it is of interest to answer the questions: What is the expected range of tree distribution change along an altitudinal gradient and what are the consequences on a landscape level? And, finally, what are the results of the changes in the potential tree abundance at timberline?

Material and methods

Study area

The study area covers the region of Switzerland, ca. 41,000 km², out of which 12,300 km² are currently forested. In the southern part of the region, forests cover 46% of the landscape. In the remaining regions (Jura, Plateau, Northern, and Central Alps), 23% of the landscape is forested (Statistisches Jahrbuch der Schweiz 1997). The climate is generally temperate humid. Conditions range from intra-alpine dry and continental to insubrian, and from a more oceanic temperate lowland climate to a cold high-elevation climate regime above today's timberline.

The statistical model

Logit regression models

Logit regression has proven to be a successful tool for testing the presence/absence of vegetation as a function of biophysical variables (Bartlein et al. 1986; Lenihan 1993; Brown 1994; Rijt et al. 1996; Guisan et al. 1998; Zimmermann and Kienast 1999). Using spatial maps of biophysical variables allowed spatially explicit plotting of the simulated tree response surfaces. The response surfaces were expressed as the probability of occurrence of a tree, ranging between 0 and 1. Highest probabilities of occurrence were achieved at sites where trees are very likely to establish and reproduce. Low probabilities of occurrence were observed at sites characterized by an unsuitable biophysical environment for the corresponding tree species.

Biotic calibration data set

Six tree species were selected to mirror the main features of tree distributions from the montane vegetation zone to the subalpine timberline: *Fagus sylvatica* (beech) and *Abies alba* (fir) are widespread under oceanic climate conditions. *Picea abies* (spruce) is a boreal-alpine species that primarily occurs in the northern part of the Alps. Pure stands of *Pinus sylvestris* (Scots pine) are typically observed on extreme soil conditions. *Pinus cembra* (Swiss stone pine) and *Larix decidua* (larch) preferably occur at high-elevation sites under continental climate conditions.

Forest Inventory data

The information used to calibrate the model originates from the Swiss National Forest Inventory (NFI). The inventory contains 10,610 sampling points in forested areas and is based on a systematic and therefore representative sampling procedure on a 1×1 -km grid. For more detailed methodological information see Brändli (1988) and Zingg and Bachofen (1988). Most of the investigated areas have experienced a complex land-use history and have been more or less intensively managed during several centuries. Thus, today's observations of trees represent an integration of both, natural and anthropogenic driving forces. Using the Forest Inventory data as a major input source we implicitly accept that the model predictions hold true for the set of changes that have driven forest development during the last several centuries.

The binary data set required to simulate tree presence/absence was compiled using the basal area of a species. Basal area is defined as the area of a stem cross section at breast height (1.3 m above ground). The total basal area of each tree species at any given location of the inventory was calculated as the sum of the individual tree's basal area. If total basal area of a tree species exceeded 0.2 m² the species was assigned to the category "present", whereas for observations below this threshold the species was categorized as "absent". This threshold was chosen in order to resemble sites where a given tree species has successfully established itself.

Since the model aims at approximating the natural distribution of trees, we eliminated all observations of *Picea abies* and *Larix decidua*, which can be clearly specified as a result of plantations. Therefore, observations of *Picea abies* below 1,000 m a.s.l. and observations of *Larix decidua* below 1,400 m a.s.l. were removed from the calibration data set.

Rikli's *Pinus cembra* data

Occurrence of the sparsely scattered *Pinus cembra* at high elevations is considerably underestimated in the 1×1 -km resolution of the Forest Inventory. We therefore supplemented the inventory with Rikli's *Pinus cembra* data (Rikli 1909). Due to the low rates of forest change at high elevations and the protection of high-elevation forests by law, we assume no major changes in occurrence of *Pinus cembra* between the beginning of the century (Rikli 1909) and the 1980s when the National Forest Inventory was surveyed.

Rikli's *Pinus cembra* data consist of observations of *Pinus cembra* on selectively mapped areas all over Switzerland. In order to avoid biases towards this more intensely sampled species, 200 (randomly selected) observations of *Pinus cembra* out of 400 were combined with the Forest Inventory data.

For model calibration, we combined the National Forest Inventory with Rikli's data set for *Pinus cembra* as a biotic input data set. To cover the entire study for statistical reasons we added zero values for non-forested plots, so that the complete data set entering the model contained 41,700 sampling points.

Biophysical explanatory variables used for model calibration

For model calibration, we selected five physiologically relevant variables on the basis of conceptual and statistical considerations. We used conceptual considerations to account for environmental key factors that restrict tree occurrence, i.e., thermic variables to express the overall energy budget of a site, hygric variables to describe the water budget, and relief energy as a surrogate for gravitation processes that increase with the steepness of a site. Following statistical considerations, the choice of the variables required a test for independence of the variables, i.e., correlation matrix, and a test for the variables' explanatory power, i.e., stepwise regression (forward selection). To perform stepwise regressions, the level of significance of a variable's entry or removal was fixed at 5%. All variables were entered in a linear and in a quadratic form. Interactions between the variables were also accounted for; however, they never contributed significantly to the regression model.

The variables finally chosen were correlated less than 64%, and contributed significantly to the regression model. The selected variables were: degree-days, radiation in July, water budget in July, summer-frost frequency, and slope angle. Since thermic variables are considered most relevant in mountainous environments, all three thermic variables were used in the model albeit of their correlation. Generation of the maps of the climatic variables is based on spatially interpolated data from standardized meteorological recordings and a digital terrain model (DTM) with a 25-m resolution. All meteorological data originated from the national network with recording stations at different altitudes. For accurate spatial interpolation of the climate, all station values were standardized to sea level using regression lapse rates to unlink regional trends from the influence of elevation. The relationship between measured values (temperature, precipitation, summer-frost frequency, and degree-days) and elevation (i.e., lapse rates) was expressed by a linear regression model. Local thin plate SPLINE-functions (Franke 1982; Mitas and Mitasova 1988) were then used to spatially interpolate climate factors at sea level to the whole study area. Finally, the climate factors were reprojected to the actual elevation using the regression lapse rates and the 25-m DTM. Similar techniques were used by Mitchell (1991), Hutchinson and Bischof (1993), and Thornton et al. (1997).

