PorTree Final Report

A project funded by the BAFU-WSL program on “Forests and Climate Change” in Switzerland

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Project Summary

The PorTree project has generated a suite of species distribution (=habitat suitability) models (SDMs) for tree species of the European Alps. These encompass all major tree species of Switzerland, and include also some that can be expected to become suitable under climate change in the near or farther future. To do so, we compiled forest inventory data for the whole Alps, spanning the whole country area of Switzerland, Austria, and Slovenia, and including the parts the Alps and adjacent areas for France, Italy and Germany. We considered it important to include the neighboring areas in order to fully capture the environmental niche of the modelled tree species as can be assessed across the Alps. Would the models only be fitted from Swiss data, then no projections are possible for warmer futures in the currently warmest regions in Switzerland (Ticino and Swiss Plateau), and no information would be available for species not yet present here. The drawback of this approach is that some national inventories do not distinguish e.g. oak, maple or ash species; therefore no consistent maps can be derived for these species across the whole Alps. Another drawback is in the fact that no consistent soil or geology data are available across the Alps, rather only climate data. The fitted models thus represent primarily the climatic habitat suitability of the modelled species. For some species, we re-fitted models from Switzerland alone. This was primarily done for two reasons: (i) some species are not modelled well from climate alone at the scale of the Alps, and/or (ii) some species are so incompletely mapped that a fitting from the whole Alps was not feasible. We thus re-fitted these models using Swiss data alone. This lead e.g. to habitat suitability models for oaks (*Quercus* spp.) and maples (*Acer* spp) fitted only as species groups across the Alps, but single species models (*Quercus robur, Q. petraea, Q. pubescens, Acer pseudoplatanus, A. platanoides*) fitted for Switzerland only with additional soil and geology information. All fitted models were projected to current and future climates using a suite of climate model projections. In addition, for few selected tree species we generated growth potential models, and we draped these models over SDM niche projections in the environmental space. This allowed us to analyze under what future conditions tree species might still grow well even if the climate takes values under which the same species is currently not observed. The results allow identifying areas where the species might not disappear rapidly despite the fact that SDMs predict unsuitable habitats in the future.

The report explains the general climate future and explains the methodology of the analyses used in the PORTREE project. In an appendix, a large collection of tree species portfolios under current and future climate conditions is presented. Each species is presented over two pages, summarizing both the model projections and the summary statistics of range shifts. This is helpful information for interested managers and stakeholders, as it illustrates, where in Switzerland what species is likely suitable or not today and in the future. However, these maps cannot be taken as projections of how fast tree species will shift their ranges through migration, and neither can projected disappearance of a species be taken as a prediction of local dieback. Rather, the models explain that the currently observed distribution will be shifted in space in order to track analogue climate conditions. If a species is projected to disappear, then this may happen fast (if physiological tolerances are exceeded) or it may happen extremely slowly during hundreds, if not thousands of years (if competitive interactions among species are changing and our target species will get outcompeted slowly over time). And it's also clear: models are always wrong at distribution edges, it's the nature of models.

We hope that the reader will find the model results useful, and take them as one additional argument (and not the full truth) in the planning and decision making of current and future forest management. With some experience, a user can also extrapolate own local expertise in combination with the modelled results, e.g. by compensating the missing soil information in some models.

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Introduction

Changing climates are expected to severely alter the phenology, growth, mortality/regeneration and eventually composition of tree species in Switzerland, Europe and worldwide. Severe climate extremes (abrupt shifts) and slowly altering climate means (gradual shifts) have started to affect these demographic responses (Gehrig-Fasel *et al.* 2007; Jolly *et al.* 2005; Lenoir *et al.* 2008; Menzel & Fabian 1999; van Mantgem *et al.* 2009). While over short periods (next 10-20 years) the effect of land use change and changes in phenology may still dominate the climate signal in its importance at the landscape scale, ongoing climate change with an increased frequency of extremes and more dramatically shifted means is expected to outweigh land use change thereafter, and severe alterations in growth, regeneration and mortality of individual tree species may be expected and can partly be observed already today (Kurz *et al.* 2008; Rigling *et al.* 2006). And several species have already undergone recent range shifts (Parmesan & Yohe 2003; Walther *et al.* 2002).

Forecasting the effects of climate change on species responses bears the difficulty that no single method will give easy answers to the many questions resulting from the uncertainty about ongoing climate change. It seems thus reasonable to evaluate possible effects of climate change from an array of methods. Often used are species distribution models (SDMs) to evaluate the geographical re-displacement of suitable habitat areas for species (Iverson *et al.* 2008; Thuiller *et al.* 2005; Zimmermann *et al.* 2006). Other methods assess the impact of climate variability on phenology (Menzel & Fabian 1999), growth (Jolly *et al.* 2005), regeneration (Ibanez *et al.* 2007), or mortality (Bigler *et al.* 2006; van Mantgem & Stephenson 2007; van Mantgem *et al.* 2009; Villalba & Veblen 1998). Common garden transplants are an alternative, yet very resource intense approach (Rehfeldt 1991).

Species distribution and climate change

The method of SDM (Guisan & Thuiller 2005; Guisan & Zimmermann 2000) is suited to analyze possible effects of climate change on species, since it assesses the macro-scale climate suitability of a species under altered climate (Thuiller *et al.* 2008). Specifically, for sessile organisms as plants, the suitability of a site for sustainable growth and maintenance of viable populations is highly important and has the potential to assist managers in decision making regarding the selection of species for forestry, conservation biology and landscape planning. The method has matured and a general agreement has been reached as to what degree the many statistical methods are capable of fitting species' distributions along environmental gradients (Elith *et al.* 2006; Guisan *et al.* 2007). Many additional effects have been evaluated, such as the importance of sample size (McPherson *et al.* 2004; Pearce & Ferrier 2000; Stockwell & Peterson 2002; Zimmermann *et al.* 2007), sampling design (Edwards *et al.* 2006), or to what degree specific sets of additional predictors, such as remote sensing variables (Pottier *et al.* 2014; Zimmermann *et al.* 2007), biotic variables (Kissling *et al.* 2012; Leathwick & Austin 2001), or the inclusion of climatic extremes (Zimmermann *et al.* 2009) help explain species distributions. Additional emphasize has been given to the modeling of the potential distribution of rare species, since small sample sizes clearly pose difficulties (Edwards *et al.* 2005; Guisan *et al.* 2006).

Tree Growth and Climate change

Various site and environmental factors determine tree growth. As summarized earlier (Kozlowski & Pallardy 1996), the requirements for tree growth are carbon dioxide, water, and minerals for raw materials, light as energy resource, oxygen, and favorable temperature for growth processes. The capacity for photosynthetic processes (i.e. foliar biomass) and the competition for resources are constraining tree growth. Tree growth processes can be ranked by order of importance in foliage growth, root growth, bud growth, storage tissue growth, stem growth, growth of defensive compounds, and reproductive growth (Waring 1987). The growth potential is further influenced by tree species interactions, tree genetics (local adaptation, seed origins), tree age, and stand density and structure (Kramer 1988). In temperate forests the potential vegetation period (determined by the seasonal global radiation budget) is limited by temperature (Kozlowski & Pallardy 1996).

Past provenance trials in Switzerland have shown that tree growth (both in tree height and volume) decreases in general with increasing altitude for the same provenances and tree species (Burger 1941; Dobbertin & Giuggiola 2006). While temperature is expected to be the most important explaining variable, other factors such as soil type, soil mineralization rate or wind and snow may also contribute to the decline in growth with altitude. However, similar decreases in tree growth were found in all the provenance trials and gradient studies Burger conducted. By using a mean temperature lapse rate of 0.6°C per 100 m change in altitude Burger's findings can be translated into height and stem increment decreases of 5-10% for Norway spruce (*Picea abies*) and 5-20% for Scots pine (*Pinus sylvestris*) per 1°C of temperature decrease (Dobbertin & Giuggiola 2006).

Long-term phenological observations show for deciduous trees that leaf duration has increased by up to two weeks in Europe over the past thirty years due to increasing temperatures (Menzel & Fabian 1999). Given sufficient water and nutrient supply, rising temperatures are therefore believed to increase forest growth. However, several studies found poor relations between leaf duration and stem growth (Jolly *et al.* 2005; Kaufmann *et al.* 2004; Leuzinger *et al.* 2005; White & Nemani 2003). Hasenauer and colleagues (Hasenauer *et al.* 1999) found for the time period 1961-1990 a parallel increase in mean annual temperature, computed growing season and actual stem growth and modelled net primary productivity on the Austrian national forest inventory grid indicating a causal relation between temperature increase and growth increase. In a European wide study using 5-year growth data from 363 ICP Forests level II plots, Solberg *et al.* (2009) found not only a strong effect of nitrogen deposition on tree growth, but also of deviation of the temperature during the vegetation season from the long-term mean. Andreassen *et al.* (2006) found in Norway that spruce plots with a 30-years' mean June temperature value below 12-13°C mostly reacted with increased growth when the summer weather was drier or warmer than normal, and vice versa. In summary, the poor relation between leaf duration and stem growth likely can be explained by the fact that early season warming does not necessarily relate directly to increased productivity. Rather, seasonal productivity changes are driven by the interplay between rising temperatures and changes in water availability, which is further outlined below.

The provenance trials described above had all been conducted in regions that were not limited by precipitation. In some dry inner-alpine valleys (such as the Rhone valley) tree height actually increases with increasing altitude related to increasing precipitation and decreasing temperature with altitude (Dobbertin & Giuggiola 2006). It is well established that tree stem growth is affected by the water availability during the growing season and previous years (Schweingruber 1996; Spiecker 1990; Spiecker *et al.* 1996). The severe drought during the temperature record-setting summer 2003 in Europe (Schär *et al.* 2004) also affected stem growth at long-term monitoring sites in Germany and Switzerland (Ciais *et al.* 2005; Jolly *et al.* 2005; Meining *et al.* 2004). Meining *et al.* (2004) report reduced stem diameter growth rates by an average of 50% in 2003 for all 10 Norway spruce Level II sites in Baden-Württemberg. In Bavaria growth in 2003 for all seven Level II spruce sites was reduced in comparison to 2002 (Meining *et al.* 2004). For European beech (*Fagus sylvatica*), growth reduction was also found at low altitude sites (510 to 780 m), but above 800 m beech showed no growth reduction. In Switzerland, tree growth of 2003 in percent of growth in 2002 decreased irrespective of species with decreasing altitude. At low altitude (≤ 1200 m) tree growth was reduced on average by one third compared to the wet year 2002 (Dobbertin & Giuggiola 2006), while the trees on plots above 1200 m a.s.l. exhibited increased stem growth (mean of 15%, (Dobbertin & Giuggiola 2006) most likely due to increased temperatures (Jolly *et al.* 2005).

Project objectives

Research objectives

We propose to develop an environmental portfolio of Central European tree species. This was aimed at building the first block of a management portfolio of tree species for adaptive forest management under climate change. To reach this goal we would ideally integrate: (i) the sensitivity and capacity of tree species to survive and grow under a range of climate conditions, and (ii) the economic analysis of markets (demand and supply) and management requirements of the same tree species. This project covers the first part only, the building of an environmental tree species portfolio, suitable to project the behavior of tree species along climate gradients. The goal of the project is to: (1) develop climate layers suitable for analyzing the growth potential and the bioclimatic envelope at sufficient spatial resolution for the European Alps and the surrounding mainland; (2) analyze the bioclimatic envelope of tree species in Europe; (3) analyze the growth response along multiple environmental gradients for some important tree species; and (5) analyze areas of risk for loss of tree species due to changing means and extremes in climate.

In order to cope with risks (see point 5 above), we propose to combine sensitivity analyses of species' ranges to climate change with sensitivity analyses of the growth potential of some important Central European tree species to climate change using existing inventory data. In order to study the full range of possible reactions, multiple data sources were necessary, and these needed to originate ideally also from outside of Switzerland. In the combination of several analysis steps, we answer the question of how trees are expected to tolerate projected climate changes at any given location using: (a) a suite of tree species portfolios, (b) projected climate change effects including uncertainties, and (c) a spatially explicit risk assessment including uncertainties for given species and projected climate changes using ensemble techniques.

Hypotheses/Expectation

There is no formally testable hypothesis at hand for this type of work, since we aimed at developing information for managers, not the testing of a scientific hypothesis. However, our expectation is to develop useful ecological information for the major tree species in Switzerland (and on some that are expected to become important under climate change) so that managers can use them for adaptive management.

Relation of the research to the program objectives

Several aspects are important for adaptive forest management under climate change. One of the most important aspects is to understand (a) whether a specific tree species is likely able to maintain sustainable populations in the future and (b) how for the same tree species the changing climate will affect its growth in the future. Both aspects are dealt with in this project using both niche models (SDMs) as well as radial stem growth analyses. Such data represent baseline data for many other projects and we thus provide such data to other projects in several forms:

- We develop maps of the potential distribution of tree species under climate change for six RCM simulations (primarily for the A1B scenario), and using six different statistical models. This allows us to project tree species risk maps in an ensemble framework.
- We develop radial stem growth models along environmental gradients for the most abundant tree species and overlay these with the ecological niche in order to study management risks where habitat models project extinction of a species.
- We provided all available climate data on current and IPCC-scenario based future climates.

