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The sensitivity of Austria's tree species to climate change

Master Thesis

of

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Preface

I want to thank all people that supported the work of my thesis, especially to my two supervisors Ao.Univ.Prof. Dipl.-Ing. Dr.nat.techn. Manfred J. Lexer and Assist. Prof. Dipl.-Ing. Dr. Rupert Seidl. Their outstanding support and contribution gave me a lot of input and motivation to conduct the scope of my work in all conscience.

For my thesis topic, I could apply my already acquired knowledge in forestry and gain new experience in the field of ecologically modeling and climate change. There, I also became acquainted with the performance of the R software for the statistical and spatial analyses.

I hope that the results of my thesis will contribute to forest science and in terms of climate change, can give a silvicultural recommendation to forest managers. Further, I want to emphasize that the tree species suitability concept here applied and the studied tree species sensitivity, can contribute and be an exemplar basis for additional ecological model approaches.

Summary

Climate change progressed considerably over the last decades at the global scale. The observed temperature increase in Austria is twice as much as at the global average, and is predicted to increase at an accelerating rate until the end of the 21st century. Also the variability of precipitation is predicted to increase, possibly leading to a higher frequency of drought events and shortened snow durations that can limit water availability to forest ecosystems. Forest tree species might have different sensitivities towards changing climate conditions, based on their specific ecophysiological thresholds and traits. The future distribution of forest tree species will depend on how forest management and species will react and adapt to a changing climate.

The objectives in this thesis were (1) to investigate the climate sensitivity of the ten most common forest tree species in Austria at their current distribution, and determine the relative roles of temperature and precipitation in overall climate sensitivity, (2) to identify the species most at risk at their current locations, (3) to indicate and quantify spatial hotspots of the risk of species loss, and (4) to quantify how species diversity is contributing to the mitigation of climate change sensitivity.

A tree species suitability model was applied, which quantifies the physiological limitations of tree species with regard to energy, water and soil regimes. The sensitivity to different generically defined climate scenarios, developed to reflect a range of different combinations of temperature and precipitation for Austria, was assessed with the model.

The analysis was conducted on two levels. The first step was to assess climate sensitivity for each species individually, considering their current distribution in Austria. Second, the risk of species loss at the level of forest inventory plots was estimated for all ten tree species jointly, to see where (ecoregions and elevations) the greatest risk for species loss might be expected, and whether species diversity and evenness at plot-level influence the risk of species loss.

The eastern parts of Austria were found to be most sensitive to climate change, especially with regard to changes in precipitation. There were strong differences in risk of species loss between ecoregions and elevation levels, with Norway spruce being the most at risk. Species diversity and species evenness at plot level had no mitigating effect on species loss. This analysis should help scientists and forest managers to prioritize adaptation strategies for a changing climate.

Kurzfassung

Seit mehreren Jahrzehnten, ist ein deutlicher Klimawandel feststellbar, wobei der Temperaturanstieg im Alpenraum im Gegensatz zum globalen Durchschnitt doppelt so hoch ist, und in Prognosen sich bis zum Ende des 21. Jahrhunderts weiter verstärken wird. Zudem sind Niederschlagsschwankungen mit einer weiten Bandbreite prognostiziert, die zusammen mit steigenden Temperaturen ein häufigeres Vorkommen von Hitzewellen, Dürreperioden und verkürzter Schneedeckendauer erwarten lassen. Baumarten werden unter diesen veränderten Klimabedingungen aufgrund ihrer ökophysiologischen Grenzen, die auf baumartenspezifischen Eigenschaften basieren, auf verschiedene Weise reagieren. Die zukünftige Baumartenverteilung hängt davon ab, inwieweit die Baumarten auf ihren aktuellen Standorten sich an ein änderndes Klima anpassen können. Dabei können sie sich entweder innerhalb ihrer ökophysiologischen Toleranzbereiche auf den aktuellen Standorten anpassen oder müssen zu besser geeigneten Standorten abwandern.

Zielsetzung für diese Arbeit war es, (1) die Klimasensitivität von den zehn am häufigsten vorkommenden Baumarten Österreichs zu untersuchen, (2) die Baumart mit der auf ihrem aktuellen Standort höchsten Klimasensitivität zu identifizieren, (3) die räumlichen Risiko-Hotspots für mögliche Baumartenverluste zu identifizieren und zu quantifizieren, und (4) abzuschätzen, inwieweit Diversität und Gleichmäßigkeit der Baumartenverteilung zur Milderung der Klimasensitivität auf Flächenebene beitragen kann.

In einer autökologischen Herangehensweise, wurde die Empfindlichkeit von den am häufigsten vorkommenden zehn Baumarten gegenüber dem Klimawandel untersucht. Es wurde ein Baumarteneignungsmodell angewendet, das Wachstumslimitierungen über ökophysiologische Grenzen, hinsichtlich Energie-, Wasserhaushalt- und Bodeneigenschaften identifiziert. Die Baumarteneignung wurde durch generische Klimaszenarien, welche eine Vielzahl von prognostizierten Temperatur- und Niederschlagsänderungen kombinieren, abgeschätzt.

Die Analyse wurde auf zwei Ebenen durchgeführt: Der erste Schritt adressiert die Artenebene, wobei das Ausmaß der Klimasensitivität jeder Baumart auf ihren aktuellen Standorten in Österreich bestimmt wurde. Zweitens wurden die potentiellen Anteile des Baumartenverlusts je Stichprobenpunkt über alle Baumarten ermittelt und nach Unterschieden über Hauptwuchsgebiete und Höhenstufen analysiert. Weiteres wurde untersucht, ob Diversität und Gleichmäßigkeit der Baumartenverteilung zu einer Milderung der punktspezifischen Baumartensensitivität beitragen.