Energy-related variables

In this study the energy-related variables are expressed by: degree-days (temperature sum above a threshold of 3 °C), radiation in July, and summer-frost frequency. Working in a mountainous environment, we suggest that plants are adapted to low-temperature regimes. Therefore, the threshold value to calculate degree-days was chosen to be 3 °C rather than 5.5 °C. This conceptual consideration does not affect the model, since degree-days maps of 3 and of 5.5 °C are highly correlated. The variable summer-frost frequency represents an important disturbance variable during the frost-sensitive, dehardened vegetation period. Physiological studies indicate that frost is responsible for damaging tissue and delay of growth processes (Tranquillini 1979; Körner and Larcher 1988).

Degree-days

Degree-days are defined as the sum of days above a temperature threshold calculated for a whole year. The threshold value chosen for this study is 3 °C. A detailed calculation of the degree-days maps is outlined in Zimmermann and Kienast (1999).

Radiation in July

Zimmermann and Kienast (1999) calculated the potential direct solar radiation for July by using the empirical formula of Müller (1984) which yields potential solar radiation for given altitudes for a surface that is perpendicular to the incoming sunlight. Shading of mountain chains as well as adjustments to actual slope and aspect of the surface points are taken into account based on a 25-m DTM. Using a Simpson-integral (Press et al. 1989), daily values for radiation on the basis of hourly intervals were achieved. Monthly totals were generated by applying a linear interpolation of the 10-day intervals. The month of July was chosen as it represents the main growing season at higher altitudes/latitudes.

Summer-frost frequency

Summer-frost frequency expresses the sum of frost events after dehardening, i.e., during the frost-sensitive time of the year. The latter is calculated as the core 90% of the vegetation period, i.e., the days with a mean daily temperature above 3 °C. The definition of this period follows the fact that frost hardening still protects tree tissues in early spring and in the autumn. Frost was defined as a sudden drop of the daily minimum temperature below -2.0 °C being preceded by a period of at least one day with an average daily temperature above 3 °C. Frost events during the frost-sensitive period were then added subsequently.

Frost was calculated on a daily basis by using minimum temperature and maximum temperature measurements. Thus the critical properties of frost, i.e., the early-morning temperature, could be captured and implemented.

$$SFrost = \sum_{i=DPE}^{DPE} \left[\frac{\max(0, (-2 - T_i))}{\max(0, (-2 - T_i))} | T_{i-1} > 3.0 \right]$$

where DPB is the beginning of the dehardened period of the year (monthly mean daily temperature >3 °C), DPE is the end of the dehardened period, T_i is daily temperature, and T_{i-1} is daily temperature of the previous day.

Hygric variable

The hygric variable is expressed by the water budget in July. The variable represents a surrogate for the potential water availability of plants. The month of July was chosen since during this time of the year, high growth activity can be perceived in mountainous regions. The water budget in July is calculated as the difference between precipitation sum and potential evapotranspiration in July. The quantification of the evapotranspiration is based on the empirical formula of Turc (1961). For calculation details see Zimmermann and Kienast (1999).

Relief energy

We mimicked gravitational processes with the variable slope. This variable was calculated from a 25-m DTM. The variable's units are in "degree of slope".

Testing the model's performance: statistical validation

Statistical validation is one of several possibilities to test the model's suitability for generating patterns with the same statistical properties as for independent observations (Rykiel 1996). Model performance was tested by means of cross-validation using contingency tables and graphic range comparisons (box plots) of the biophysical variable for independent observations and for corresponding model predictions. To perform the contingency tables, 50% of the calibration data set was randomly selected for recalibration of the logit regression model. Resulting regression equations were then applied to the independent 50% of the remaining calibration data set. Using contingency tables we then checked for correct assignment of observed and of modelled species. Contingency-table performance relied on thresholds for observations of the National Forest Inventory as basal area >0.2 m² (the same threshold as used in the model calibration data set) and $P > 21\%$; P = simulated probability of presence for the predictions of *Fagus sylvatica*, *Abies alba*, *Picea abies*, and *Larix decidua*; $P > 11\%$ for *Pinus cembra* and for *Pinus sylvestris*. We tabulated the percent-values of correctly estimated pixels for observed established tree species as well as for modelled established trees, and checked for the magnitude of the assignment using contingency coefficients.

Notched box plots were used for graphic range comparisons. The ranges of biophysical variables derived from 50% of the calibration data set (randomly selected) were compared with the corresponding simulated probabilities of presence using the remaining, independent 50% of the calibration data set. Overlapping percentiles of the notched box plots of both predicted and observed show that there is no statistically significant difference between the ranges considered (McGill et al. 1978; Velleman and Hoaglin 1981).

Climate change scenarios

Many complex temperature-change scenarios have been developed in order to predict possible future changes in the temperature regime. The Intergovernmental Panel on Climate Change assessments (IPCC, WMO, UNEP 1996) and downscaling approaches for the Alps (Gyalistras et al. 1994; Fischlin et al. 1995) suggest that the magnitude of the expected changes in mean annual temperature for Europe ranges between 2 and 3 °C. Since it is likely that the proposed changes of the climate will have a proportionally larger effect at high altitudes (Beniston et al. 1997; Beniston and Rebetez 1996), differing impact risks are suggested along altitude.