How to interpret SDM outputs

Projected changes in potential habitats

Species distribution models (SDM) fit the observed current distribution of a species to a range of climate and other predictors. When projecting this model to change climate scenario maps, rapid – basically immediate – range shifts are projected (Figure 1). Several points need to be considered when interpreting this type of model output:

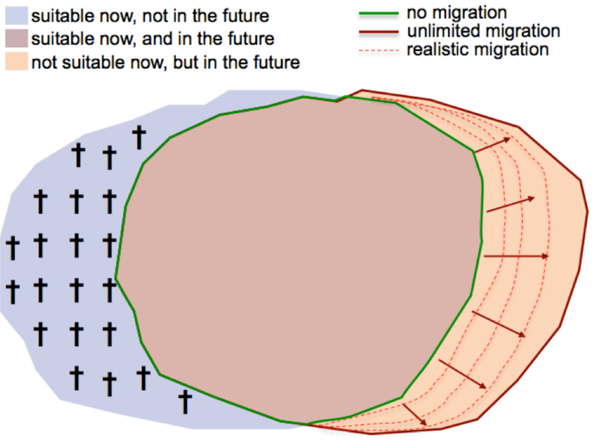

Figure 1. Schematic representation of shifts in suitable habitats from species distribution models. Three zones can usually be distinguished, depending on whether the habitat is projected to be suitable now and/or in the future.

(1) A projected range shift by – say – 2080 does not mean that the species is expected to ultimately go extinct in the whole range that no longer is simulated to be suitable (blue part in figure 1). Rather, the model says that "*under current climate conditions, the species has not been observed with sufficient evidence under such conditions the species might experience in the future at these locations*". This only answers that there is no evidence the species should be there in the long run. But it does not answer, how fast the species will disappear. If the future climate conditions impose direct physiological stress, then the species might disappear fast (as can e.g. be observed with Scots pine in the lowest altitudes of the Valais, where in the recent two decades the species has disappeared do to increased drought extremes. However, in many cases a species will still find physiologically suitable conditions. It is rather the competition with better performing species that will result in range loss over time. Such competition based range shifts take 100s if not 1000s of years, and can also be mitigated by forest management.

(2) Each model has zones of errors. There is no "error-free" model. In SDMs we always expect errors to be visible at the edge of the distribution. It does not mean that just outside (or just inside) of the predicted edge we expect the species to disappear/appear. Rather, it is a probabilistic model, and we optimize the cut level in order to have better visualization capacity (and because probabilities are also difficult to interpret). Yet, it's clear that we expect most deviations from the true reality at range edges.

(3) SDMs as produced here are fitted from all forest inventory points across the European Alps. This has the advantage that all possible habitat conditions under which the species can be observed in the Alps are used to fit the niche model. This guarantees that the model more broadly represents the full niche of the species. However, it has the disadvantage that it does not give sufficient attention to Swiss data points. The plots in Switzerland may stand for local adaptation of Swiss provenances that are not equally well captured when fitting a model with all data points of the Alps. We may specifically see differences to Swiss inventory points for species that have their center of distribution outside of Switzerland (the Swiss provenances might represent local adaptations to conditions at the edge of the distribution; see e.g. *Ostrya carpinifolia*), or for species that have a very broad environmental niche (see e.g. *Pinus sylvestris*). We consider the advantage of fitting a more complete niche of the species as very high due to the need to predict to conditions we cannot currently observe in Switzerland. This requires fitting models for a larger range of current climate conditions.

(4) Due to fact that we fit models over the whole European Alps has one significant disadvantage, though. The lack of Alps-wide soil, geology, or land-use data prevents us from calibrating these important environmental variables into the models. To overcome this, we can only fit models for Swiss data alone, where these environmental predictors are available. Most of the presented species are fitted directly at the Alps-scale. Only models of few species that cannot be successfully predicted from the Alps-wide data basis are calibrated from Swiss data alone, in order to assess their likely future response under climate change. These models are clearly assigned as fitted from Swiss data in appendix S1. This allows to easily recognize the different model calibration reference. When fitting Swiss data points alone, we have added three predictor variables: (i) a categorical geology variable (calcareous vs. non-calcareous bedrock), (ii) soil depth, and (iii) distance to water (standing or running).

(5) In appendix S1 we present a range change statistic for each species at the Swiss and in many cases at the European scale. The European scale is meant to represent the whole European continent. These statistics are only available for some of the modeled species, and were calculated from models originating from the EU FP7 MOTIVE project. The models were calibrated using the ICP Forest Level I plots, a network of ca. 6500 plots allocated in a ca. 16km regular lattice over forest areas of Europe. If a species has only a Swiss range statistic, then no European models were available for this species.

(6) Not all national forest inventories that we used in this project distinguish the tree species always to the species level. Some countries failed to distinguish specifically the different species of oaks (*Quercus spp.*), maples (*Acer spp.*) and ash (*Fraxinus spp.*). Instead of fitting Alps-wide models for the individual species from some selected regions only (which would have biased clearly the model calibration), we decided to present only the genus level models. For oaks, the models lump generally the species *Q. robur*, *Q. petraea*, and *Q. pubescens* (but not *Q. ilex*, nor *Q. cerris*). For maples, the models generally combine the specie *A. pseudoplatanus*, *A. platanoides*, and *A. campestre*. For ashes, the models combine the species *F. excelsior* and *F. ornus*.

RESULTS 1: *Expected changes in climate*

The global climate is currently warming and this trend is expected to continue towards an even warmer world, associated partly with drastic shifts in precipitation regimes (IPCC 2007). The global temperature has been warming by ca. 0.6°C (±0.2°C) during the 20th century (IPCC 2001), but the land areas have shown a higher increase in temperature within the same period. Here, we report on the current state of the art in climate model projections for Europe, with an outlook to the soon available 5th IPCC assessment report.

It is challenging to project how the climate might look like in 50-100 years, a duration that is relevant for forest management. In climatology many models are used in ensemble mode to generate possible climate futures. Each model and each simulation can be considered one possible representation of how the climate might evolve during the 21st century. For forest management and decision-making, we have to live with the fact that no exact forecast is possible. Rather, we have to implement our planning based on projected trends including their uncertainty. The periodic reports by the Intergovernmental Panel on Climate Change (IPCC) summarize the state of the art of how scientists see the development of the future climate and the associated impacts on ecosystems, economy and society. Now, the 5th assessment report has recently been published, and some comparisons to the last two reports are already possible. The 3rd Assessment Report (IPCC 2001) had assumed that the global climate might be warming by 1.4-5.9°C, with no probabilities given for different increases, and with extreme scenarios projecting even far higher temperature increases. The 4th assessment report (IPCC 2007) provided a more narrow range of the likely future climate stating that temperatures will likely be between 2.0 and 4.5°C warmer than during the 1961-1990 period (with a likelihood of 66%). It also said that temperature increases by more than 4.5°C cannot be excluded (see Rogelj et al. 2012), but that the most likely temperature increase by 2100 is 3.0°C. First comparisons from global climate modeling studies for the 5th IPCC assessment report project an increase of 2.4-4.9°C as medians from three different scenarios of radiative forcing (following different emission scenarios that are similar to those used in earlier reports). A fourth scenario is added that assumes a more rigorous and rapid reduction of greenhouse gases than was ever used before, predicting a median temperature increase of only 1.1°C during the 21st Century. Overall, the model simulations for the 5th IPCC assessment report expect that the likelihood of having global temperature increase exceeding 4.9°C is 14%, thus also likely, but that the most likely warming scenario at the global scale is still 3.0°C. Thus, in general, the newest scenarios do project similar average warming trends as we have seen in the 4th IPCC assessment report, although some scenarios point to somewhat higher warming trends than were calculated for the 4th report (see Rogelj et al. 2012). Figure 1 shows global climate data simulations for the 4th and 5th assessment report.

The global climate is simulated using so-called general circulation models (GCM), which project the climate future on physics-based processes and first-principles. For regional applications such as e.g. Europe, such GCM model output has a too coarse spatial resolution, usually in the range of 1°-2.5° Lat/Lon per model cell. In order to obtain more realistic climate projections at a regional to local scale, two types of downscaling are often combined. First, so-called regional climate models (RCM) are calculated to certain larger regions of the World (e.g. all or parts of Europe). These models contain the same physical mechanisms as the GCMs, are fed by GCM output, and simulate the climate development within the study region by using GCMs data as boundary input to the study region. The output of these models is at high temporal and moderate spatial resolution, ranging typically between 5-50km per cell. This is a much better spatial representation of the climate in regions and the output is somewhat sensitive to mountains and their effects on the climate system, though often the output is still too coarse for management and decision-making. Therefore, a further statistics-based downscaling procedure is applied (Pielke & Wilby 2012) in order to scale the output from RCMs to finer spatial resolution ranging from e.g. 100m to 1km, which can be considered well-suited for management applications.

Climate projections for the PORTREE project

For the PORTREE project, we have used five different RCMs driven by four different GCMs resulting in six GCM/RCM combinations in order to study the impact of likely climate changes on forest species and ecosystems. Table 1 gives an overview of the models used, which originate mostly from the ENSEMBLES EU project, using GCM runs that were calculated for the 4th IPCC assessment report (IPCC 2007). A summary of the methods used to downscale is given in the methods brief below.

Table 1. Climate models used to assess the impact of climate change on forest ecosystems and tree species ranges in the PORTREE project. RCM models are labeled in bold face, while the GCMs used to feed the RCMs are in normal font.

Model **RCM**/GCM	Scenario: **A1B**	**A2**	**B1**	**B2**
CLM/ECHAM5, run by MPI	x	x	x	–
RACMO2/ECHAM5, run by KNMI	x	–	–	–
HADRN3/HadCM3, run by HC	x	–	–	–
HIRHAM5/Arpège, run by DMI	x	–	–	–
RCA30/CCSM3, run by SMHI	x	x	–	x
RCA30/ECHAM5, run by SMHI	x	x	x	–

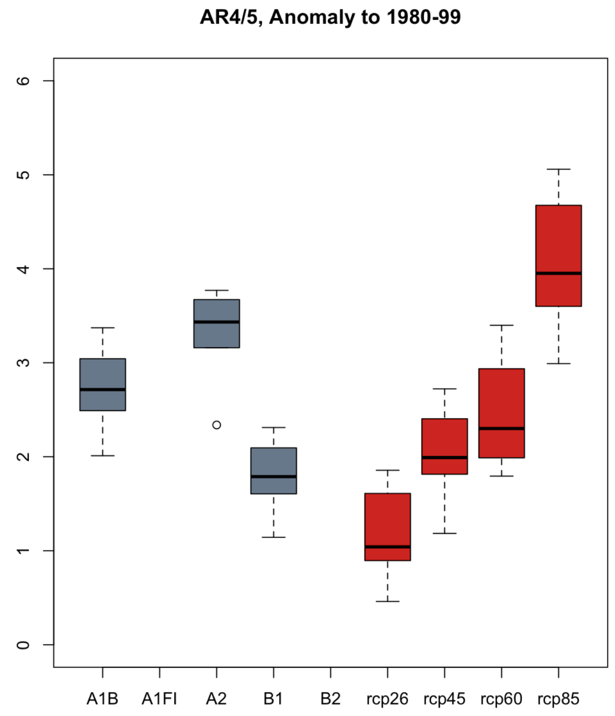

Figure 1. Comparison of global circulation model (GCM) simulations for the 4th (steel blue) and the 5th (maroon) IPCC assessment report (AR). It indicates the larger spread of possible climate futures projected with AR5 data, compared to AR4, despite simulating the same global mean climate.

Figure 2 illustrates the projected climate change trend from the six used RCM simulations over all of Europe by the example of annual and seasonal (summer and winter half) means, and by the uncertainty in projected summer climates. Figure 3 zooms into the Alps for the same type of climate summaries. Over the Alps, we can summarize the major trends in projected climate changes as follows:

For temperature, we observe a general warming trend in the range of 1.8 to 4.0 °C over the Alps by mean of the 2051-2080 period, with least warming in the winter half, and highest warming in the summer months. The Alps generally face higher warming trends than the surrounding mainland, specifically in the winter months. In summer, the warming is more pronounced in the Western Alps and generally in the South of the Alps, while the northern ranges and lowlands will face a lower warming. Uncertainty among the six models is highest in the higher altitudes of the Alps, and generally increases towards the Eastern part of the Alps.