Die Ergebnisse zeigten, dass vor allem die östlichen Teile Österreichs besondere Klimasensitivität aufweisen. Besonders veränderte Niederschlagsbedingungen würden Baumarten in tieferen Lagen der kollinen und submontanen Höhenstufe stark negativ beeinflussen. Es gab große Unterschiede von

potentiellen Artenverlusten zwischen den einzelnen Hauptwuchsgebieten und Höhenstufen, wobei die Hauptwuchsgebiete Mühl- und Waldviertel, sommerwarmer Osten und östliche Randalpen, sowie die kollinen und submontanen Tieflagen unter 700 Höhenmetern am stärksten betroffen sind. Diversität und Gleichmäßigkeit der Baumartenverteilung hatten keinen mindernden Einfluss auf die Klimasensitivität der aktuellen Baumartenverteilung. Die vorliegende Analyse sollte Wissenschaftler wie Praktikern helfen, Prioritäten in der Klimaanpassung zu setzen.

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Abbreviations

AFI = Austrian Forest Inventory

C/N = Carbon-to-Nitrogen

GAR = Greater Alpine Region

GCM = Global Circulation Model

IPCC = International Panel on Climate Change

PNV = Potential Natural Vegetation

RCM = Regional Climate Model

SMI = Soil Moisture Index

TSM = Tree Species Suitability Model

VPD = Vapor Pressure Deficit

ZAMG = Zentralanstalt für Meteorologie und Geodynamik

1 Climate change and sensitivity of forest tree species

1.1 Climate change variability

1.1.1 Observed climate change

The effects of global warming are already visible today and have enormous economic, environmental and social impacts on mankind. IPCC (Solomon *et al.*, 2007) states that the impacts of climate change are accelerating at a higher rate than expected a decade ago. Therefore, the states of the European Union have set an ambitious objective for climate change mitigation: to limit global warming to a maximum increase of 2°C in temperature, with the 19th century as the baseline temperature (UBA, 2006).

There is a significant difference between the already observed warming in the Greater Alpine Region (GAR) and northern hemisphere in Europe. The HISTALP database (Auer *et al.*, 2007), which concentrates on monthly climate data, states that mountains do not show any lesser or greater warming than lower elevations, but due to differences in sunshine, cloudiness and air pressure, there is higher climate variability over the whole GAR. Thus, one can expect a higher impact of climate change over the whole GAR, which includes many neighboring countries in Europe, besides Austria (Auer *et al.*, 2007). The temperature increase in Germany is up to 0.8°C and nearly doubled by up to 1.5°C in the Alps, which is twice as much as the global average over the last hundred years (UBA, 2006; Auer *et al.*, 2007).

The 2003 heat wave has shown the potential consequences of extreme climate events on the environment and economy. The whole eastern and southeastern part of Austria had during the vegetation period from January until the end of August 2003 only 300mm precipitation in total, i.e. only 50% of the expected mean precipitation in that period. The whole extent of subsequent damages in forestry was only visible in the following years after the drought event (Formayer and Frischauf, 2004).

1.1.2 Expected future climate change for temperature

The warming in Europe is predicted to be higher than the global mean temperature increase for this century (Solomon *et al.*, 2007). European projections predict an increase of the mean annual temperature due to increase of hot summer days and warmer days in the winter (UBA, 2006). Under the scenario A1B of Solomon *et al.* (2007), the expected warming for the northern European region varies between 2.3°C to 5.3°C for the period 2088 to 2099, compared to the mean annual temperatures of 1961-1990 (Solomon *et al.*, 2007). The A1B scenario is the balanced emission

scenario of the IPCC that considers an increase in the world population and a continued high CO₂ emission until 2050 (Schüler *et al.*, 2012; Solomon *et al.*, 2007).

Compared to the intercontinental scale of Europe, Lindner *et al.* (2010) also speak of higher increases in temperature within mountainous regions in the future. Comparing expected climate change to the climate of the period of 1961-1990, a study from the Max Planck Institute for Meteorology predicts a temperature rise between 2.5°C and 3.5°C by the end of the 21st century in Germany (UBA, 2006). The possibility of an increase of more than 4°C in winter temperatures across the Alps is likely to make days with frost rarer, leading to a higher probability of rain precipitation rather than snow, and a shorter winter period (Matulla, 2009; UBA, 2006; Roberts, 2008). On the basis of the emission scenario A1B of the regional climate projections in Europe, the expectations for an increase in mean annual temperature in Austria tend to be between 2.3°C and 5.3°C by 2099 (Solomon *et al.*, 2007; Matulla, 2009). Considering the currently unabated increase in emissions, one might even consider increases of up to 6.4°C in 2100, which are results of the IPCC's 2007 emission scenario A1FI (Niedermair *et al.*, 2007). A regional study of the Province of Styria shows an increase of 0.30°C per decade projected for a 30 year period from 1971-2000 to 2021-2050 (Gobiet *et al.*, 2012). Theoretically, that would result in an increase of 3°C within one hundred years. But overall, predictions of temperature increases until 2100 range (under A1B emission scenario) between 2.3°C and 5.3°C for different regions of central Europe, inter alia for Austria (Solomon *et al.*, 2007).

1.1.3 Expected future climate change for precipitation

Eitzinger *et al.* (2009) report small changes in precipitation patterns with slightly increases in winter and slight decreases in summer for Central Europe. At the continental temperature zone of Europe the annual rainfall will increase up to 10%, mainly in winter (Lindner *et al.*, 2010). Meanwhile, summer precipitation is predicted to decrease by up to 10%, whereas the precipitation changes in mountainous regions differ in general locally due to their high heterogenic geomorphology and are very uncertain to predict (Lindner *et al.*, 2010).

Figures of IPCCs regional climate projections show an annual area-mean precipitation change for the period 2080-2099 relative to 1980-1999 with a precipitation increase of +10% in winter and a decrease by up to -20% in summer for Austria. A similar pattern was reported by Schüler *et al.* (2012) with the relative change of total precipitation between 1971-2000 and 2071-2100 predicted to amount between +5% to -25% (Schüler *et al.*, 2012). Strauss *et al.* (2012) speak about precipitation scenarios of reduced precipitation sums of -20% and elevated precipitation sums of +20% for the years 2008-2040 relative to 1974-2007. As a consequences of changes in temperature and

precipitation, climate simulations also predict a major change in the average snow levels until the end of the 21st century (2071-2100) compared with the same period of 1961-1990, declining between -30% and -50% within the Alps (MPI-M, 2006). However, changes in precipitation may vary more at smaller scales in areas of complex terrain (Solomon *et al.*, 2007).