To cover a variety of potential patterns of global change in our models, a set of warming scenarios was applied: a moderate, an intermediate, and a strong warming scenario (Table 1). We transformed the expected warming of the mean annual temperature into a shift of the degree-days, i.e., +100 degree-days for moderate warming, +200 for the intermediate scenario, and +400 for the strong warming. Warmer conditions are likely to provoke alteration in the hydrological characteristics of a region. Climate models suggest an increase in precipitation of +10%, and +20% in the Alps, particularly during winter (Glogger 1998). As precipitation in winter also affects water availability during the vegetation period, we designed a scenario that accounts for increases of the water budget by +20%. However, this scenario was not considered any further since no differences in tree responses were observed between the hygric/warming and the warming-only scenarios.

Graphic display of impact of warming in a mountainous environment

Temperature is an important factor in governing vegetation zonation in mountainous environments. Although the correlation between elevation and temperature is strong, the relationship between altitude and temperature is not entirely constant. Within relatively short horizontal distances the thermic conditions may vary considerably within an altitudinal belt, resulting in distinct mountainous ecoregions on larger spatial scales (e.g., central, northern, and southern Alps). Thus, tree shifts along elevation are not a reliable measure of the scenario simulation. Phenology, however, is much more in equilibrium with temperature than elevation over large spatial scales. We therefore employed a phenophase-based biotemperature, rather than an altitudinal gradient, to plot the model-derived results of tree distributions.

Schreiber et al. (1977) provide biotemperature maps that are available on a 1:200,000 and 1:500,000 resolution. The

Table 1

Global change scenarios performed in the study. Scenario 4 was dropped in the course of the study (for details see text)

	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Degree-days	+100	+200	+400	+400
July water budget	-	-	-	+20%

Table 2

Correlation matrix for the five biophysical variables used in the model

	Degree-days	July radiation	Summer-frost	July water budget	Slope
Degree-days	1.00				
July radiation	-0.64	1.00			
Summer-frost	-0.56	0.33	1.00		
July water budget	-0.17	-0.04	-0.01	1.00	
Slope	-0.31	-0.12	0.13	0.25	1.00

Table 3

Model validation summary based on contingency tables. All associations are significant ($P < 0.001$) at a level of significance of 5%. Thresholds to simulate tree occurrence are chosen as follows: $P > 21\%$ for *Fagus sylvatica*, *Abies alba*, *Picea abies*, and *Larix decidua*; $P > 11\%$ for *Pinus cembra* and *Pinus sylvestris*

Tree species	Number of pixels of validation data set	Correct estimations		Contingency coefficient
		Absolute	(%)	
<i>Fagus sylvatica</i>	5,336	4,741	89	0.56
<i>Abies alba</i>	4,198	3,519	84	0.35
<i>Picea abies</i>	5,306	4,254	80	0.46
<i>Larix decidua</i>	5,336	4,957	93	0.35
<i>Pinus cembra</i>	5,272	5,249	97	0.43
<i>Pinus sylvestris</i>	5,430	5,292	97	0.11

Table 4

Altitudinal distribution of warming-induced gains of forested pixels above today's timberline

Altitudinal belt (m a.s.l.)	Number of newly forested pixels ($P < 3\%$)	
	<i>Picea abies</i>	<i>Pinus cembra</i>
2,125–2,250	+73	+27
2,250–2,375	+517	+292
2,375–2,500	+2,207	+129
2,500–2,625	+786	+1

maps are based on the phenophases of more than 100 different plants (herbs, shrubs and trees). The phenophases are classified into 18 biotemperature units, ranging from “cold” at high altitudes (mean annual temperature ca. 0–1 °C) to “warm” (mean annual temperature >12 °C) at low altitudes. Each biotemperature unit covers approximately 100 m in an altitudinal gradient. The elevation covered by the biotemperature gradient ranges between ca. 250 and 2,300 m a.s.l.. To display the model-derived simulations in this study comprehensively, Schreiber's biotemperature gradient was subdivided into the four distinct and frequently addressed vegetation belts: the colline belt (250–600 m a.s.l.), the montane belt (600–1,500 m a.s.l.), the subalpine belt (1,500–2,000 m a.s.l.), and the alpine belt (2,000–2,300 m a.s.l.).

To achieve detailed information on the behavior of tree distribution characteristics at their upper distribution limit, a biotemperature-independent test was performed. For each tree species, the difference between the model-derived number of total pixels for the entire region of Switzerland was calculated for both, today's temperature condition and temperature conditions under global warming. We then checked for newly forested pixels, i.e.,

pixels that have simulated absence of trees under today's climate conditions, but achieve simulated tree presence as a result of warming (Table 4).

Results

Model

Correlation matrix of biophysical variables

The correlation matrix of the applied biophysical variables is displayed in Table 2. Results show that the hygric- and relief-energy variables are relatively independent with a correlation maximum of 25%. The thermic variables (degree-days, radiation, and summer-frost frequency), however, are relatively highly correlated (64% at maximum).

Model performance

The results of the cross-validation are shown in Table 3 and Fig. 1. Results suggest that at least 80% of the pixels of the independent data set were correctly assigned (Table 2). The χ^2 statistics show that there was a statistically significant interrelation (confidence level 95%) between simulated and observed tree occurrences.

The contingency coefficient expresses the magnitude of the association between simulated and observed tree occurrence. It is relatively high for *Fagus sylvatica* (0.56), *Picea abies* (0.46), *Pinus cembra* (0.43), *Abies alba*, and *Larix decidua* (0.35). This indicates that these species are generally simulated where they are observed.