For precipitation, the annual trend is not very strong, with some regions South of the Alps obtaining a bit more, while most of the regions obtain a bit less precipitation annually. However, the seasonal differences are large. The summer half year is projected to obtain significantly less rainfall, with some regions in the Central Alps obtaining only 70% of the current summer rainfall amounts, and with only small regions in the Southwest and in the East of the Alps obtaining roughly the same amount as today. The winter half is projected to be wetter for most regions, especially the Southwestern Alps, with the Po plain and some Mediterranean regions obtaining less rainfall than today (-20%). The uncertainty among models, calculated as the standard deviation in projected climate values among all six models, is highest along the Mediterranean coast in the West,

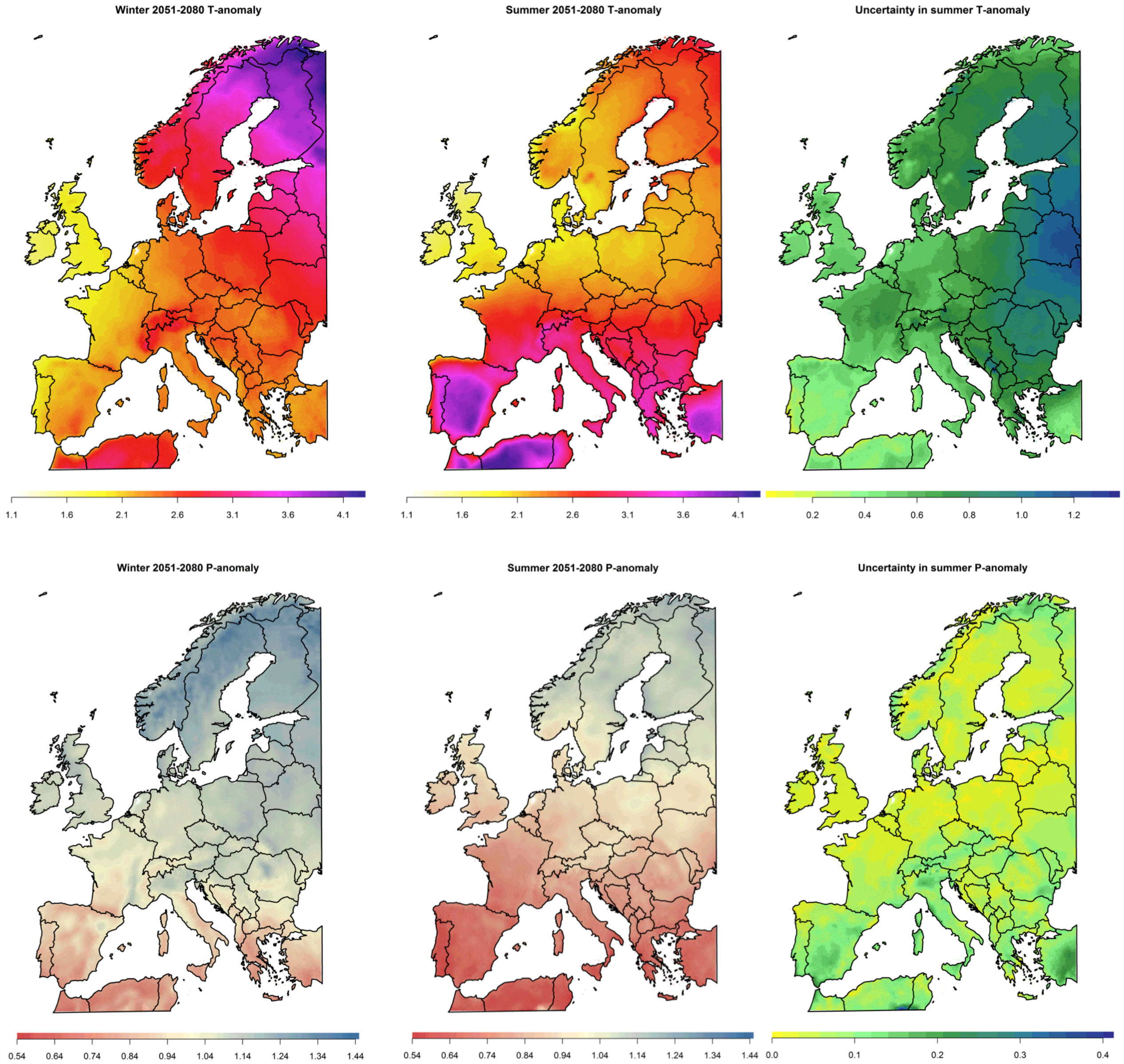

Figure 2. Climate anomalies for the A1B scenario by 2080 (deviations of the 2051-2080 period from current, i.e. 1961-1990) averaged over the six RCM models used in the PORTREE project. *First row*: Anomalies for winter and summer temperature (in °C), and uncertainty (st.dev. in °C) of summer temperature among all 6 RCMs; *Second row*: Anomalies for winter and summer precipitation (in % compared to current), and uncertainty (st.dev in %) of summer precipitation among all 6 RCMs.

and is also comparably high in the Po plain and at higher elevation in the Alps, while in the plains north of the Alps, the six models show comparably high agreement.

The projected climate simulated differs quite significantly among the six models (Fig. 4). The HadRM3/HadCM3 model projects the highest (ca. +5° C), while the RCA30/CCSM3 model foresees the lowest (ca. +2.8° C) average summer temperature increase by 2100. With regards to precipitation, the HIRHAM/Arpège model projects the strongest (ca. -30%), while the RCA30/ECHAM5 model foresees the lowest (ca. -5%) reduction in summer precipitation over Europe. The year-to-year climate variability is significantly higher in the HIRHAM/Arpège and in the HadRM3/HadCM3 than in the CLM/ECHAM5 model. These differences indicate uncertainties with regards to climatic extremes we may face and with regards to the degree of climate change we will face in forest management decisions.

We also observe strong spatial variation in projected climate patterns, both among models (Fig. 3D) and throughout the projected time series (Figs. 5 & 6). The HadRM3/HadCM3 model reveals high spatial variation and additionally strong fluctuations around a warming trend until 2100 (Fig. 5), meaning that temperatures cannot be expected to gradually warm up. Early in the 21st century, regions north of the Alps are partly projected to show higher temperature increases than those south of the Alps, while after 2050, the South (and partly the West) of the Alps show clearly higher summer temperature increases. After 2030, 2055 and 2070, clear jumps to higher anomaly levels are observed in this model. The HIRHAM/Arpège model reveals a very high spatial variation and considerable temporal fluctuations in summer precipitation anomalies (Fig. 6). This means that despite a general drying trend, some wet years are projected to occur, although with decreasing frequencies. On the other hand, such high fluctuations over time also indicate that very dry years are expected to occur more frequently. Some regions in the Southwest of the Alps show specifically high temporal fluctuations, with very wet years occurring infrequently.

A significant change can also be expected from a change in seasonality (Fig. 5). The CLM model projects a "mediterranization" of the climate, by projecting significantly lower summer precipitations than today, and by simulating increased spring (March, April) and autumn (November) rainfall compared to today, and notably so after ca. 2050.

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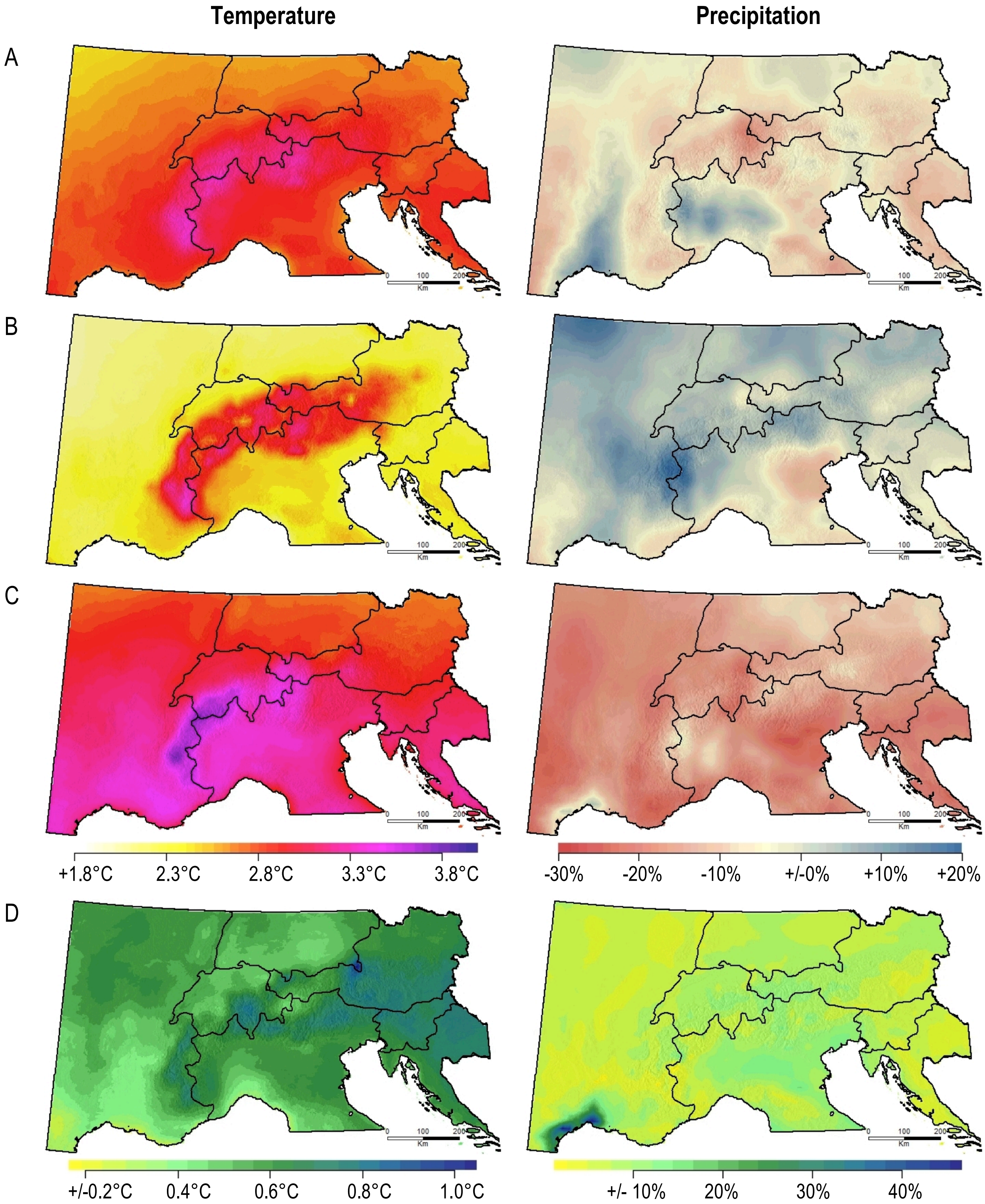

Figure 3. Climate anomalies for the A1B scenario by 2080 (deviations of the 2051-2080 period from the current, i.e. 1950-2000 climate) averaged over the six RCM models used to assess the impact of climate change on forest ecosystems and tree species ranges in the PORTREE project. **A**: Anomalies for annual temperature and precipitation; **B**: Anomalies for winter months (October-March); **C**: Anomalies for summer months (April-September); **D**: Uncertainties in summer anomalies among all 6 RCM models (calculated as the standard deviation among individual summer anomalies of the six models).

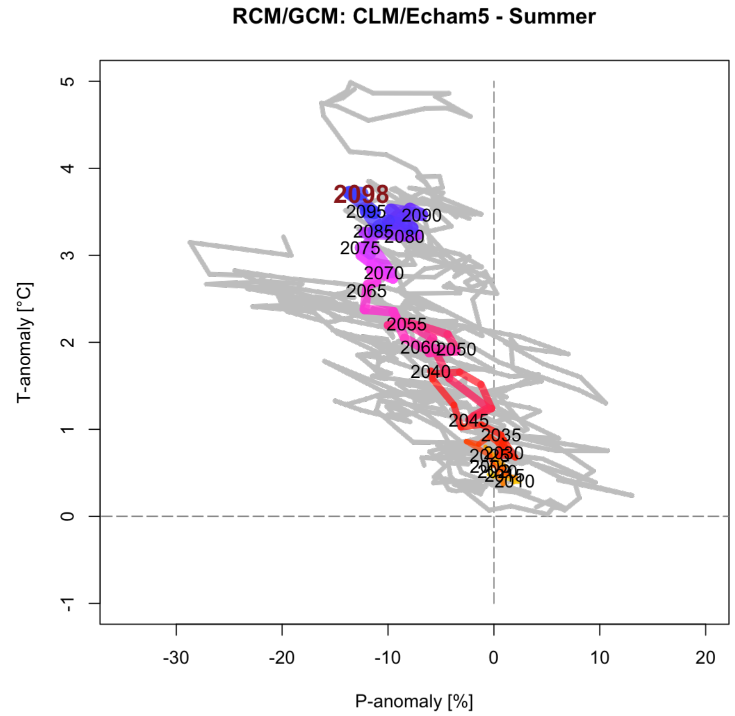

Figure 4. Temporal evolution of 5-year summer mean temperature and precipitation anomalies for six RCM climate projections of PORTREE (grey) for the A1B scenario, with the CLM/ECHAM5 model highlighted in color.