In summary, the risk of increased summer droughts and decreased snow levels with subsequent shorter durations of snow cover is expected to lower the water availability in the growing season in central Europe during this century (Solomon *et al.*, 2007).

1.2 Uncertainties and climate models in an ecological context

Generally, by its very definition, the future is uncertain. One way to embrace the uncertainties of future environmental conditions in climate change impact research is to conduct scenario analyses, i.e. to ask “what if” questions. In this regard the application of models is a powerful tool to address uncertainties. Yet models, being simplifications of reality, contain uncertainties themselves. It is thus important to know the underlying assumptions and to evaluate models in detail against independent data, in order to make analyses about future scenarios more robust (Wiens *et al.*, 2009).

General Circulation Models (GCM) describe potential future conditions at coarse resolution and provide the bases for projections of, e.g., habitat distribution models of species in ecology (Wiens *et al.*, 2009). Here, one has to distinguish between two types of downscaling strategies to predict different resolution scales, namely statistical and dynamical downscaling. The first is based on empirical relationships between measured climate data at local to regional scale and climate simulation output of GCMs. The latter uses Regional Climate Models (RCM) operating at much finer scales than GCMs which are driven by output from GCMs within a limited regional to continental frame (Spak *et al.*, 2007; Wiens *et al.*, 2009; Strauss *et al.*, 2012).

However, here generic climate change scenarios were applied, rather than using RCMs for the investigation of the sensitivity of tree species to changing climate conditions. In order to study tree species responses to a variety of changes in temperature and precipitation, generic changes to present climate were studied. To bracket the range of studied changes, the wide range of predicted changes from literature were consulted (cf. section 1.1). Since temperature and precipitation are main drivers of plant growth and survival and are likely to change considerably under climate change, the focus was set on a variety of combinations of these two factors within this analysis (Walther *et al.*, 2002; McCain and Colwell, 2011; Leitgeb and Reiter, 2009).

1.3 Tree species sensitivity to climate change

1.3.1 Climate change in forests

According to many studies, the climatic drivers of climate change in the 21st century have the tendency to increase the frequency of disturbance regimes, such as droughts, fires, storms, floods or late frost events in spring, coupled with subsequent large insect infestations and fungal decay decreasing forest productivity (Lexer *et al.*, 2002; Seidl *et al.*, 2011; Formayer and Frischauf, 2004; Lindner *et al.*, 2010). Dry periods will increase and cause more droughts as well as heavy precipitation that will lead to a higher risk of floods (MPI-M, 2006). On the other hand, prolonged vegetation periods with higher temperatures and higher CO₂ concentrations lead to higher photosynthetic rates. These changes result in a positive effect of climate change: A higher photosynthetic activity can contribute to increasing forest productivity and higher temperatures can expand forests to higher elevations (Kapeller *et al.*, 2012; Schüller *et al.*, 2012; Roberts, 2008). The trend of climate change in Europe differs from global trends with increases of forest area and decreasing demand for agricultural land (Schröter *et al.*, 2005). This allows land management changes that could decrease the vulnerability of ecosystems to climate change (Schröter *et al.*, 2005). According to Russ (2004), the positive effects of forest growth in Austria are occurring in up to 90% of rural private forest ownerships at higher elevations, where unmanaged and managed forests succession takes over former patches of pastures. Yet, Schüller *et al.* (2012) states that these prolonged vegetation periods, together with higher temperatures and increasing water deficits, can also increase drought events, with a higher risk of species loss by insect infestations. A higher water deficit might result from higher mean annual temperatures, even if the annual precipitation sum remains constant. The underlying processes are higher transpiration rates resulting in a higher demand for water (Schüller *et al.*, 2012). The main driver for highly sensitive reaction of tree species is considered to be in the hydrological cycle of forests and therefore the highest impact is to be deduced by water deficiencies (Roberts, 2008).

1.3.2 Species sensitivity in mountainous forests

The dimension of species sensitivity towards climate change will differ within geographic regions and locations, because of the high heterogeneity in geomorphology, micro-climate and soil formation (Lindner *et al.*, 2010). Looking at the spatial variations of climate change sensitivity, the latter authors mention that with increasing temperatures, there will be a positive impact on forest growth in northern and western Europe and a negative impact in the more water-limited eastern and southern parts of Europe. Here, in addition to the Mediterranean, mountain regions seem to be most

vulnerable among all European regions (Schröter *et al.*, 2005). Analogies can be drawn with Austria's location in Europe, as it is the transition zone between the generally well water-supplied temperate maritime climatic zones of northern and western Europe, and the drier temperate continental climatic zone of eastern and southeastern Europe. As Austria is very heterogeneous in geomorphology, climate change variation in forests strongly differs at a local scale from the lowlands and foothills up to the high Alps (cf. Lindner *et al.*, 2010).

Considering the sensitivity of European mountain forests, their structure and composition will eventually change, as will species competition due to increasing climate change (Lexer *et al.*, 2002; Skvarenina *et al.*, 2004; Roberts, 2008). Migration rates of European tree species differ due to different climatic conditions geographically, and depend on species traits, species competition, habitat- and climatic conditions (Meier *et al.*, 2011). The tree line ecotone of alpine forests responds with an upward shift of the tree-line to higher elevations by greater variability in air temperature (Chen *et al.*, 2011; Camarero and Gutierrez, 2004; Bodin, 2011; Bolli *et al.*, 2007), whereas Austria's foothills and lowlands become more unsuitable for some species that will migrate to higher elevations with more suitable conditions for regeneration (Roberts, 2008). Additionally, bark-beetle infestations will expand with rising temperatures geographically over larger areas of coniferous forests in Europe (Seidl *et al.*, 2009). Seidl *et al.* (2011) evaluated climate sensitivity of trees in the Eastern Alps under the current forest management strategy. The findings of the ecosystem modeling showed a high vulnerability towards climate change in the second half of the 21st century, where forest productivity and forest health decreased drastically at water-limited sites on calcareous bedrock (Seidl *et al.*, 2011). However, future events might affect each tree species differently within a forest stand, and ultimately change the current species composition.