The low contingency coefficient observed for *Pinus sylvestris* (0.11), however, suggests that the association between modelled and observed established trees is weak, although the amount of correctly assigned pixels is high

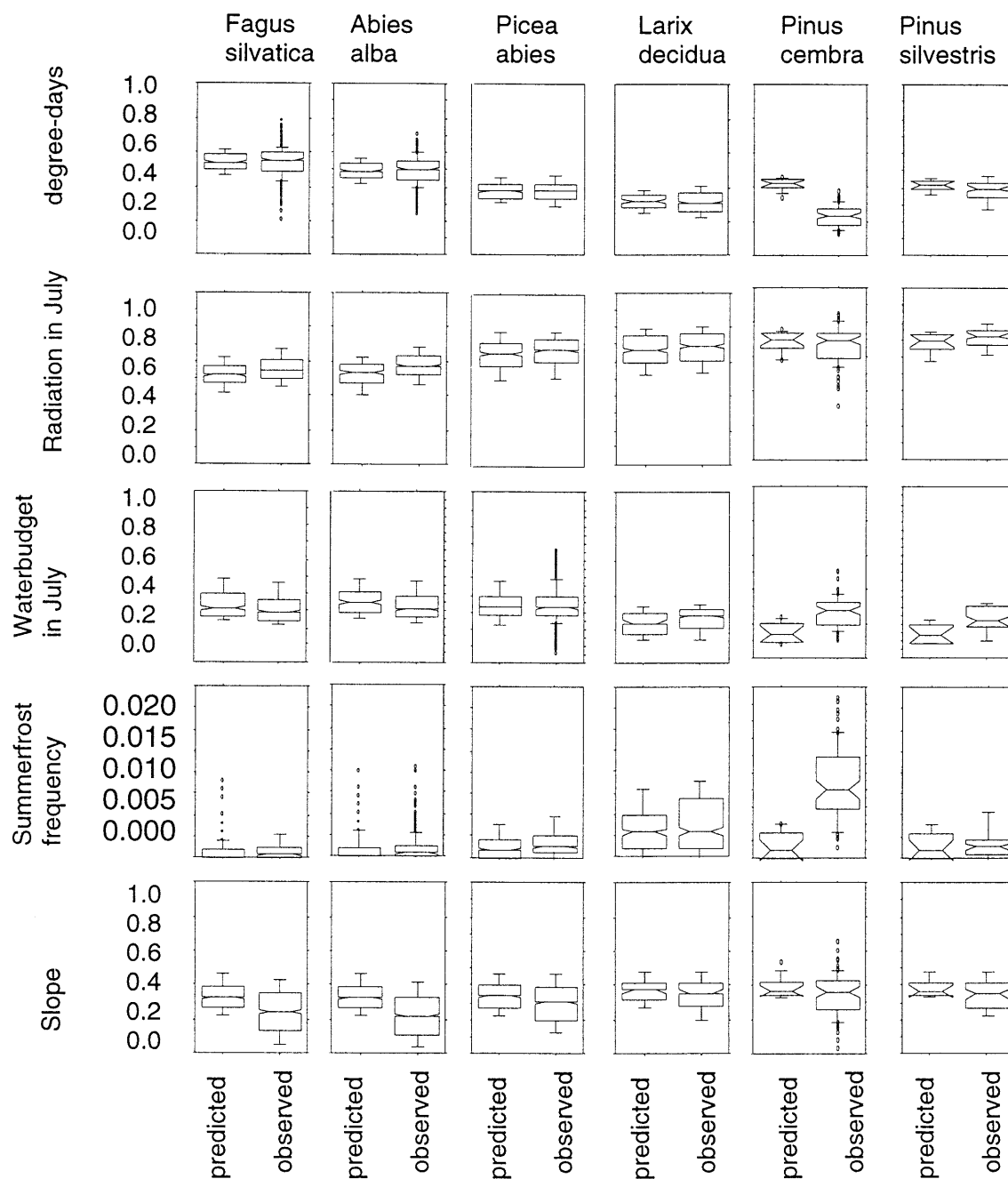


Fig. 1

Notched box plots of six tree species and five biophysical variables. Thresholds for tree presence are: basal area $>0.2 \text{ m}^2$ for observations of the Forest Inventory; $P > 21\%$ for *Fagus sylvatica*, *Abies alba*, *Picea abies* and *Larix decidua*; $P > 11\%$ for *Pinus cembra* and *Pinus sylvestris* for predicted trees

(97%). For *Pinus sylvestris*, the model “oversimulates” tree occurrence, i.e., trees are simulated where they are not observed. This may indicate that the trees potentially occur at many other sites, where they are actually not observed due to, e.g., environmental conditions not being taken into account in the model. The association between tree observation and simulation, however, is statistically significant for all species.

Notched box plots generally show good coincidence between the percentiles of both observed and predicted trees (Fig. 1). This indicates that there is no significant difference between modeled and observed trees, except for *Pinus cembra*, where for the variables summer-frost frequency and degree-days, values for predicted and observed trees do not overlap. We recognize that the model performance for this species is likely to be weak. Nevertheless, general model performance exhibits statistically significant relationships between simulated probabilities of presence and observed occurrence of tree. This allows us to conclude that the model is reasonably valid within the environmental space characterized by five biophysical variables.