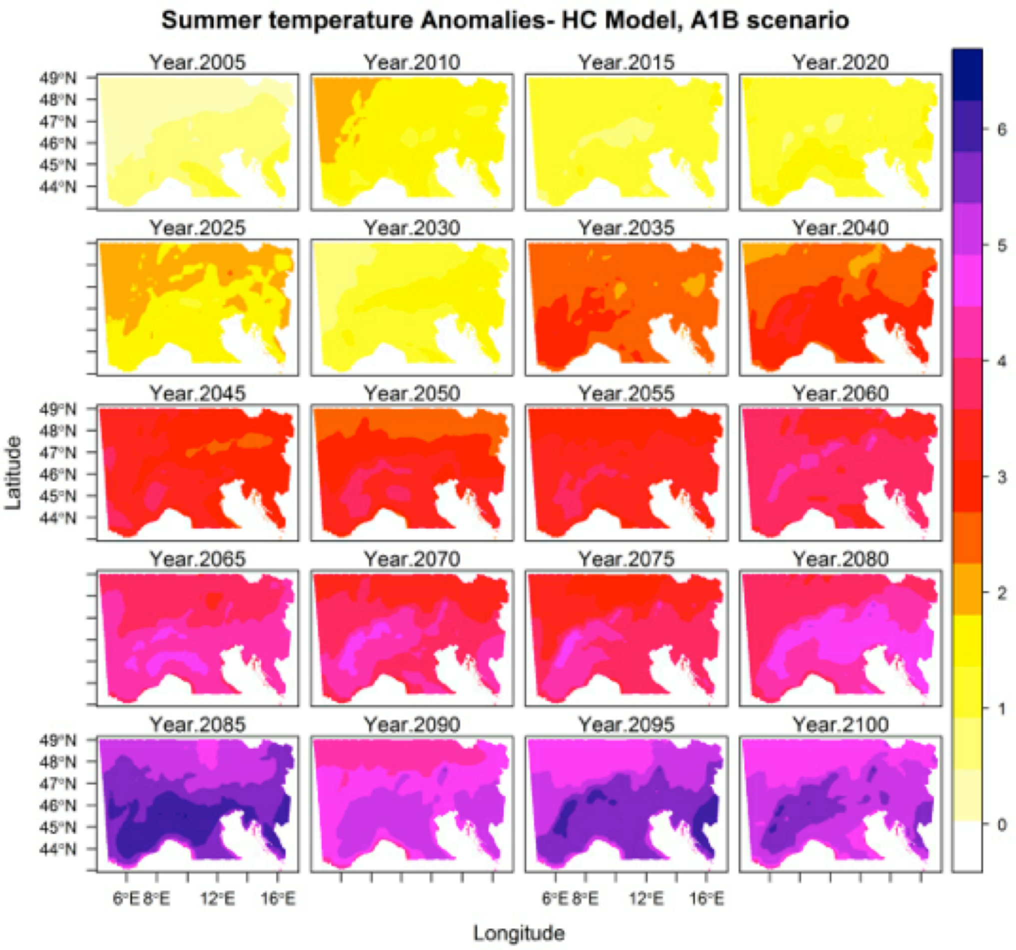

Figure 5. Spatial time series of absolute (°C) summer (April-September) temperature anomalies for the A1B scenario from 2001 until 2100 compared to the current climate (i.e. 1950-2000) over the Alps for the HadRM3/HadCM3 model used in the PORTREE project. Anomalies represent 5-year averages starting in 2005 for the 2001-2005 period.

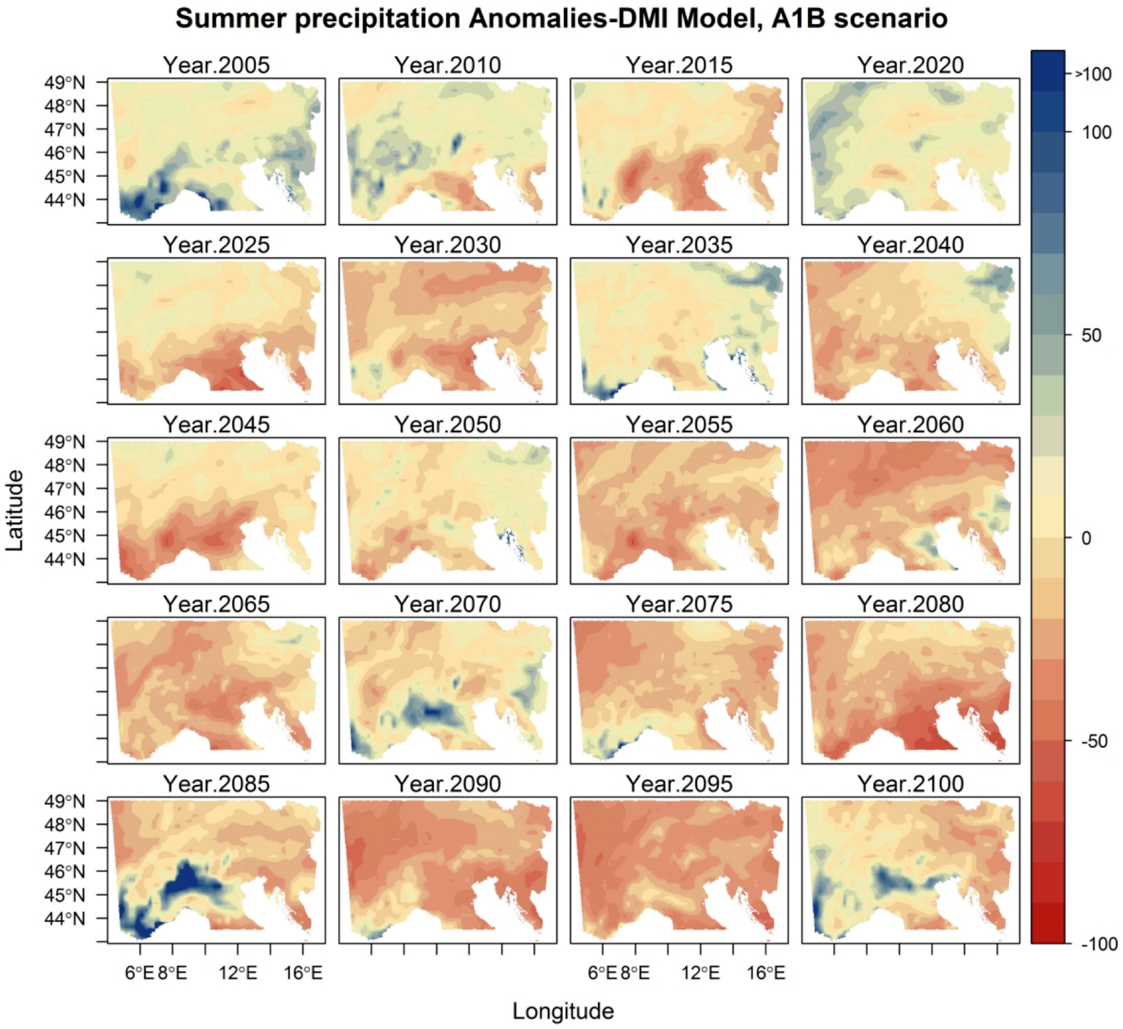

Figure 6. Spatial time series of relative (% change) summer (April-September) precipitation anomalies for the A1B scenario from 2001 until 2100 compared to the current climate (i.e. 1950-2000) over the Alps for the HIRHAM/Arpège model used in the PORTREE project. Anomalies represent 5-year averages starting in 2005 for the 2001-2005 period.

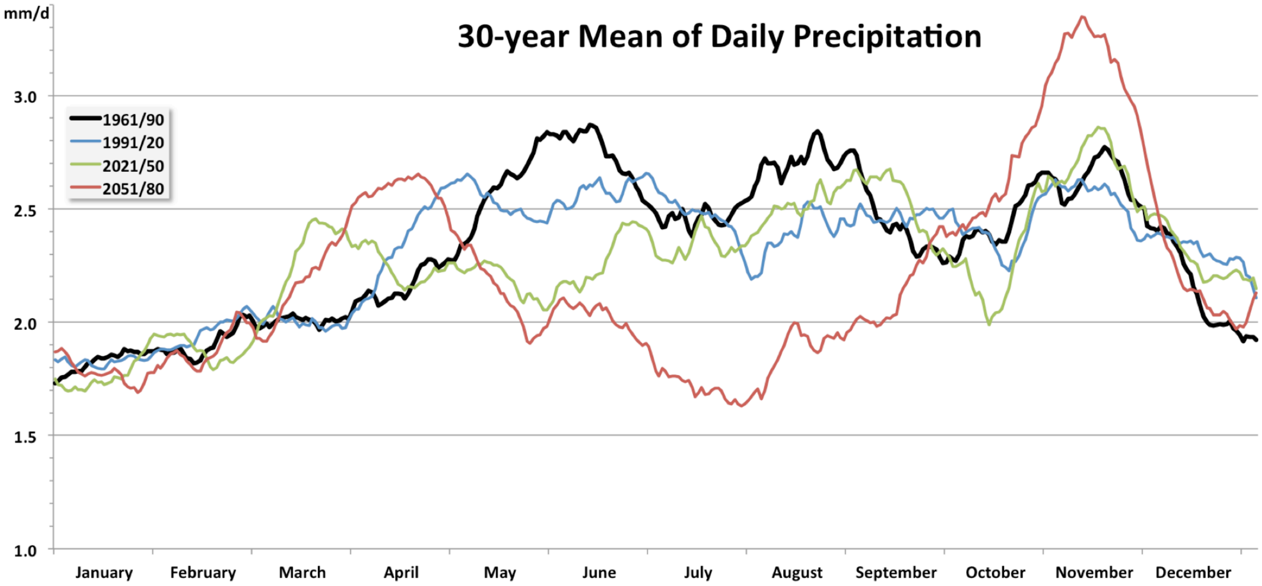

Figure 7. Change in precipitation seasonality across the European Alps as projected by the RCM model CLM that was driven by the ECHAM5 GCM. A trend to drier summer months and somewhat wetter spring (March/April) and autumn (November) months is apparent, specifically visible after 2050, when the RCM simulation projects a strong change to the precipitation regime.

RESULTS 2: *Projected range shifts in trees*

We present species distribution models (SDMs) fitted from six statistical models to simulate the ranges and their expected shifts following climate change. We used six models because the choice of a specific model has been shown to significantly contribute to uncertainty in projections. More specifically, we used the following statistical methods: [1] Classification and regression trees (CART), [2] Flexible discriminant analysis (FDA), [3] Generalized linear models (GLM), [4] Generalized additive models (GAM), [5] Artificial neural networks (ANN), and [6] Generalized boosted regression trees (GBM). Therefore, given the use of six statistical models and six (RCM-based) future climate model runs, we generated 36 different possible futures per species and time slice. This allows for assessing the projection uncertainty from both the variability in modeled climate and the variability originating from the choice of statistical methods. From these 36 models, we then built ensembles of model projections and classified these as follows: (1) a species is unlikely to find suitable habitat if less than 30% of the projections indicated presence of a species; (2) a species is moderately likely, associated with high uncertainty, if 30-60% of the projections suggested that the species is there; and (3) a species is most likely present with rather low uncertainty under projected climates if in >60% of the 36 model projections presence of a species is simulated to occur. Such a simple classification avoids an over-interpretation of the obtained results. More details on the data used and the statistical modeling procedures are given in the methods brief below.

Range shifts at the European scale

Figure 8 illustrates the projected range shifts of *Picea abies* (L.) Karst. at the European scale, as fitted from ICP Forest Level I data (Lorenz 1995). Norway spruce (*P. abies*) and many other species from Central and Northern Europe are expected to loose much terrain at low altitudes and in Central Europe, and will retract to higher altitudes and latitudes following climate change. Currently, Norway spruce is planted at lower altitudes than it would naturally inhabit in many locations in Southern and Central Europe. Obviously, these lower altitudes encompass climatic conditions that are still contained within the fundamental niche of the species now, and the distribution model under current climate does include these areas as (marginally) suitable habitats. However, much of this area will soon become unsuitable. This is specifically visible for the simulations of the 2051-2080 period, where for Norway spruce clearly only higher elevations and latitudes are projected to remain suitable. Larger parts at low altitudes and all of Central Europe become unsuitable or remain only suitable with high uncertainty. This uncertainty arises from highly contradicting projections by both climate and SDM model combinations.