1.3.3 Species genetics and adaptation to climate change

“The different components of the current climate change affect differently each hierarchical level of the ecosystem, leading to cascading effects and complex feedbacks when responses are analyzed in processes ranging from the molecule to the whole ecosystem” (Valladares, 2008).

Valladares (2008) states that trees experience highly heterogeneous environmental conditions in their lifetime, thus having a high level of genetic diversity, but in the short term have a low evolutionary rate. In other words, trees can be persistent to extreme abiotic and biotic conditions because they are diverse, having a high genetic variance and develop adaptation strategies (Geburek, 2006) - but their intrinsic traits can adapt only to some extent to the rapid speed of climate change.

Still, Petit and Hampe (2006) add that trees are also highly fertile throughout their whole lifetime, allowing the species to respond to high selection intensity and therefore to adapt to fast environmental changes. Genetically, trees are well-adapted to climatic variation, but the tremendous rate of climate change has the potential to exceed, over a short period of time, their ecophysiological thresholds on forest sites, where trees are less adapted or no longer suitable. Lindner *et al.* (2010) says, "Adaptive capacity consists of the inherent adaptive capacity of trees and forest ecosystems and of socio-economic factors determining the capability to implement planned adaptation". A promising adaptation response would rather depend on natural selection and natural species distribution, which allows tree populations to endure changing environmental conditions (Lindner *et al.*, 2010). This is a fundamental consideration for the adaptation of trees to climate change that is emphasized in the next section. Trees have long life cycles with high potential for reproduction, but adaptation may not be realized with the pace of climate change.

1.3.4 Current forest distribution and potential natural forest vegetation

Forests play a very important ecological and economical role in Austria. Besides their productive function supplying the timber and paper industry, they have an important protective function that secures mountains from soil erosion and protects human infrastructure from gravitational natural hazards such as avalanches. The vast changes to our global environment and the uncertainties of climate change have shifted a greater emphasis on tree species choice as a major element of adaptive management strategies. For example, Norway spruce was cultivated excessively on sites in Europe that were outside its natural (Spiecker, 2000). As the climate change expected for the 21st century is likely to increase high water deficits, this species might no longer be able to cope with such site conditions at its current forest distribution (Lexer *et al.*, 2000; Tatarinov *et al.*, 2000). This is not only the case for Norway spruce - many other coniferous and deciduous tree species are affected by such drastically changing climate conditions.

Lexer *et al.* (2001) conducted a study with the forest model PICUS v1.2 to assess the sensitivity of Austrian forests at their current forest distribution for different climate change scenarios. At low elevation sites where management has been promoting coniferous species outside its natural range, the orientation on the PNV was found to be most stable to changing climatic conditions than the current forest composition. In the grid of sample plots of the Austrian Forest Inventory (AFI) in Figure 1, similarities of the current forests to simulated PNV were compared under present climate conditions (shown as 'Baseline'-scenario) for the evaluation of the model used in the study of Lexer *et al.* (2001). The similarities between current forests and simulated PNV were especially high in the

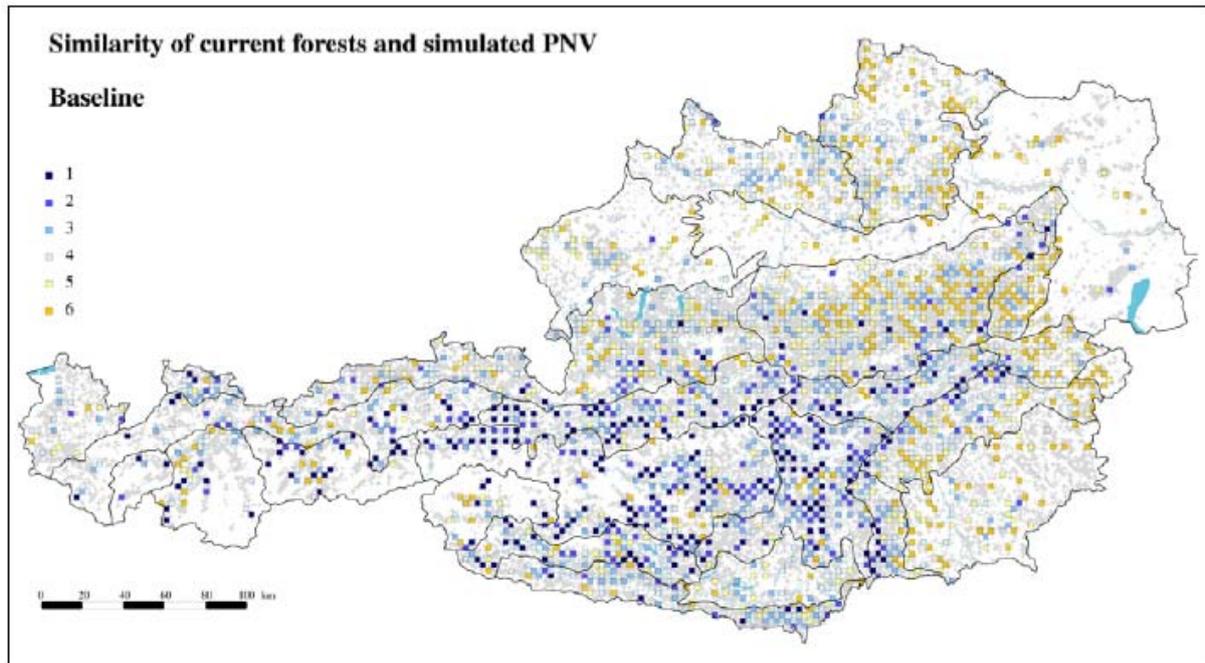


Figure 1: The species composition of current forest equals (Class 1) or differs strongly (Class 6) with the simulated PNV and is quantified by the Austrian Forest Inventory grid of 2589 inventory points with trees > 5 cm DBH (reference source: Lexer *et al.*, 2001).