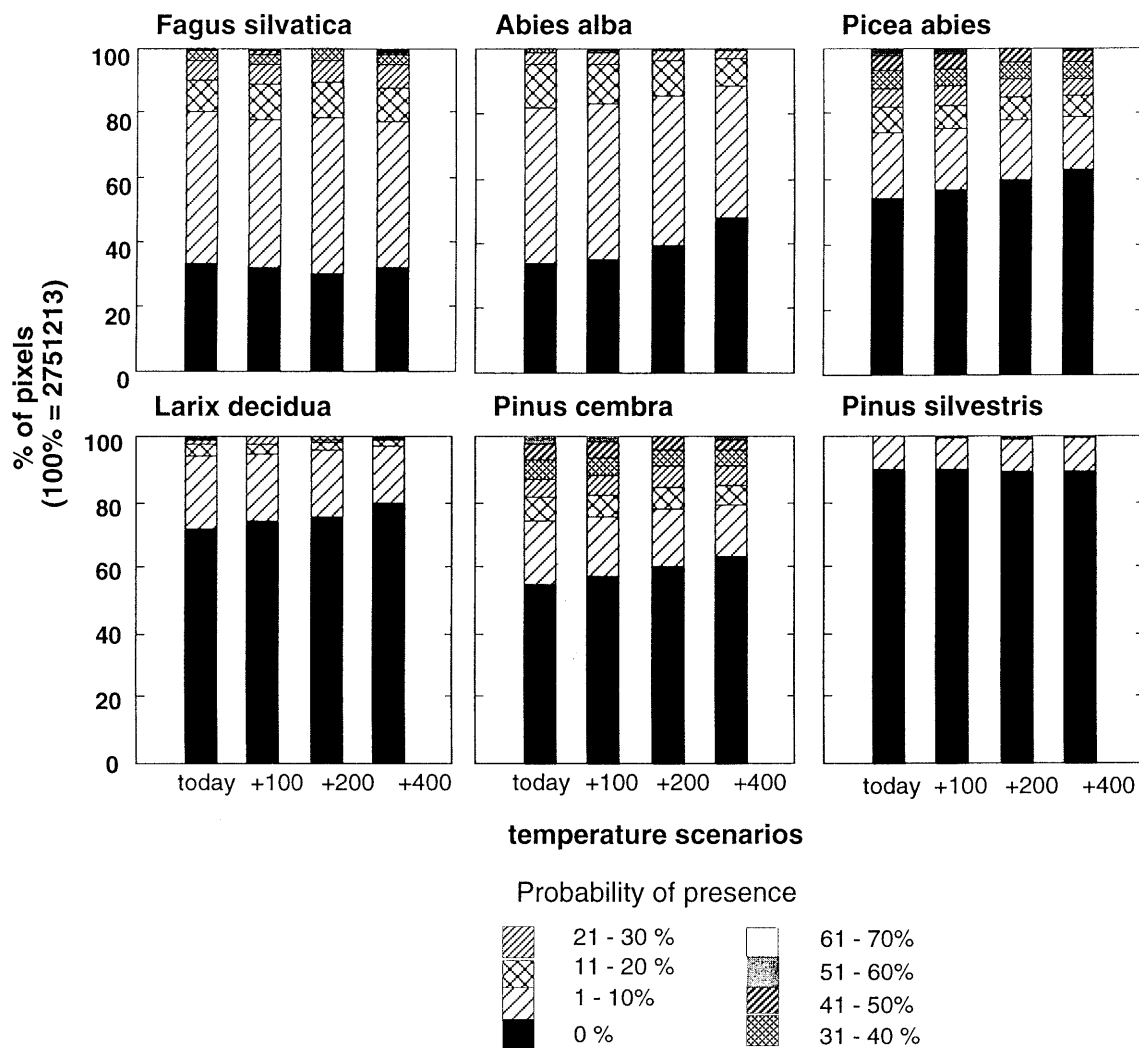


Fig. 2
Tree abundance for today's temperature conditions and for three warming scenarios

Tree responses to warming

Overall changes in tree abundance

We compared the tree abundance under today's temperature conditions with the simulations of three global change scenarios (+100, +200, and +400 degree-days relative to today's conditions). Figure 2 shows the relative values for predicted potential tree abundance over the entire study area. Simulations for classified probabilities of presence suggest that warming provokes only minor overall alterations of the potential tree abundance. Classes with high probabilities of presence do not indicate changes in tree abundance as a result of warming. Minor increases in the pixel class "absent" (0% probability of presence) for the species *Abies alba*, *Picea abies*, *Pinus cembra* and *Larix decidua* are observed. This indicates a small relative loss of presence of the corresponding species. Since the changes are not prominent, we conclude that rare trees are expected to stay rare and frequent trees are expected to stay frequent with warming.

Shifts of tree abundance along a biotemperature (altitudinal) gradient

An overview of the potential shifts of tree occurrence along a biotemperature (altitudinal) gradient for the warming scenario +400 degree-days is given in Fig. 3. To describe the distribution characteristics we distinguish between two major features: (1) overall distribution ($P > 1\%$, $P =$ simulated probability of presence) separating tree presence from absence, and (2) core areas ($P > 21\%$) describing the main distribution range of the trees. The most striking responses of tree distributions to warming can be summarized as follows:

When describing the effect of warming on the altitudinal distribution of the core area ($P > 21\%$) of *Fagus sylvatica*, the loss of the distinct distribution peak (at ca. 800 m a.s.l.) is most pronounced. The flattening of the distribution is accompanied by an uphill shift of the distribution peak from 800 to 1,000–1,200 m a.s.l. The overall distribution ($P > 1\%$) does not change considerably except for the boundaries. The boundaries shift uphill from ca. one biotemperature unit at the lower distribution limit (from ca. 300–400 m a.s.l.) to two biotemperature units at the upper distribution limit (from ca. 2,000–2,200 m a.s.l.), respectively.