At the European scale, we simulated 38 tree species of which only *P. abies* is shown here (Fig. 8). These simulations were carried out in collaboration with the EU-FP7 collaborative project MOTIVE, in which the PORTREE team was leading the workpackage 2 and had the responsibility to generate potential range maps and project future ensembles for forest trees in Europe (lead: NE Zimmermann). A more complete set of species can be checked out and downloaded from a special website[1]. From these analyses, it became obvious that mostly the

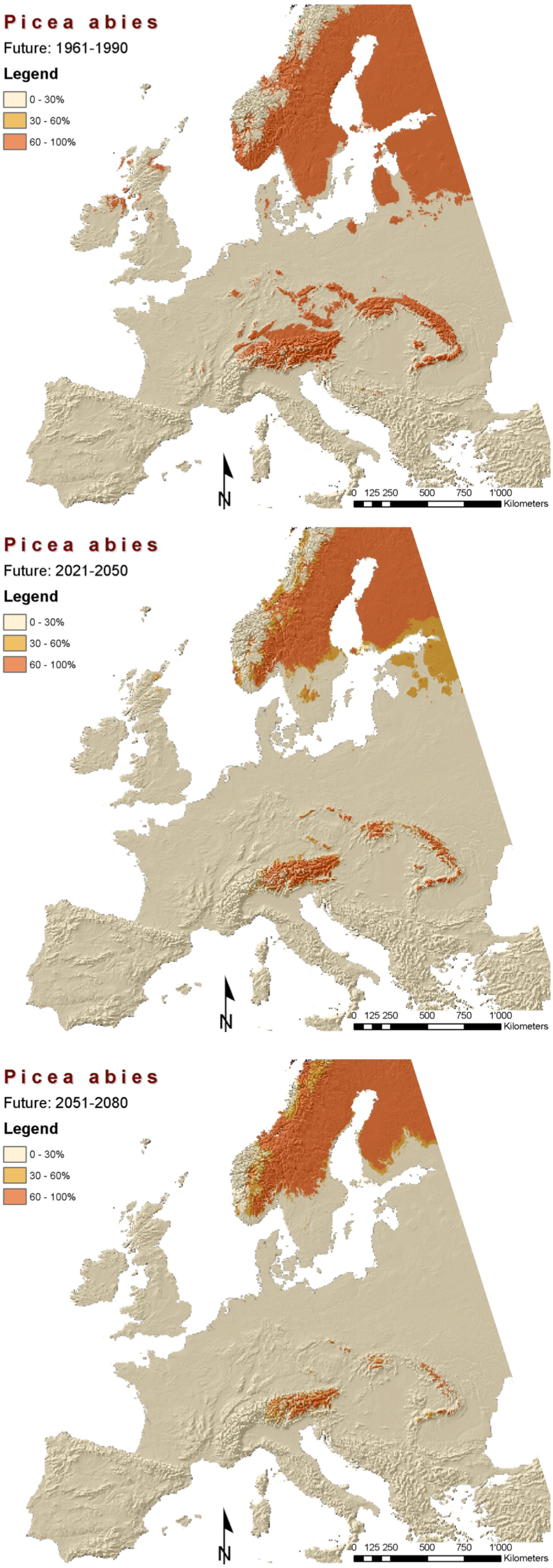

Figure 8. Ensemble projected change in habitat suitability for *Picea abies* in Europe following climate change in response to 6 RCM climate models using the A1B scenario and calibrated from 6 statistical models. The legend gives the agreement for simulating suitable habitat among all climate model x statistical model combinations from current (top) to the 2051-2080 period.

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[1] http://www.wsl.ch/lud/motive

more drought-tolerant species such as *Quercus petraea* (Mattuschka) Liebl., *Quercus pubescens* Willd., or *Pinus sylvestris* L. can be expected to become more abundant at lower altitudes throughout Europe, while other species such as *Fagus sylvatica* L., *Acer pseudoplatanus* L., *Tilia* spp., *Ulmus* spp. or *Abies alba* Mill. are likely further reduced in their ranges similar to Norway spruce. Species from (Sub-)Mediterranean regions such as *Quercus ilex* L., *Ostrya carpinifolia* Scop. or *Quercus suber* L. are expected to expand their ranges to the North, but these species will most likely not reach the areas currently suitable for beech or spruce by the end of the 21st century. Different pine species are also expected to extend their ranges quite considerably. However, they will likely not extend to very fertile soils either, and some of the pines like e.g. *P. sylvestris* might face indirect threats from insects and other pest outbreaks, rather than direct threats from climate change alone. In summary, the projected range shifts will affect the forest structure quite considerably. Among all species modeled, we can expect a shift in plant functional types in Europe between now and the end of the 21st century. Figure 8 summarizes the expected in-/decrease in broadleaf and needleleaf trees in Europe under the A1B scenario.

It becomes obvious (Fig. 9) that the two functional types respond quite differently, with broadleaf trees increasing in abundance mainly in Central and Northern Europe, and decreasing in Western and Southern Europe of the (sub-) Mediterranean and Atlantic regions (Lindner *et al.* 2014). At the same time, needleleaf trees rather show a bi-modal response with both an increase in high latitudes/altitudes and also an increase in the Mediterranean and Atlantic regions and in the Eastern European dry zones.

Range shifts at the scale of the European Alps and Switzerland

At the scale of the European Alps, we fitted – specifically for the PORTREE project, and in collaboration with the EU InterReg IIIB Alpine Space project MANFRED – for a larger suite of tree species ensembles of species distribution models (SDMs), often also termed climate envelope models (CEM). We used presence/absence information from forest inventories of France (Alps only), Northern Italy, Austria, Southern Germany, Slovenia and Switzerland in order to build a database of tree species presences and absences across the Alps. We compiled data for >30 tree species at a total of >80'000 inventory plots, although some countries did not distinguish all species at the same taxonomic level (some countries did e.g. not distinguish the different oaks or maples). For fitting the SDMs, used the following variables as predictors of species distribution in our models: (1) degreeday sum with a 5.56°C threshold, (2) temperature seasonality (standard deviation of monthly values), (3) summer precipitation (sum of April to September monthly values), (4) winter precipitation (October to March), (5) potential yearly global radiation, (6) slope angle in degree, (7) topographic position (difference between the average elevation in a circular moving window applied to a 100m digital elevation model and the center cell of the window (Zimmermann *et al.* 2007), (8) aspect value (ranging from 0 (south) to 100 (north), and (9) distance to running waters. These parameters were then used to explain the spatial distribution of a species. For some species, we fitted models only for Swiss inventory points, mostly for two reasons: either the species was not distinguished well in European inventories (e.g. oaks, maples), and therefore no sound data basis was available to calibrate models from the whole Alps; and/or the models using the above mentioned predictors did not reveal sufficiently sound model results. For models calibrated for Switzerland only, we added (10) soil depth, (11) calcareous/non-calcareous bedrock, and (12) distance to running and standing water (thus replacing the less precise layer (9). See "Methods brief" for details.

The statistical model calibration evaluated, which parameter had predictive power and what parameter could be discarded or downweighted because it did not significantly add to explain the spatial distribution of a tree species. More details on the data compilation and on the modeling procedures are given in the methods brief below. For developing projections of SDM ensembles under future climates, we used the same six RCMs (see appendix S3 for more details on the RCMs and on the downscaling procedures). All simulations were carried out at a 1km spatial resolution, and all input/output parameters are available in addition at a 100m spatial resolution that would allow generating the same output at these fine spatial grids.

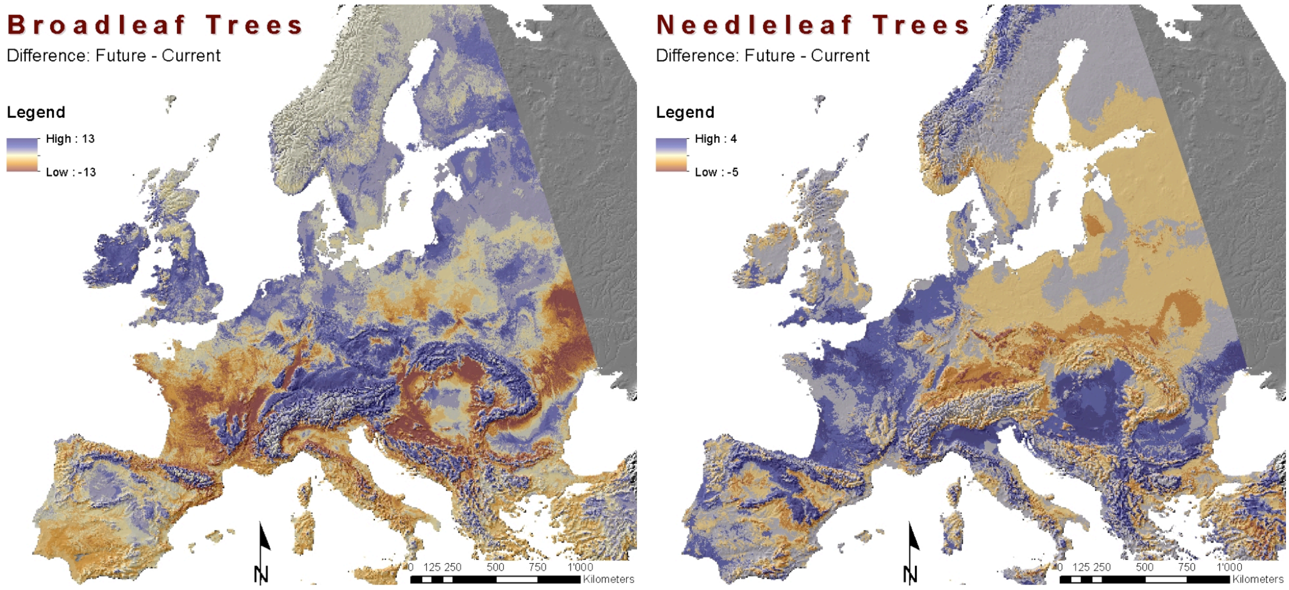

Figure 9. Changes in plant functional type composition from single species habitat suitability changes following climate change. The two panels indicate to what degree broadleaf (left panel) and needleleaf (right panel) tree species are expected to increase (blue) or decrease (red) in numbers. The results represent ensemble SDM simulations from six climate scenario (A1B) simulations and six statistical models.

Figure 10 illustrates the potential future range shift in two species *Fagus sylvatica* L. (European beech) and *Picea abies* (L.) Karst. (Norway spruce) in eight panels, indicating the areas that are suitable for the two species under current and under future

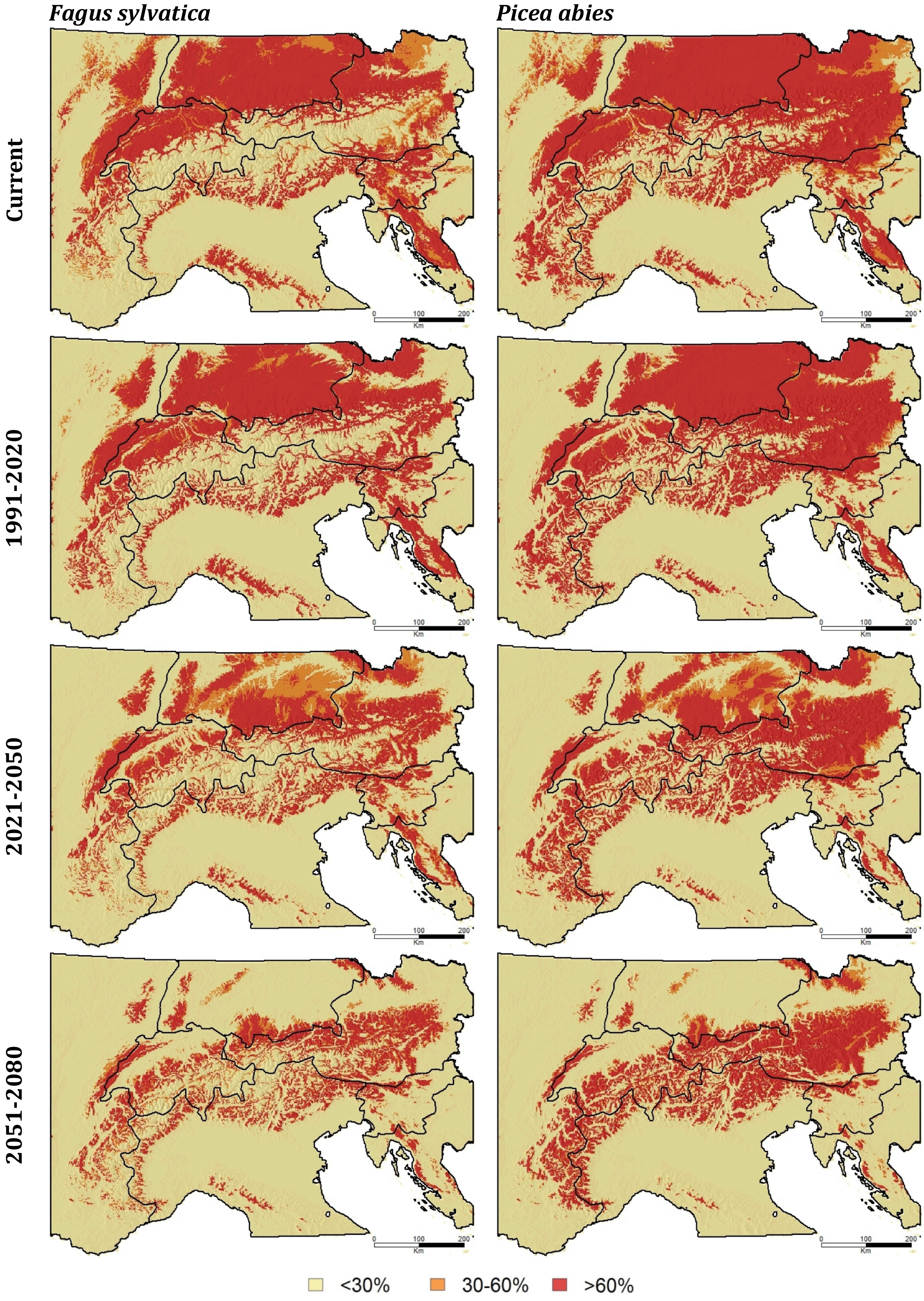

Figure 10: Projected future habitat suitability from ensemble SDM modeling of *Fagus sylvatica* and *Picea abies* for current and projected future climate in three time periods. Dark red colors represent high agreement that models suggest presence, respectively from six statistical and six climate models. Beige colors indicate high agreement that the species is absent, while intermediate orange colors indicate high uncertainty whether the species is present or absent for the given time period.

climate conditions in three different time steps towards the end of the 21st century. Both species are expected to loose much terrain at low altitudes, and will retract to higher altitudes following climate change. Currently, Norway spruce is planted at lower altitudes than it occurs naturally. Obviously, these lower altitudes are still within the fundamental niche of the species, and the simulated maps also capture the extended range of the species to lower altitudes under both current and future climates. However, compared to beech, it extends to higher altitudes, reaching treeline in many parts of the Alps. This is specifically visible for the simulations of the 2051-2080 period, where for Norway spruce clearly higher elevations are projected to be suitable than for beech. For both species, larger parts at low altitudes become unsuitable, while the habitat suitability in large areas in Southern Germany are projected to be highly uncertain for both species. This uncertainty arises from highly contradicting projections by both climate and SDM model combinations.