elevation areas, whereas low similarity was found for the north, east and southeast of Austria (cf. Figure 1, Lexer *et al.*, 2001). However, this study suggested that there where the orientation on the potential natural forest vegetation (PNV) is considered, those forest stands would be more stable against natural disturbances and better adapted to a changing climate. Although the orientation to the PNV does not have to be necessarily the better choice when making silvicultural decisions, it still seems to be a lagging point of most forest ownerships in practice and should be therefore more in focus (Lexer *et al.*, 2001). In particular, Norway spruce has been promoted outside its natural range in the submontane and lower montane elevation belts since the 19th century (Lexer *et al.*, 2001; Kilian *et al.*, 1994). Hence, one can assume that Norway spruce might be most threatened to climate change in the future.

Beyond the facts of climate change mentioned previously, with a change in forest micro climates, there is also the uncertainty of the degree of changes in environmental conditions that control the suitability of a single species. The difference between species- or ecosystem sensitivity can be explained as follows: If a species is under a changing climate been predicted to be absent from a site where it currently occurs, the species is set at risk to species loss at this site (Nitschke and Innes, 2008). On the other hand, an ecosystem may not be at risk by the absence of a single species and therefore, would rather represent a risk to diversity loss (Nitschke and Innes, 2008). Here raises the

question whether a tree species at their current forest distribution can tolerate changing climatic conditions.

In the short term, all effects of climate change will have a challenging impact on forest ecosystems and their slowly adapting long-living tree organisms. Forest managers will have to seek advanced forest adaptation strategies to limit damaging costs and loss of forest revenues due to future extreme events. Many forest managers want to know where tree species at their current distribution are likely to remain, expand or become vulnerable with changing climate conditions over the rest of the century (Coops and Waring, 2011). The determination of how sensitive the current tree species distribution in Austria reacts to future climate change variability has been analyzed during this study.

2 Objectives and hypotheses

One of the biggest challenges in the context of the effects of climate change on forestry is the assessment of the sensitivity of tree species to such climatic changes. This study focuses on the ten most relevant commercial tree species of Austria and analyzes their climate sensitivity with an ecophysiological model of tree species suitability. The aim was to determine the sensitivity of species at their current forest distribution to a variety of changes in temperature and precipitation for the entire Austrian forest area. The specific objectives were

- (1) to investigate the climate sensitivity of the ten main species in Austria at their current distribution, and determine the relative roles of temperature and precipitation in overall climate sensitivity,
- (2) to identify the species most at risk at their current locations,
- (3) to indicate and quantify spatial hotspots of the risk of species loss as a prerequisite for silvicultural decision making, and
- (4) to quantify how species diversity is contributing to the mitigation of climate change sensitivity.

The hypotheses with questions regarding these objectives above:

1. Given their current distribution, which tree species is the most sensitive to climate change and has the highest risk of species loss?

Based on the previous work (Lexer *et al.*, 2001; Spiecker, 2000; Kahle *et al.*, 2005; Levanič *et al.*, 2009; Kapeller *et al.*, 2012; Schöler *et al.*, 2013; Leitgeb *et al.*, 2013), it is hypothesized that Norway spruce reacts most sensitive to climate change because it has been cultivated excessively outside its natural area. Furthermore, Norway spruce is highly sensitive to drought and could also get under pressure on sites where it occurs naturally. Thus, Norway spruce is expected to have the highest risk of species loss.

2. Are Austria's dominant tree species more sensitive to precipitation or temperature?

The hypothesis with regards to this research question is that tree species are more sensitive to changes in precipitation than to changes in temperature (Choat *et al.*, 2012). Water deficit has a bigger impact on tree species survival than the continuously global increasing of temperature (Allen *et al.*, 2010).

3. Where in Austria's elevation zones and eco-regions is the current forest composition particularly at risk from substantial climate-mediated species loss?

3.1. Due to less precipitation and higher temperatures in the low-lying areas, those areas are expected to be less buffered to climate changes than higher elevation regions.

3.2. Due to less precipitation and higher temperatures in these areas, changes in the ecoregions of the northern and eastern plain as well as in the northern and eastern foothills of the Alps are expected to be most pronounced.

4. To what extent is species diversity reducing the risk to substantial species loss of one or several species at a forest stand?

The hypothesis is that if species diversity and evenness are high, the risk for substantial species loss is smaller as with one or only a few species dominating an inventory point (Zhang *et al.*, 2012).

3 Material and Methods

3.1 Site- and climate data

Site data

Leitgeb and Reiter (2009) state that in addition to climatic conditions determined largely by precipitation and temperature, the physical and chemical soil conditions also play a critical role for tree species suitability. In this analysis of limiting factors of tree species in Austria, soil data of the inventory plots of the national Austrian Forest Inventory (AFI) were used. The AFI is the most substantial monitoring system of Austria's forests. It surveys the condition and changes of forest ecosystems in Austria on a statistical basis since 1961 (Schadauer, 2004). All inventory plots of the AFI consist of a systematic sample point grid of about 10.000 inventory points. The grid consists of 3.9 x 3.9 km² permanent installed sample plots that are clustered to square tracts of four sample plots at a square size of 200 x 200 m² (Lexer, 2001, Lexer, 2000). Based on this grid of the AFI, available soil parameters for 6.500 points were determined from a subsample of plots that were analyzed in depth in the Austrian Forest Soil Survey (Seidl *et al.*, 2009). The final set thus includes not only different soil groups but also pH values and C/N ratios.

Climate data

The variability of macro climatic conditions is regionally responsible for changes in species distribution and composition. Häckel (1993) describes the climate as the sum of all weather conditions of a location. The regional climate determines the distribution of plant communities, whereas local climate, e.g. at valleys or slopes, and soil conditions simultaneously influence the local variation of species (Schwarz, 2002).