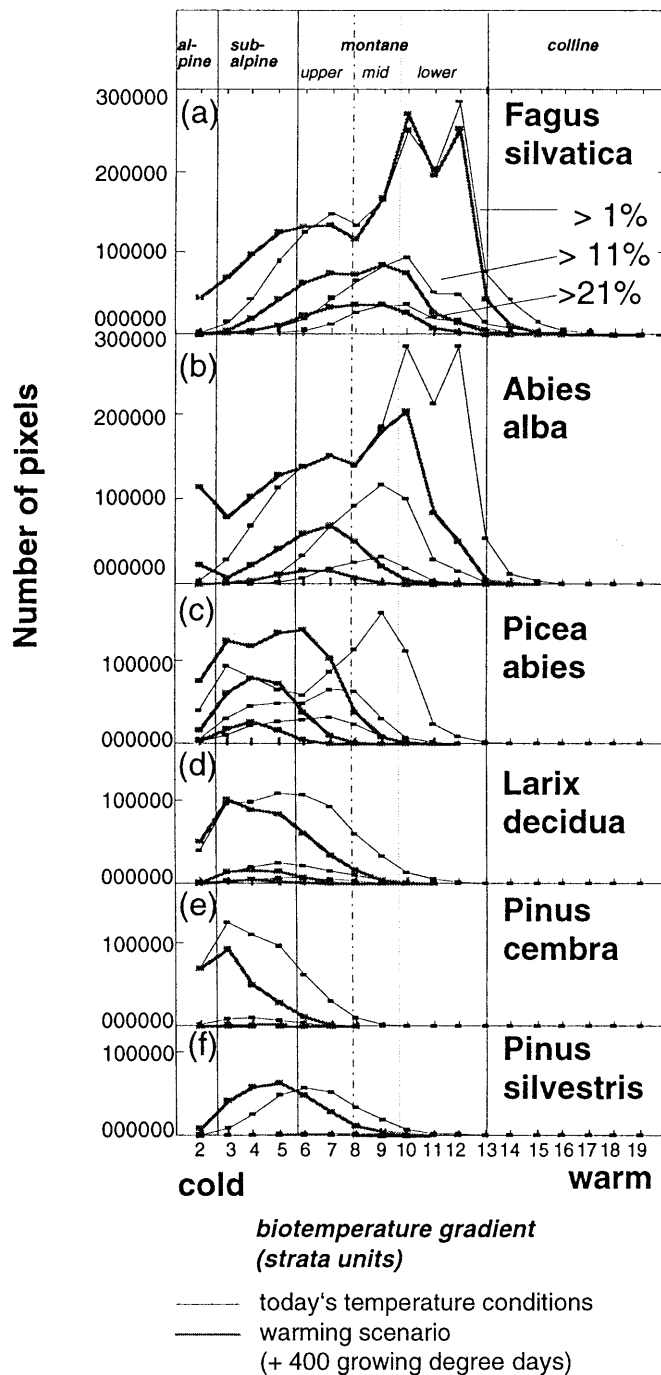


Fig. 3

Distribution of probabilities of presence of six tree species along a biotemperature (altitudinal) gradient (Schreiber et al. 1977) for warming scenario +400 degree-days. Biotemperature gradient consists of 18 units, each covering ca. 100 m in altitude. The following classes of probability of presence are shown: $P > 1\%$, $P > 11\%$, and $P > 21\%$

The core area of *Abies alba* ($P > 21\%$) responds to warming with an uphill shift of the lower boundary of ca. one biotemperature unit (from 1,000–1,100 m a.s.l.). The distribution peak at 1,000 m a.s.l. shifts ca. three biotemperature units uphill and is newly observed at an elevation of ca. 1,300 m a.s.l. The overall distribution of *Abies alba*

($P > 1\%$) at its lower distribution boundary moves up two biotemperature units (from 500–700 m a.s.l.), and one biotemperature unit at its upper distribution boundary (from 2,100–2,200 m a.s.l.).

As a consequence of warming, the distribution peak of *Picea abies*' core area ($P > 21\%$) shifts up four biotemperature units, from 1,300–1,700 m a.s.l. The core area boundaries are modelled to change their ranges from formerly 900–2,000 m a.s.l. to 1,200–2,200 m a.s.l. This shift covers approximately three biotemperature units. The range of the overall distribution of *Picea abies* is expected to shift one biotemperature unit at its lower distribution limit (from 1,000–1,100 m a.s.l.). The upper distribution limit at ca. 2,100 m a.s.l. stays relatively constant with warming.

The core area of *Larix decidua* indicates an uphill shift of one biotemperature unit, (from 1,600–1,700 m a.s.l.). The lower distribution boundary is expected to shift ca. one biotemperature unit (from 800–1,000 m a.s.l.), while the upper distribution boundary at ca. 2,200 m a.s.l. does not change considerably as a result of warming. The core area as well as the distribution boundaries of *Pinus cembra* are not observed to shift considerably as a consequence of warming.

The distribution peak of the *Pinus sylvestris* core area shifts three biotemperature uphill units (from ca. 1,400–1,700 m a.s.l.) as a result of warming, while the overall distribution stays relatively constant.

Shifts of tree abundance near the timberline

In this section, we consider warming-induced changes of tree distributions in the subalpine belt and their potential implications for the timberline habitat. Summarizing the results of Fig. 3, the upper boundary of the overall distribution of the trees does not climb significantly uphill into the alpine zone as a consequence of warming. Hence, trees cover roughly the same distribution as they do under today's temperature conditions.

Results from the biotemperature-independent investigation show that warming leads to an insignificant gain in forested pixels at the upper timberline, indicating only minor warming-induced impacts (Table 4). The difference between the model-derived number of total pixels for both today's and increased temperatures showed that only two species (*Picea abies* and *Pinus cembra*) out of six have the potential to cover newly forested pixels (Table 4). Moreover, these newly forested pixels have only very low probabilities of presence ($P < 3\%$).

The insignificant increase in forested pixels at the upper timberline indicates that here the effect of warming is very small.

Summary of the effects of warming on tree distributions in a mountainous landscape

For today's climatic conditions the lower montane belt (800–1,000 m a.s.l.) is predominantly covered with *Fagus sylvatica* ($P > 21\%$ in Fig. 3), which co-occurs with *Abies alba*. At 800 m a.s.l., *Fagus sylvatica* has a distinct peak of presence, indicating the core area of its establishment. The mid-montane zone between 1,000 and 1,100 m a.s.l. is

covered by associations of *Fagus sylvatica* and *Abies alba*. They are observed together with *Picea abies*. In the upper montane belt (1,200–1,500 m a.s.l.), *Fagus sylvatica*, *Abies alba*, and *Picea abies* occur jointly at altitudes between 1,200 and 1,500 m a.s.l. Here, *Abies alba* has the highest probability of presence, indicating the main distribution of this species. The subalpine (1,500–2,000 m) belt is primarily covered with *Picea abies*, occasionally occurring together with *Pinus cembra*, *Larix decidua*, and *Pinus sylvestris*.