Many tree species have been simulated for the range of the Alps, and only few species are displayed here. A more complete set of species can be checked out and downloaded under a special website[2]. It becomes obvious that mostly the more drought-tolerant species such as *Quercus petraea* and *Quercus pubescens* can be expected to become more abundant at lower altitudes throughout the Alps, while other species such as *Acer pseudoplatanus*, *Tilia* spp., *Ulmus* spp. or Abies alba are likely further reduced in their ranges similar to beech and spruce (Fig. 11). Species from (Sub-) Mediterranean regions such as *Quercus ilex* or *Q. suber* are expected to extend their ranges to the North, but these species will not (or only barely) reach the areas currently suitable for beech by the end of the 21st century. Therefore, we can mostly expect sub-mediterranean, drought tolerant species to invade the spatial domain that is currently dominated by beech, namely: *Q. petraea*, Q. *pubescens*, *Ostrya carpinifolia* or *Fraxinus ornus* (see Fig.2). Different *Pinus* species are also expected to extend their ranges considerably. However, they will likely not extend to very fertile soils either, and some of the species like e.g. *P. sylvestris* might face indirect threats from insects and other pests, rather than direct threats from climate change alone. They may rather dominate at higher altitudes when summer precipitation is reduced, and larger parts of the Alps become considerably drier.

In fact, none of the individual SDM models is capable of projecting the effective fate of the different tree populations. The maps simply illustrate the habitat potential at certain time periods in the future. Species may still survive for quite a while at locations that become unsuitable. They will eventually face one or both of the following two threats: (1) physiological stress from a climate that they cannot tolerate, and (2) stronger competition by other, better adapted species or by antagonists such as insects, fungi, etc. that may profit in turn from a drier and/or hotter climate, and that may infest trees that are less vigorous because of a combination of the two causes (1) and (2). Forest management can usually deal more or less well with the second type of threat if it is primarily due to changes in tree species competition. Dealing with changes in antagonists in forest management is more difficult, as the example of the Scots pine dieback in the Alps illustrates (Bigler *et al.* 2006; Dobbertin *et al.* 2005; Dobbertin *et al.* 2007). Here, a rapid dieback at the lowest altitudes of the Scots pine distribution has been observed over the last 10 years, which is the area that is projected to eventually become unsuitable in the future from ensemble SDMs as well.

In appendix S1, we present a detailed summary of a range of important tree species for Switzerland. There, we combine the outcome of the ensemble range projection under future climates, and we present the summary statistics in the form of a table. In addition, we discuss the major implications of the projected changes in the light of management support. Table 2 provides an overview of model accuracies; details are given in appendix S4. For beech and spruce, appendix S5 gives all individual maps from the single models used to build the ensembles.

RESULTS 3: *Growth trends and spatial risks*

Range shift projections by SDMs project partly drastic extinctions over large parts of the area a species currently inhabits. One may ask, whether such dramatic extinctions are actually realistic. In fact, the method only projects to the future what we observe today. This means that in those areas, where we do project extinction in the future, we will then have climate conditions under which we do not have current observations of presence of the species. Therefore it is likely that the projections are correct, but we do not know how fast these changes will occur. The application of SDMs to different climates of the past have provided evidence that especially late successional, dominant tree species were well projected, and matched well the historical, pollen-based reconstructions of their ranges (Pearman *et al.* 2008). Early successional tree species were less well predicted by this method, as they usually do not dominate developed stands, and depend much on the presence or absence of more competitive species.

Now, we may ask, how fast such changes will occur. And we can further ask, if a species that grows now at a location close to areas that are soon predicted to have an unsuitable habitat will face immediate threats once the habitat becomes unsuitable. Here, we do not answer the first question. We would need a dynamic model and a well-developed seed dispersal and regeneration routine, something that might be simulated by models such as TreeMig (Lischke *et al.* 2006) or combinations of TreeMig with SDMs (Meier *et al.* 2012). However, we attempt to answer the second question by evaluating the growth response of three important tree species within their climate envelope. This envelope, or the simulated range of the species, represents the realized niche of a species. It encompasses all locations where the climate is suitable to maintain viable populations and where the given set of competing species does not drive the species out of its range (Hutchinson 1957). It also includes past management effects on species abundance and distribution. According to Hutchinson, this realized niche is different from the fundamental niche in that it also includes the effect of competitors, while the fundamental niche only considers abiotic factors, such as climate or topography. Usually, the realized niche is a subset of the fundamental niche, it contains those parts, where the species can deal with the competitors usually found at these locations, while in other parts it cannot compete against these other species in the long run. Leaving the fundamental niche would cause immediate physiological stress, while leaving the realized niche may simply only mean that competition by other species increases strongly.

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[2] http://www.wsl.ch/lud/manfred

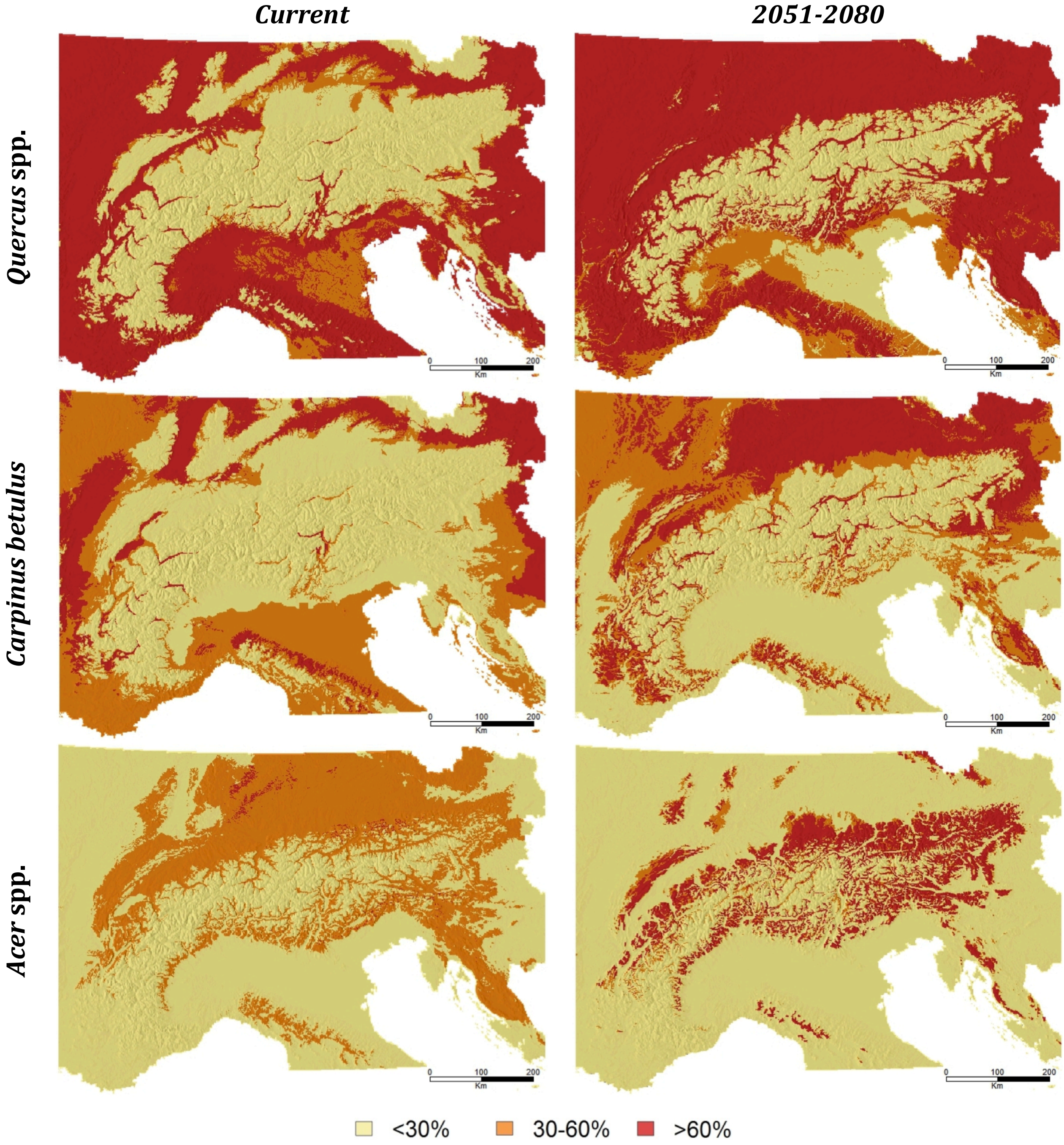

Figure 11: Projected future habitat suitability from ensemble SDM modeling of *Quercus* spp. and *Carpinus betulus*, and *Acer* spp. for current and projected future climate in three time periods. Dark red colors represent high agreement that models suggest presence, respectively from six statistical and six climate models. Beige colors indicate high agreement that the species is absent, while intermediate orange colors indicate high uncertainty whether the species is present or absent for the given time period.

For us, it means that we need to evaluate, what range edges of a species primarily will cause physiological stress and what range edges are primarily constrained by competition from other species. One way of finding out is to set up a suite of competition experiments, but this is time-consuming for trees. Another method to explore this is to analyze the contours of the maximum growth of tree individuals along range shaping climate gradients. If the maximum growth observed among trees is low towards the edge of a range, then the species is at risk of experiencing physiological stress, if the range edge is exceeded in ecological space. If, however, the maximum growth is still high or very high at a range edge, then the threat comes primarily from competition by even better growing species, once climate exceeds the limits of the edge. The latter is manageable in forestry, since competitors can be dealt with over the life span of a tree, and the immigration of such competitors will take time anyway. Figure 12 illustrates how *Picea abies* shows very high growth towards the warm edge of the (persistence) niche, which is located at ca. 2000 degreedays. However, the center of the species niche is more towards cooler climates (max 1700 degreedays). However, we see that the species can tolerate quite warmer climates, especially if the summer precipitation is not too low. The fitted growth niche (orange-red) exceeds partly the persistence niche (grey) due to the fact that we only used high-resolution data from Switzerland for the growth model, while the species distribution was fitted from the forest inventory data of the Alps.

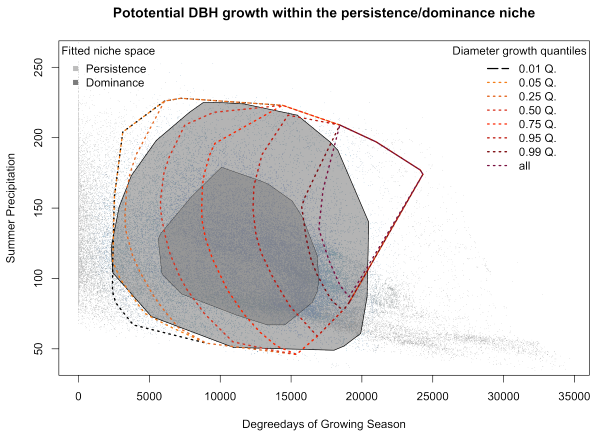

Figure 12: Growth quantiles of *Picea abies* according to a complex growth model fitted to trees from the forest inventory of Switzerland (LFI) and plotted over the persistence niche. Grey background dots represent all PORTREE points.

The fitted tree growth is sensitive to climate, tree size and stand density on Swiss forest inventory (LFI) plots. For projecting growth onto the environmental niche space, we kept tree size and stand structure constant and let all other variables vary per plot. We finally extracted quantiles of maximum growth among all LFI plots. The climate parameters used in the growth model are the same as in the niche model, and therefore we can plot the growth quantiles on top of the niche model.

The finding in figure 12 indicates that *P. abies* is not immediately at risk of extinction under a warming climate as long as there is not a decrease in precipitation. We therefore assigned two areas that lay outside of the realized (persistence) niche of the species, but likely well within comparably high maximum growth rates (see figure 13). The first – low risk – area is the zone just outside of the realized niche adjacent to highest maximum growth rates. This climate zone (here exemplified also with *P. abies*) will eventually be colonized by other, competing tree species, such as *Fagus sylvatica*, *Quercus robur*, *Quercus petraea*, etc., but P. abies is not likely experiencing physiological stress, and forest management can cope with the competition stress to Picea abies. A second – high(er) risk – area is a zone farther away from the realized niche. It might still be within the fundamental niche, but this is less certain. Therefore it is less obvious that the species still can be reasonably safely managed until the end of the 21st century.

These two zones can be mapped in space in order to visualize the management implications according to these concepts. Figure 14 illustrates these findings for *Fagus sylvatica*, and tells an interesting story. Compared to the SDM ensemble output, the low-risk zone indicates that most of the area that is projected to become unsuitable likely still provides sufficient growth potential for *F. sylvatica* until the end of the 21st century at comparably low risk. The major risk comes from invading competitors, but likely not from climate stress. Such threats can usually be managed well. The high-risk zone even maps all of the projected loss-zone of the ensemble SDMs as being suitable until the end of the 21st century. We call this assumption “high risk”, because the zones mapped as suitable compared to the “low risk” zone have a larger ecological (climatic) distance to the habitats that *F. sylvatica* currently inhabits, and therefore the risk of running into growth stress increases in the future. appendix S2 contains all growth analyses results.