For the tree species sensitivity assessment, a baseline of current climate was required to serve in the evaluation of the TSM approach but also as a contrast to potential future climate scenarios. This climate data was taken from a network of weather stations from the central institute of meteorology and geodynamic in Vienna (ZAMG) and from the hydrographic service (Lexer, 2001). All climate data were interpolated from a comprehensive network of over 600 weather stations from eight climate sub regions regarding the influence of elevation, topography (aspect, slope, horizon) and maritime- or continental climate in Austria (Lexer *et al.*, 2000, Schwarz, 2002). This allows the estimation of climate conditions for the approximately 10.000 AFI sample plots (Lexer *et al.*, 2000). The climate data for all the necessary climate variables for the analyses were taken from the climate data records over a 30 year period from 1961-1990. These variables include information of mean annual GDD,

monthly minimum winter temperature, mean annual temperatures of July and August, mean annual precipitation, mean annual SMI as well as the growing season SMI, i.e. May to September, and the VPD of July and August.

3.2 Conceptual model approach

3.2.1 Niche concept and model approach

This study about the assessment of species sensitivity due to risk of species loss under climate change, is based on an ecological modeling approach of the fundamental niche or bioclimatic envelope of a species, considering physiologically limiting factors or parameterization from empirical data (Coops and Waring, 2011; Wiens *et al.*, 2009). These models have become a central point for the understanding of climate change impacts on species and their habitats (Wiens *et al.*, 2009). The term niche has existed for almost 100 years, and was first used in an ecological context in 1917 by Grinnell (Schmitt, 1987). He defined the ecological niche as a subdivision of a habitat that allows individuals of a species to survive and grow under given environmental conditions within this subdivision (Wiens *et al.*, 2009). Hutchinson further developed niche-theory in his seminal work (Schmitt, 1987). He, like Grinnell, defined the fundamental ecological niche as the environmental conditions in which a species could survive and reproduce (Hutchinson, 1957). But as an essential challenge to the original Ginnellian niche concept, he first mentioned the realized niche as a subset of the fundamental niche which is driven by biotic interactions and species competition (Wiens *et al.*, 2009; Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Silvertown, 2004). Through a competitor species, another species could be excluded from a part of its fundamental niche, making the remaining subset the realized niche (Guisan and Thuiller, 2005). Here, one has to distinguish between abiotic limitations on species distribution that defines the fundamental niche and biotic limitations on species distribution that defines the realized niche (Hutchinson, 1957). In general, ecological models use these two approaches: While the vast majority of niche models only include abiotic drivers and thus attempt to address the potential fitness of plants by the fundamental niche (Austin, 1992; Zimmermann and Kienast, 1999), models of vegetation dynamics also consider biotic processes such as competition in their calculations (Soberón and Peterson, 2005; Lischke *et al.*, 2006; Nitschke and Innes, 2008).

Here, the focus is on the former approach, excluding any biotic interactions, such as disturbances and interspecific competition of plant communities. The thresholds and environmental limitations for species occurrence can be built into such niche models in at least two different ways: Predictions of the future species behavior can be based on observation of the present tree species distribution and

the respective environment at its occurrence for calibration of the fundamental niche for a species (Zimmermann and Kienast, 1999). These models are described in more detail in the following chapter. Here, a more process-oriented approach is used, taking a species' ecophysiological thresholds into account in order to define its fundamental niche. This approach is described further in section 3.3 below.

3.2.2 Species Distribution Models (SDM) and climate change

Humboldt already recognized and investigated the role of climate for single species and their natural distribution (Lexer, 2001; Humboldt, 1807). Plants are continuously exposed to a wide range of limiting factors in their natural environment and climate change may alter this complex combination (Valladares, 2008). To predict future changes in ecosystems is challenging, as nature has a high degree of heterogeneity and complexity (Guisan and Zimmermann, 2000). One approach is to investigate species distribution and its potential changes by a correlative approach. The key assumption of such SDMs is that the occurrence of a species is given under suitable climatic conditions, and can change if climate changes. SDMs are thus a statistical fit of observed species occurrence with currently observed soil- and climatic variables as predictors. Guisan and Thuiller (2005) state that SDMs and their outputs of habitat suitability maps have been in science a successful approach for the investigation of species distribution. These models explain how relationships between species and their environment are driven by three types of influence on species distribution: limiting growth factors that are defined as factors driving the species ecophysiology, secondly resources which are compounds assimilated by organisms and thirdly disturbances that are affecting environmental systems (Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000; Huston, 2002). These relationships between species and their environments can cause different spatial patterns in species distribution (Guisan and Thuiller, 2005).

Guisan and Zimmermann (2000) state that in addition to the dynamical SDMs, modeling of single species rather than communities are more likely to be closer to a realistic prediction. The reason thereto can be explained by the physiological limitations and characteristics of each species, where species do not move as an entity but rather respond individually to changing climatic conditions (Guisan and Zimmermann, 2000). Thus, the climate sensitivity at the level of individual species is analyzed in this study. There has been a study of species versus community approach by Zimmermann and Kienast (1999) where they focus on the importance of the individual behavior of species as an important driver of shifting species composition. Individual life history traits, such as a species specific physiology, adaptation capacity, competitive ability or migration rate, are individual

species characteristics that have consequences on the dynamic behavior of single species (Zimmermann and Kienast, 1999). However, both approaches can develop these powerful and complex statistical models (SDMs) and whether one is modeling a species or a community approach depends on the aim of the study (Zimmermann and Kienast, 1999).

3.3 Tree Species Suitability Model (TSM) and parameterization

Past observations that are used to parameterize statistical SDMs do not represent all potential future environmental conditions. Another approach to model species sensitivity to a changing environment is to use thresholds determined in physiological studies (Liu *et al.*, 2013; Nemani *et al.*, 2000). Nitschke and Innes (2008) say: “The static nature of statistical models can be overcome by using mechanistic models that are driven by empirically derived parameters”. The model used for this study describes the relationship between the environment and a species’ ecophysiological thresholds. Whether a species is more or less suitable in its current distribution under a changed climate depends on the specific environmental conditions prevailing at a site as well as on the species’ traits and thresholds. This is determined with the tree species suitability model (TSM), which is described in more detail below.