The potential scenario of global warming for landscape appearance may be described as follows. In the montane belt, *Picea abies* is retreating to higher altitudes, whereas *Fagus sylvatica* is well established, particularly in the lower montane belt. In spite of the loss of its distribution peak at 800 m a.s.l., *Fagus sylvatica* forms associations with *Abies alba* at mid elevations of the montane belt. *Picea abies* has completely retreated from the mid montane belt, indicating a segregation of the species *Fagus sylvatica* and *Picea abies*. The segregation is even more pronounced at the upper montane belt, where *Picea abies* draws back its peak of presence towards the subalpine belt. As a result, *Fagus sylvatica* and *Abies alba* are the predominant species of the upper montane belt after warming. In the subalpine belt, *Picea abies* is potentially well established. Here, *Picea abies* is occasionally associated with *Abies alba* and *Fagus sylvatica*, or *Larix decidua* and *Pinus cembra*.

The results show that warming leads to an uphill shift of the core areas for *Abies alba*, *Fagus sylvatica*, *Pinus sylvestris*, *Larix decidua*, and *Picea abies*. Magnitudes of the altitudinal shift range between 100 and 300 m. Additionally, warming leads to a pronounced segregation of *Fagus sylvatica* and *Picea abies* in the montane and the subalpine belt, respectively. A characterization of the risk of warming also shows that tendencies towards losses of tree abundance may be caused: the species suffer moderate (*Abies alba*, *Fagus sylvatica*, *Pinus sylvestris*) to severe (*Larix decidua*, *Picea abies*, *Pinus cembra*) losses in their core distribution areas. Thus, results of the presented risk assessment suggest major reorganizations of the species compositions of forests in the montane and the subalpine belt of Switzerland.

Discussion

We have presented an ecological sensitivity assessment in order to analyze individual tree responses to predicted global warming. Before drawing final conclusions, several critical points of the modeling environment are discussed below.

Model

Approach

The model developed in this study is a spatially explicit model of tree species presence/absence. The model is driven by physiologically relevant spatial data derived

from long-term climate observations. The presented approach relies implicitly on the equilibrium concept suggesting that trees are in “equilibrium” with their environment and, hence, may be simulated as a function of their environment. Additionally, the model is driven by a limited number of variables, namely (1) thermic and topographic properties and (2) water availability, which are assumed to account for the highly heterogeneous landscapes of a mountain chain (i.e., the Alps). Variables such as population dynamics (e.g., competition) cannot be accounted for in a spatially explicit equilibrium model, as this would require a dynamic modeling approach.

General advantages and disadvantages of spatially explicit models are extensively discussed by Malanson (1993), Beerling et al. (1995), Franklin (1995), Guisan et al. (1998), and Kienast et al. (1998). Currently, the dynamic-transient and process-oriented models may be considered to be more appropriate tools for predicting the impact of warming upon vegetation (Mellillo et al. 1993; Woodward and Smith 1994) since this type of model accounts for temporal aspects. However, most case studies that rely on an individual-based approach are applied to small spatial scales due to data limitations. Large-scale assessments therefore often rely on the equilibrium approach. Such time-independent assessments are a most valuable tool to assess the risks of a changing environment for the following reasons: trees are long-living organisms and their life spans commonly cover several hundreds of years (Loehle 1988). From a statistical point of view, trees apparently survive many common and uncommon climatic events during their lifetime. Thus, it is likely that the process of evolutionary selection favors trees, which are characterized by tolerating long-range climatic changes (Loehle and LeBlanc 1996). By this, it is rather delicate to predict (1) the time-frame for expected changes and (2) the threshold of climatic change that causes responses of trees. We therefore do not propose a prediction of the time-frame for potential changes in tree distribution caused by warming. We rather present a risk assessment that identifies potential alterations of tree distributions for a worst-case warming scenario (+400 degree-days), which is independent of the response time of the trees.

Biophysical variables

The conceptual model framework, the model setup, and the final credibility in the model’s biological interpretation rely on the availability and quality of the calibration data set. The data used to calculate the variables are (1) long-term climate records (30-year monthly normals) and (2) standardized high-quality measurements that are physiologically interpretable. As the meteorological stations are not evenly spread over the area, it is likely that sites at high altitudes are particularly underrepresented. We therefore assume that the data used for calculation of the variables are biased towards low-elevation stations. We overcame this bias partly by calculating the climate-elevation relationship on a high-resolution 25-m DTM which accounts properly for the complex topography in mountainous regions. Thus, the biophysical input variables rely on a

combination of high-quality climate series for long time periods and on a high-resolution, accurate DTM. Due to the large-scale character of the presented risk assessment, the applied biophysical variables most likely account for the main characteristics of the complex mountainous climate-vegetation relationship.

The simplification of complex natural systems by applying only five environmental variables in our model can hold in situations such as the Alps where the environment is predominantly driving the distribution of vegetation, and where vegetation is not regulating climate due to feedback mechanisms as much as, e.g., in equatorial forest ecosystems. Statistically significant results from model performance support this general acceptance of environmental factors driving vegetation in mountainous environments.

Biotic calibration data set

The biotic calibration data derived from the Forest Inventory are statistically representative for the entire study area. The 1 × 1-km grid gives detailed information on tree occurrences and composition. Relying on the Forest Inventory as a calibration data set, we accept that the required criteria to distinguish between forest and non-forest lead to an underrepresentation of scattered open stands. This type of forest occurs particularly at high-elevation sites. Adding supplementary data to the Forest Inventory such as Rikli's *Pinus cembra* data (Rikli 1909) improved the database to some extent.

The use of the Forest Inventory implicitly accounts for changes in natural factors (e.g., disturbance events such as wind, avalanches, or climatic fluctuation such as the Little Ice Age) and management impacts (e.g., cutting, artificial regeneration, grazing) which have affected tree distributions during the past centuries. As the forests in the lowlands are generally easier to access, they are more intensely managed than the remote high-elevation sites. Management schemes in Switzerland increasingly use "selection cutting" and apply "natural regeneration", indicating that management increasingly influences forest structures rather than species composition. Therefore, a predictive model calibrated with the Forest Inventory as a major data source will simulate potential natural rather than realized niches of trees, particularly at high elevations. The trend-high management impact at low-elevation sites, low impact at high-elevation sites, and a management scheme that has only minor effects on forest species composition will also hold true for future periods, which improves the quality of our predictions.