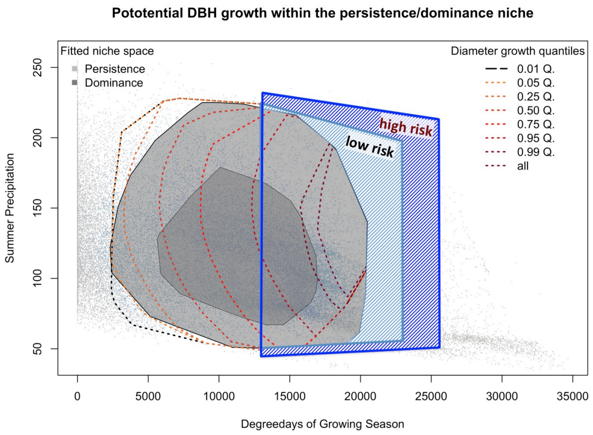

Figure 13: Two conceptualized risk (low, high) zones outside of the realized niche of *Picea abies* adjacent to niche edges that indicate high growth rates originating from a complex growth model fitted to trees of the forest inventory of Switzerland LFI). The light blue (low risk) zone is close to the persistence niche, with a high likelihood of *P. abies* still growing well under the absence of competition. The darker blue (high risk) zone is also adjacent to the high growth niche edge of *P. abies,* but farther away in climatic terms, and thus it is less certain if *P. abies* can be maintained under exclusion of competition.

One threat is still there, irrespective of such considerations. If climate becomes more extreme or more variable than projected by the applied RCMs (e.g. if the A1B scenario is exceeded in the future, or if on an annual basis the climate develops more extreme single events than projected in these RCMs, then the zones projected to be lost under the ensemble SDMs are no longer easily manageable. Severe growth stress or even mortality might occur there, and even in areas that are mapped suitable by the ensemble SDMs. The projection of extremes is difficult, and not yet well handled by RCMs. Also, the effect of extremes on range constraints and spatial patterns in trees is not well understood, and only preliminarily analyzed regarding its effects on species ranges (Zimmermann *et al.* 2009).

Management implications

General implications

For forest management, the projected climate anomalies may require specific actions to avoid significant loss in timber value. Least changes are likely required for mid to high altitudes. Here, the evaporative demand of a warming climate is balanced by sufficient amounts of precipitations both in winter and summer. Forest productivity can be expected to increase, and more thermophile species may soon find suitable habitats in this region. Maintaining a comparably high diversity in tree species is likely the best option to prevent severe negative effects if one or the other species should become difficult to keep viable. Slowly facilitating the ingrowth (partly planting) of more thermophilous tree species may help the transition towards the projected changes. For the lower altitudes in Switzerland, the projections are still quite unclear. While there is a general warming and drying trend projected, the models disagree as to how much the warming will be, and whether precipitation will increase or decrease in certain areas in summer. But even if no changes in total precipitation amount will occur, there are likely two effects visible for forest management. First, evaporative demands due to warmer temperatures can likely not be fully balanced, specifically because summers become slightly drier, the result will be a net water loss for tree growth; the general tendency is a climate seasonality shift towards a more Mediterranean-type climate, away from a summer maximum and winter minimum in rainfall towards two rainfall peaks in spring and fall, with comparably dry summers. In some regions, this trend may be less pronounced. Most severe changes with negative consequences for timber production can be expected for the areas south of the Alps. Here, precipitations are decreasing both in summer and winter, and temperatures are increasing in both seasons more (winter) or less (summer). This will result in much drier growth conditions, and has likely severe effects on the already water-limited forests. Only (and not shown in figures), the temporal variability for this region is specifically high with regards to rainfall, so that we may still expect some wet years in-between very dry years. This may mean that natural forest regeneration may still be possible, but growth might partly be severely limited.

While the general climate trends are still uncertain, as seen from the uncertainty maps originating from 6 RCM models, projections of climate extremes are even more difficult to make or to foresee. Several models, and even more so the deviation among models, are projecting that both the climate variability and the uncertainty of projections will become larger towards the end of the 21st Century (Figure 4). In general, we can expect that both temperature and precipitation extremes will increase. This has the consequence that forest management becomes more difficult or less foreseeable, because a larger range of possible conditions needs to be considered in the planning and decision-making.

By analyzing growth patterns over the persistence niches for some tree species, we were able to show that some areas projected to have unsuitable habitats might still be reasonably well manageable well into the 21st century, projecting a less pessimistic future than is usually obtained from ensemble, static SDMs. Due to the growth response of the analyzed trees, we believe that there is enough evidence that the threat is not immediate for many tree species if the niche thresholds are slightly exceeded climatically. It is – however – not easy to project exact borders for such a behavior, since only massive experiments can provide the true physiological basis for such statements.

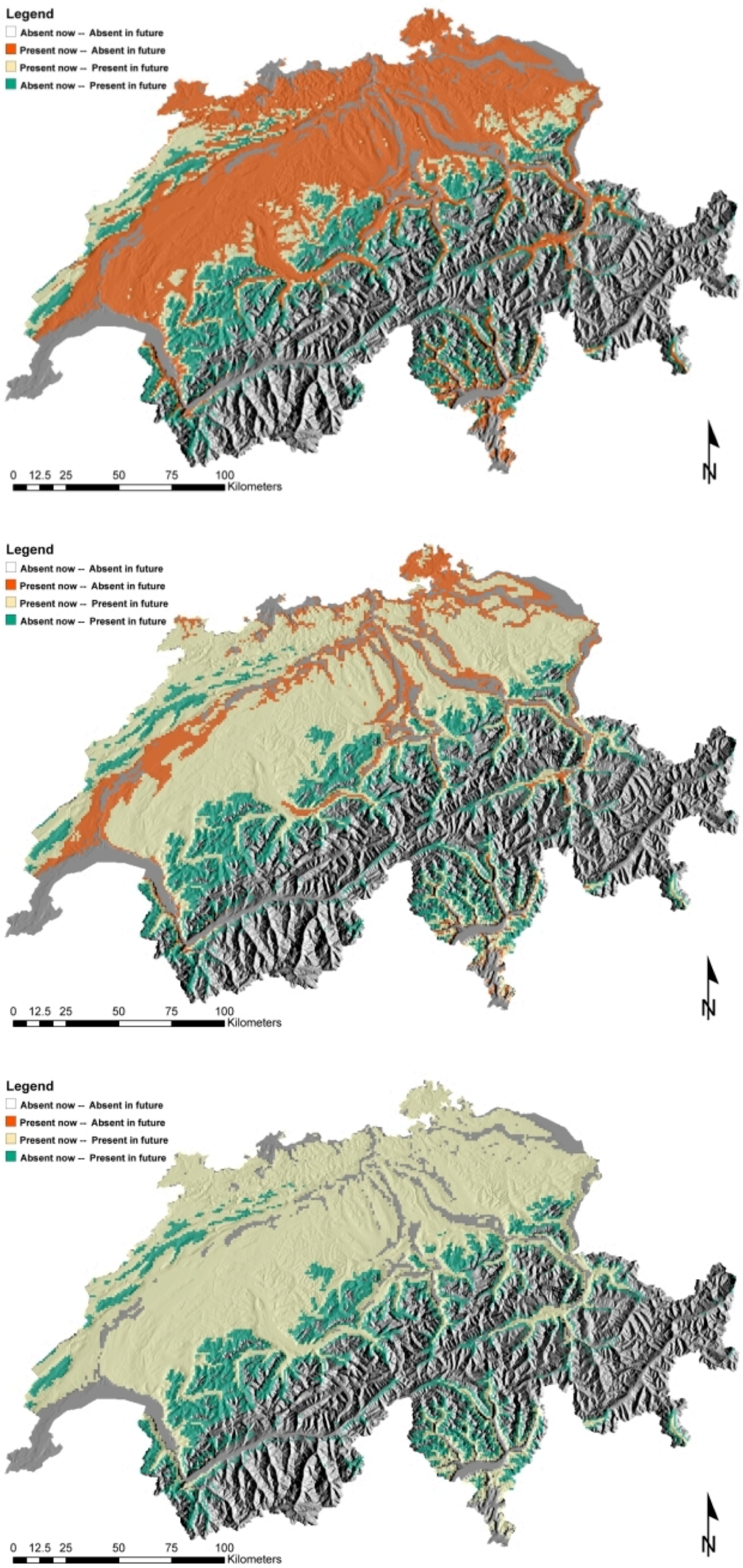

Figure 14: Risk of extinction (**orange**) of *Fagus sylvatica* in Switzerland under ensemble projections using the A1B scenario, 6 RCMs, and 6 statistical SDMs by 2080. The three panels map the risk based on three different assumptions. **A**: SDM based projection of extinction risks maps the area, where *F. sylvatica* has suitable habitat today, but will no longer do so in the future. Yellow indicates overlap in suitable habitat under current and future (2080) climate conditions, while green maps the areas that are not suitable today, but will become suitable by 2080. **B**: Takes the SDM projection of A, and maps the low risk zone of figure 13 into the orange range loss part of A in yellow, meaning that the projected range loss in A might not immediately cause threats, as long as forest management deals with competition by other species. **C**: Like B, but with the high risk zone mapped in yellow into the orange area of A.

Moreover, it is important for forest managers to understand that SDMs do not project an exact spatial future. No detailed soil information was available for the SDM models, so the results only apply for the "average" soil conditions under a given climate. If a location has a deeper than average soil, or if trees have access to ground- or additional (if only temporary) surface waters, or if soils can hold larger amounts of water and nutrients (than average), then our models are likely too pessimistic. On the contrary, forest stands on very shallow, sandy or rocky slopes might experience higher drought stress even now, than is projected by the SDM models. Careful comparative assessments by forest managers can help guide towards the future, by using both the model input and the field observations to plan the next management steps.

We would like to encourage forest managers to undertake own "experiments". Most scientific experiments do not last long enough to be useful for adult trees. Managers of a forest might want to experiment a little bit by planting single or few trees from species that are expected to soon find suitable habitats. This helps develop a local view of these species. On the contrary, carefully observing a set of trees that might soon lose their suitable habitats may provide a strong insight into the local behavior of a species, and the risks that might be assessed from this behavior.

Concluding remarks

The SDM methodology has the advantage of rapidly informing managers and practitioners about: (1) the areas that likely become suitable soon, (2) the areas that are not expected to undergo significant changes, and (3) the areas that likely – and eventually – become unsuitable for maintaining viable tree populations naturally. The disadvantage of the method is that it cannot inform managers about the speed of the projected changes, nor to what degree forest management might allow to continue growing a species that is currently here. Immigration into formerly unsuitable areas are not easy to predict, since the invading species have to compete against the already inhabiting species, and the replacement process might take a long time. This is primarily because invading species cannot establish in densely timbered forest stands. Even more difficult is to forecast at what rate tree species might go extinct, or render financial benefits when planted or managed under slowly deteriorating climates. In fact, most species grow better under warmer climates, and therefore not all areas that are "too warm" for a species are immediately at risk of loss. However, when at the same time increasing drought levels exceed species-specific thresholds, then trees might rapidly decline in growth or in maintaining viable populations. This illustrates, how difficult the forecasting of rear edge populations of a species range is under changing climate conditions. Careful observations need to be combined here with model results.

SDMs can be improved, by adding more informative predictors, such as soil information or site productivity estimates. However, the difficulty to obtain these predictors with identical units and sufficient quality over large areas spanning the entire range of a species renders this type of model improvement often very difficult. On the other hand, doing it only for smaller areas often results in models that do not span the capacity of the species well, because a smaller area that represents only a portion of the ecological niche of a species can be calibrated from data of such spatial domains. Yet, model improvements have to be sought constantly, and novel GIS techniques combined with the increasing availability of ecologically meaningful remote sensing data allow constant refinement of model predictors.

Methods brief

Multiple sources of climate and tree / forest data were required to solve the PORTREE questions at the scale of Switzerland and the European Alps in order to guarantee that enough gradient is sampled for each tree species. These data sets needed to include presence/absence (P/A), growth and stand composition, as well as mortality over the last 10-20 years. Finally, for all sites, spatially explicit climate data are required, ideally as daily, or at least as monthly and seasonal/annual maps of important climate variables including their projections under a range of IPCC scenarios.

Tree and inventory data

We used the following tree/stand data sets (in collaboration with EU-projects, where we were key partners):

- For PORTREE models at the scale of the European Alps, national forest inventory data (A, CH, D, F, I, SLO) using presence/absence (P/A) of tree species per plot were compiled. Range statistics on the Swiss scale were calculated within Switzerland from these PORTREE models (See appendix S3).

- For models at the European scale: ICP-Forest Level 1 data: data including P/A and "composition" of species per all ~6500 plots. These data were used to calculate the range statistics at the Europe scale.