The concept of the TSM is based on a mechanistic model, where generality and realism are prioritized over accuracy of prediction (Guisan and Zimmermann, 2000). TSM is a model that is oriented towards physiological processes and aims to represent its structure and parameters, but does not explain such processes. This mechanistic model approach was developed by Lexer and Seidl (in prep.) based on previous work by Steiner and Lexer (1998), Steiner (1998) and Pichler (2000). It is based on the assumption that a tree species is not suitable for a site if one or several physiological thresholds are exceeded. Here, suitability is defined by prior knowledge and understanding of the physiological responses of tree species to climate and soil factors (Lexer and Seidl, in prep.). This assumes that increasing environmental stress above a certain threshold excludes a species from growing successfully at a given site (Larcher, 2003). Therefore, the effect of individual limitations is evaluated for each factor by means of response functions on a unit scale from 0 to 1, where at 1 there is no limitation and at 0 there is full limitation due to a factor. These response functions are subsequently combined to a single value of stress at this unit scale and whose interconnections will be explained later below, after the definition of the limiting factors.

Climatic- and soil factors are grouped according to three main limiting factors of tree species, namely energy, water and soil (Figure 2). These are the main site factors determining growth and survival of

trees (Kramer, 1988). Miller (2006) states that the response of plants to a combination of several abiotic stresses is unique and cannot be estimated from responses of plants to each of the several stresses applied individually. The interactions between environmental limitations are thus an important part in TSM. The model considers limitation, intensification and compensation between limiting factors. The limitation refers to Liebig's law of the minimum, where the single most limiting element determines the growth and survival of organisms at any given time (Danger *et al.*, 2008). This is a common combination of limiting factors in ecosystems, however, also intensification and compensation can occur. Two or more factors can, for instance, intensify in their limiting role on plants, e.g. the effect of atmospheric drought, increasing the water loss from the stomata can be intensified by soil drought, i.e. when water supply from the soil is limited. Hence, the limiting effect of these two factors is intensifying, and affected by factors such as precipitation, evaporation, temperature and radiation levels (Schwarz, 2002). Third is compensation, where the abundant availability of one resource compensates a limiting factor. Low nutrient availability that might limit a species' growth could, for instance, be compensated by sound rooting access to the soil, granting that trees can access the available nutrients. All these three types of interactions are considered in TSM in the specific context of individual factors (Figure 2).

The selection process of relevant abiotic parameters has to be performed with care, as this is the most sensitive part of the model development (Zimmermann and Kienast, 1999). In the following the X limiting parameters of climatic- and soil conditions that are considered in TSM (Lexer and Seidl, in prep.) are described. For this work, TSM parameters for the ten most common tree species were amended and compiled relative to their current standing volume at the forest stands in Austria (Hauk, 2011). Silver birch (*Betula pendula*) was substituted for grey alder (*Alnus incana*), since the latter mostly occurs in riparian areas and is of limited relevance for upland forest management, but also since the specific water cycle processes at these sites are not well represented in TSM. Hence, following tree species were selected for this work: Norway spruce (*Picea abies*), silver fir (*Abies alba*), European larch (*Larix decidua*), Scots Pine (*Pinus sylvestris*), European beech (*Fagus sylvatica*), pendunculate oak (*Quercus robur*), mountain maple (*Acer pseudoplatanus*), European ash (*Fraxinus excelsior*), hornbeam (*Carpinus betulus*) and silver birch (*Betula pendula*).

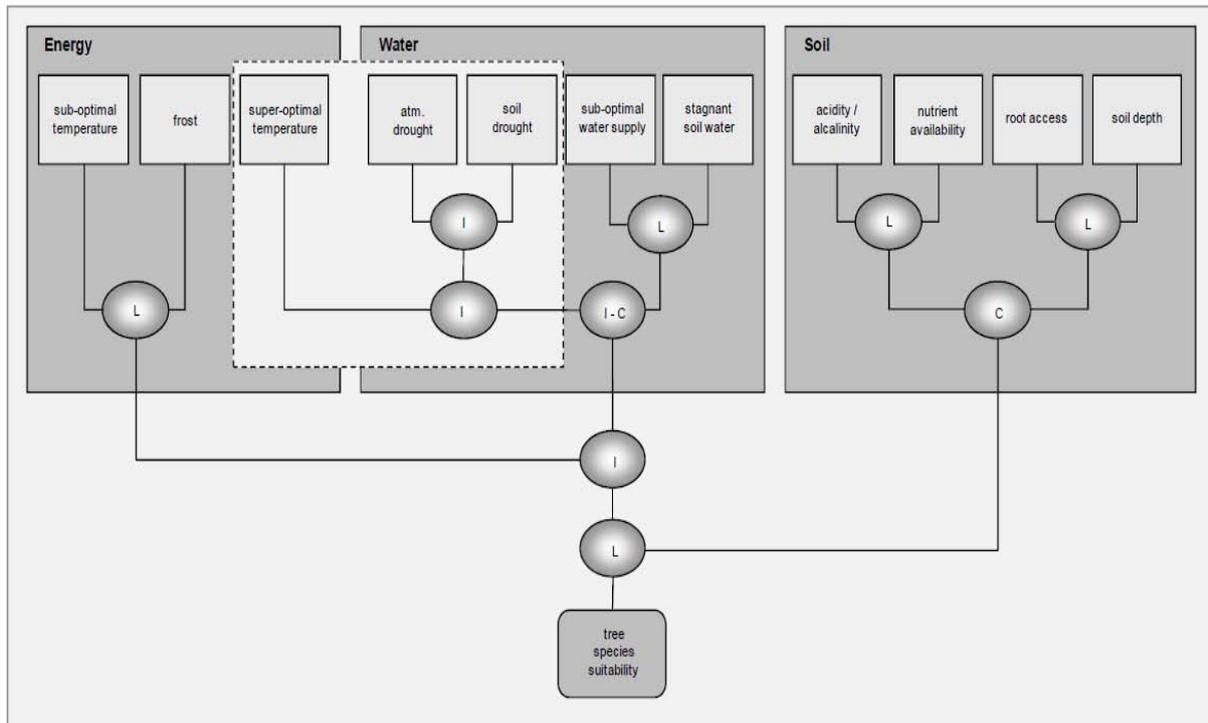


Figure 2: Flow-chart of the Tree species Suitability Model (TSM). Square boxes = drivers, ellipses = interactions: L: Liebig's law, I: intensification, C: compensation (Lexer and Seidl, in prep.).