General restrictions for the predictions of a model calibrated with the Forest Inventory include: (1) competitive and dispersal abilities of the trees do not alter, (2) trees change their response neither to climate nor to climate's constraints, and (3) the anthropogenic impact on land-use and forest management will continue to be similar in the future. We summarize that the model enables us to simulate key large-scale distribution characteristics of trees rather than to predict details along the boundaries of their distribution.

Warming-induced shifts of the geographic distribution range of trees

Simulations of climate-induced shifts of forests provide a reliable tool for powerful risk assessments of potential future landscape changes. Evidence from different approaches and various scientific disciplines ranging from paleoecological studies (e.g., Huntley 1991; Huntley et al. 1995) to investigations on recent observations (e.g., Kienast 1991; Brzeziecki et al. 1994, 1995; Bugmann 1997; Iverson and Prasad 1998) show major shifts of species, and hence reorganizations of forests as a result of climate changes. According to Iverson and Prasad (1998), warming scenarios were responsible for 36 out of 80 investigated trees of North America shifting 100 km northward. Seven of the trees under investigation even had the potential to shift 250 km. In Europe, the effect of warming potentially causes drastic reductions in *Picea abies* ranges (Huntley et al. 1995; Sykes et al. 1996). Results suggest that *Fagus sylvatica* spreads towards the Arctic Ocean and *Abies alba* retreats to northern Fennoscandia, leaving behind only scattered occurrences in central Europe (Huntley et al. 1995).

Along altitudinal units, several investigations of tree associations give evidence of distributive shifts of the vegetation towards higher altitudes as a result of warming (Kienast 1991; Brzeziecki et al. 1994, 1995). Mountain forests are particularly sensitive to climate change (Fischlin et al. 1995; Bugmann and Fischlin 1996) as rapid changes in thermic properties govern vegetation zonation along altitudinal gradients on small spatial scales: mean temperatures decrease ca. 0.5 °C per 100 m in altitude (Walter and Breckle 1986). In the following, we compare predictions based on the vegetation community approach (Brzeziecki et al. 1994, 1995) with results from the species-specific model presented in this study in order to identify the risk of warming along elevation. In contrast to community-based models (Brzeziecki et al. 1993, 1994, 1995; Kienast et al. 1998), the individual tree-species model is able to identify sensitive zones where new plant compositions might occur as a result of climate changes.

Our results suggest that the core areas of four out of six main tree species (*Fagus sylvatica*, *Abies alba*, *Picea abies*, *Larix decidua*) shift ca. 100–300 m uphill as a consequence of warming. Contrary to this, the distribution potential of the core areas of *Pinus sylvestris* and *Pinus cembra* remain about the same. Brzeziecki et al. (1994, 1995) suggest that with warming, *Fagus sylvatica*-dominated communities are predicted to occur between 1,000 and 2,100 m a.s.l., whereas we simulate *Fagus sylvatica* to occur between 1,100 and 2,000 m a.s.l. for the same warming scenario. According to Brzeziecki et al. (1994, 1995) *Picea abies*-dominated communities are predicted to occur between 1,000 and 2,000 m a.s.l., whereas we simulate *Picea abies* to occur between 1,100 and 2,000 m a.s.l. for the same warming scenario. Summarizing the results, *Fagus sylvatica* and *Picea abies* communities are expected to shift uphill at the same magnitude as we predict from the single-species approach and we basically find the same segregation tendencies for both the individual-species and the community approach. This is remarkable since the two

models (1) are based on two different biotic calibration data sets and (2) are simulated using two different statistical approaches. Generally, the ranges of the single-species approach are simulated to be somewhat smaller than the ranges of the community approach. We assume the simulations of the single-species approach to reflect the niche (in the sense of Hutchinson (1957)) of the tree more accurately than the simulated communities. Simulations of the community distribution obviously lead to an overestimation of tree distribution pattern, as the community approach integrates over a complex multi-species vegetation unit.

The warming-induced decline of the two continental tree species *Larix decidua* and *Pinus cembra* is remarkable. Kienast (1991) shows similar results using a dynamic modelling approach. His results suggest that *Pinus cembra* is outcompeted by the invading *Picea abies* in the subalpine zone.

Trees at the timberline habitat

In general, simulations suggest no significant uphill movement of timberlines as regards overall tree distributions. We therefore conclude that both today's climate and future warmer conditions are most likely to provide a similar altitudinal range for timberlines. Historic evidence, for example, suggests that missing or unspectacularly small responses of timberlines to alterations in the climatic pattern do not necessarily provoke tree lines to fluctuate proportionally to the well-dated climatic oscillations pattern during the Holocene (Bortenschlager 1977; Ives 1978; Wijmstra 1978; Ives and Hansen-Bristow 1983; Scuderi 1987; Bortenschlager 1993; Rochefort et al. 1994; Graumlich and Brubaker 1995).

As for timberline habitats, our results suggest that tree distributions at timberlines are not strongly affected by warming.

Conclusions

The presented model is a powerful tool to assess the risk of global warming on individual tree species occurrence on a regional scale. According to the main results of the study, we evaluate the risk of warming as follows:

1. Within the region of Switzerland (41,000 km²) rare trees stay rare and frequent trees stay frequent with increasing temperatures.
2. Major warming-induced effects on tree distributions are observed along a biotemperature (altitudinal) gradient. We expect extensive reorganization of the forests in the montane and the subalpine belt. The reorganization is primarily characterized by a segregation of *Picea abies* and *Fagus sylvatica*: *Picea abies* retreats almost completely from the mid and the upper montane belt to the subalpine belt. Consequently, the subalpine belt is primarily covered with *Picea abies*, while the mid to upper montane belt is mainly characterized by *Fagus sylvatica* and *Abies alba*.

3. Today's climatic conditions provide roughly a comparable distribution potential for timberlines as under warming conditions.

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