- For growth models, we could only use Swiss data (LFI). We used (a) stand basal area, (b) period length (in ¼ years) between inventory periods per plot, and (c) individual tree DBH as predictors for the growth model calibration in addition to the climate variables listed below. We used individual tree radial DBH increments as dependent variable in the growth models.

Current climate, climate downscaling and topography data

We used three sources for our climate and topography data, namely Worldclim, PRISM precipitation for the Alps, and an SRTM (90m) derived digital elevation model across the Alps resampled to a spatial resolution of 100m.

- For topography analyses, we assembled SRTM-based elevation data (Rabus *et al.* 2003), originally available at 90m spatial resolution, and resampled it to 100m resolution for the European Alps.

- Worldclim data (Hijmans *et al.* 2005)is globally available for monthly mean temperature and precipitation (mean period of 1950-2000) at a ca. 1km spatial resolution. It is an excellent data source for continental scale, contemporary climate data. For the scale of the Alps and the PORTREE model calibration, we used the monthly temperature maps (Tmin, Tave, Tmax,). Precipitation maps were not used due to the low number of precipitation stations used in Worldclim, which resulted in a lack of representing dry interior valleys.

- PRISM-derived (Daly *et al.* 1994) precipitation maps (Prcp) were used for the Alps. This product has been developed at ETHZ for the European Alps, using ca. 6000 rainfall gauging stations (Schwarb *et al.* 2001). While first only available as annual and seasonal maps, it now contains monthly mean precipitation maps for the Alps and was made available by C.

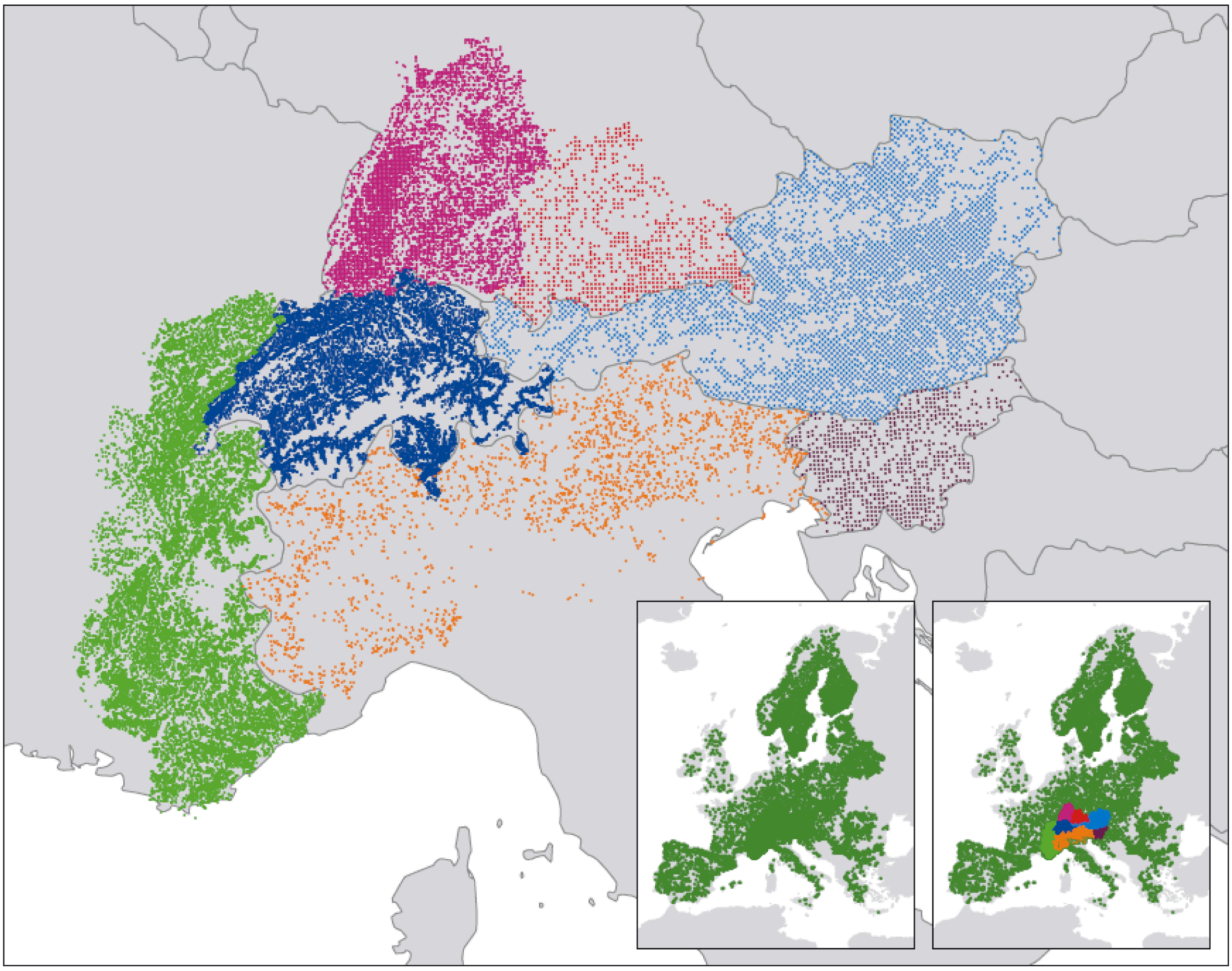

Figure 15: Data sets used for the PORTREE model development. Main panel: forest inventory plots per country (data from Germany for Baden-Württemberg and for Bavaria have separate colors). Inset panels: The two panels illustrate the ICP Forest Level I plots in Europe (left), and the Alpine forest inventory data draped on top of the ICP Forest data.

Frei, MeteoSchweiz. The PRISM method is also – in a modified version – the new core of the climate interpolation and mapping method at MeteoSchweiz. The data is available at a 2 km spatial resolution.

Before extracting predictor variables, we downscaled all monthly climate data to the 100m spatial resolution of the topography data, using moving window regression approaches (Zimmermann *et al.* 2007). The 100m data was then processed to predictor variables and values were extracted for each inventory point location.

Future climate projections and downscaling of projections

Before processing the current climate and topography data to predictors, we processed and downscaled climate change projections to the same spatial resolution of 100m. The following data were used:

- RCM climate data from the EU project ENSEMBLES[3]. We primarily were interested in the basic climatology output variables Tmin, Tave, Tmax, Prcp. We used the A1B scenario, since this scenario was available for all models. Other scenarios were only available occasionally. We used data from 6 RCM/GCM model combinations (see table 1) for our analyses.

We downscaled AR4 IPCC scenario simulations for forecasts in the Swiss study areas. IPCC scenarios based on AR4 were not yet easily available in a downscaled form (<=1km resolution), and primarily were only available at very coarse spatial resolution (ca. 20km pixels). The latter was too coarse to be easily downscaled statistically. We thus used RCM output from the ENSEMBLES project, which has made the four basic IPCC scenarios (A1B, A2, B1, B2) available. However, only the A1B scenario was consistently available trough all RCMs, therefore we decided to use this scenario for the "Wald & Klimawandel Program". The other scenarios were downscaled where available.

Predictor variables for model calibration

After downscaling current and potential future climates to a 100m spatial resolution, we derived a series of predictor variables for model calibration. Specifically, we generated the following predictors:

(1) degreeday sum with a 5.56°C threshold, based on the monthly Tave maps (see Zimmermann & Kienast 1999); (2) temperature seasonality (standard deviation of monthly values, according to Worldclim routine), (3) summer precipitation (sum of April to September monthly values), (4) winter precipitation (October to March), (5) potential yearly global radiation (see Zimmermann *et al.* 2007), (6) slope angle in degree, (7) topographic position (difference between the average elevation in a circular moving window applied to a 100m digital elevation model and the center cell of the window (Zimmermann *et al.* 2007), (8) aspect value (ranging from 0, i.e. south, to 100, i.e. north; Meier *et al.* 2014), and (9) distance to running waters

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[3] http://www.ensembles-eu.org/

(from an European coverage of running waters). These parameters were then used to calibrate predictive models of the spatial distribution of PORTREE species. For some species, we fitted models only for Swiss inventory points, mostly for two reasons: (i) the species was not distinguished well in European inventories (e.g. oaks, maples, ashes), and therefore no sound data basis was available to calibrate models from the whole Alps (see appendix S3); (ii) the models using the above mentioned predictors did not reveal sufficiently sound model results. For models calibrated for Switzerland only, we added (10) soil depth from the soil suitability map of Switzerland (Eidg. Justiz- und Polizeidepartement (EJDP) 1980), (11) calcareous/non-calcareous bedrock (Allenbach *et al.* 2008), and (12) distance to running and standing water (thus replacing the less precise layer (9).

Statistical SDM analyses and map projections

We analyzed the distribution of tree species (P/A; = persistence area) along environmental gradients using: [1] Classification and regression trees (CART), [2] Flexible discriminant analysis (FDA), [3] Generalized linear models (GLM), [4] Generalized additive models (GAM), [5] Artificial neural networks (ANN), and [6] Generalized boosted regression trees (GBM) in order to build model ensembles. The selected climate and other environmental variables are (a) known to be relevant to tree species in general, (b) have partly been shown to be of physiological relevance, and (c) had all a Pearson correlation coefficient <0.7 among each other to avoid collinearity problems when fitting the models. Model accuracies are summarized in table 2, and available in an extended form in appendix S4.

We thus had 6 climate models (for future projections) and six statistical models fitted for each tree species. This resulted in six maps per species under current climate. For future conditions, this resulted in 36 maps per species and time step. Projections were generated at 1km spatial resolution, but can also be generated at higher spatial resolution.

Each map first represents probabilities to find a specific tree species at each landscape pixel. These probabilities are then classified into binary P/A maps for integrating into ensemble maps. Probabilities were converted into binary maps by optimizing the probability cut-level so that the AUC values (Fielding & Bell 1997) in a cross-validation test exercise per species and statistical model was optimized. It thus represents the most accurate re-classification of probabilities into simulated presence/ absence values for each species and model.

These maps all represent likely futures of a tree species, and we used all maps to construct ensemble projections that fulfilled the following criteria: First, we excluded models of inferior quality (AUC < 0.7), second we mapped per pixel how many of the 6 SMDs for current, and 36 SDMs for future conditions mapped "presence" of the species. Finally, we reclassified these summed presences and absences so that we generated 3 zones. Namely: (1) a zone were less than 30% of the models project "presence", meaning that there is high agreement of "absence", (2) a zone where more than 60% of all model combinations project "presence", meaning that there is comparably high agreement among models, and finally (3) a zone where 30-60% of the models project "presence", meaning that there is high uncertainty among statistical/climate models as to whether the species is present or absent at these pixels. All models were evaluated based on Kappa, AUC and TSS.

Table 2. Model accuracies given by cross-validated AUC (area under curve). The AUC values are tabulated for each species as mean and st.dev among all six statistical models used. Models with AUC values <0.7 were excluded and therefore did not contribute to the statistic.

Species	**Mean**	St.dev
Abies alba	**0.84**	±0.034
Acer campestre	**0.83**	±0.071
Acer pseudoplatanus	**0.78**	±0.028
Alnus glutinosa	**0.84**	±0.035
Alnus incana	**0.84**	±0.018
Betula pendula	**0.79**	±0.024
Carpinus betulus	**0.91**	±0.008
Castanea sativa	**0.98**	±0.012
Corylus avellana	**0.89**	±0.019
Fagus sylvatica	**0.84**	±0.045
Fraxinus excelsior	**0.84**	±0.017
Fraxinus ornus	**0.86**	±0.063
Larix decidua	**0.84**	±0.035
Ostria carpinifolia	**0.92**	±0.029
Picea abies	**0.85**	±0.032
Pinus cembra	**0.94**	±0.032
Pinus nigra	**0.82**	±0.047
Pinus sylvestris	**0.84**	±0.020
Populus tremula	**0.76**	±0.027
Prunus avium	**0.80**	±0.029
Prunus padus	**0.82**	±0.062
Quercus ilex	**0.97**	±0.007
Quercus petraea	**0.89**	±0.012
Quercus pubescens	**0.85**	±0.051
Quercus robur	**0.88**	±0.023
Robinia pseudoacacia	**0.96**	±0.010
Ulmus glabra	**0.88**	±0.020

Statistical growth analyses and growth projections

In order to analyze the growth potential along environmental gradients, we fitted the (radial increment or DBH) growth of individual trees as a GLM function with the following variables as predictors: (1) DBH of the dependent tree individual, (2) stand basal area (stand BAI) of the surrounding LFI plot, (3) the period length between the two inventory periods used to assess individual tree radial growth (in ¼ years), and (4) the basic nine climate variables used for the SDM model calibration. By this, the individual tree growth model is sensitive to the size of the tree, the stand density (BAI) and the length of the inventory period, in addition to all climate parameters used.

The growth model was then plotted on top of projected SDM persistence domains (see Figure 12 & 13) by keeping stand and tree size of each plot at a median value among all individuals per species, by setting the inventory period length to 10 years, and by then plotting the modelled growth onto all LFI points with the respective climate values. In a post-processing, we mapped isolines of maximum simulated growth per plot region, thus representing potential growth rates of a species draped over the persistence niche of the same species. The two niches (persistence & growth) do not fully match on top of each other because the persistence niche is fitted from the PORTREE inventory points across the Alps, while the growth niche is fitted only from LFI data.

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