3.3.1 Energy limitations

Sub-optimal temperature

Sufficient amount of utilizable solar energy is a prerequisite for positive net primary production. The temperature regime of a site is key determinant of whether trees can utilize solar energy through photosynthesis processes (Steiner, 1998) and thus has a high significance for forest growth and survival. Growing degree days (GDD) which are the sum of the temperatures above a threshold temperature of 5,5°C, can be used as a composite indicator to quantify both the length of the vegetation period and the temperature limitations (or lack thereof) during the vegetation period (Steiner, 1998; Lexer and Hönninger, 2001, Lexer, 2001; Lexer and Seidl, in prep.). The response of tree species to this temperature limitation was modeled as the left side of a quadratic function by Lexer and Seidl (in prep.) where the response increases when the minimum threshold, GDD_{min} , is exceeded and moving closer to the optimum GDD_{opt} (Equation 1). The parameter values of these two indicators in this study rely on Pichler (2000), Lexer (2001) and Lexer and Seidl (in prep.).

Equation 1: GDD

$$f_E = \begin{cases} 0 & GDD < GDD_{\min} \\ \frac{4 \cdot (GDD_{\min} + 2 \cdot (GDD_{opt} - GDD_{\min}) - GDD) \cdot (GDD - GDD_{\min})}{(2 \cdot GDD_{opt} - 2 \cdot GDD_{\min})^2} & GDD_{\min} < GDD < GDD_{opt} \\ 1 & GDD > GDD_{\max} \end{cases}$$

Sub-optimal temperature

Plants cannot survive temperatures of higher than 46°C to 56°C due to unshaded soil surfaces of semiarid regions (Körner, 2006). Values for the maximum temperature of a positive net photosynthesis in this study were set to exceed 40°C for coniferous tree species, following a study of Bergh *et al.* (2003). Trees do not necessarily directly die at such temperatures, but they stop their gross photosynthesis activity at these levels, shut their stomatal conductance or drop their leaves to mitigate water deficits and prevent tree mortality. If such conditions occur repeatedly, they result in negative net temperature gain and ultimately mortality, posing a major limit for the fundamental niche of a species. The parameter set of optimum and maximum temperatures used in this work relies on parameters by Bergh *et al.* (2003), Bergh *et al.* (1998), Jarvis (1999) and Lyr (1996).

Frost

Frost is a major limitation to trees particularly in the seedling and sapling stage. Fall temperatures below this threshold could be causing subsequent cell damages to species (Larcher, 1995). The species sensitivity to low temperature extremes vary to a higher degree than to high temperature extremes and are therefore more significant and difficult to estimate (Lindner *et al.*, 2010). Damage by early or late season frost is expected to increase with earlier times of bud breaks and is assumed to occur at temperatures below 0°C; but whether this leads to mortality depends on the variability of the minimum temperature thresholds of a plant which determines its frost-hardiness (Larcher, 2005; Christensen *et al.*, 2007; Nitschke and Innes, 2008). Frost limitations (Equation 2) are defined as the minimum of the monthly temperatures of the months December to February (Lexer and Seidl, in prep.; Steiner, 1998; Lexer, 2001). The threshold values were defined according to Steiner (1998). For

species for which winter frost hardiness was assumed to be high and the factor generally not limiting the parameter values were set to infinity (cf. Steiner, 1998).

Equation 2: Frost

$$f_F = \begin{cases} 0 & f_F < 0 \\ \left(1 - \frac{F}{F_{\max}}\right)^{0.05} & 0 < f_F < 1 \\ 1 & f_F > 1 \end{cases}$$

3.3.2 Water limitations

Atmospheric drought

The vapor pressure deficit (VPD) is an indicator of water limitations due to atmospheric drought and limits leaf gas exchange by closing the stomata to avoid further transpiration which is modeled as quadratic function in Equation 3 (Pietsch *et al.*, 2005; Lexer and Seidl, in prep.). In this function, TSM uses the optimal vapor pressure deficit, i.e. where no water limitations on the stomatal conductance occur, and the maximum value of vapor pressure deficit that triggers the full closure of the stomata as parameters. VPD parameter values were based on Pietsch *et al.* (2005), Hölscher *et al.* (2005) and Jochheim *et al.* (2009).

Equation 3: Vapor Pressure Deficit (D)

$$f_D = \begin{cases} 0 & D > D_{\max} \\ 1 - \left(\frac{D - D_{opt}}{D_{\max} - D_{opt}}\right)^2 & D_{opt} < D < D_{\max} \\ 1 & D < D_{opt} \end{cases}$$

Soil drought and sub-optimal water supply

In addition to temperature, water is another indispensable factor for tree growth and survival. Water budget declines can be expected with continuous increases of annual temperatures by higher evapotranspiration rates and reduced precipitation over the total landscape area of Austria.

Precipitation drains away quite rapidly, thus snow serves as an important water source until the vegetation period begins (Schüler *et al.*, 2012). Snow levels can play a key role for inducing early drought periods at a local scale in the future. A decrease of snow levels may also be one of the long term consequences of decline in water resources for trees during the growing season at the foothills and the Alps. Change in soil water capacity is as important as change in precipitation, as both could be an intensifying factor to water stress of tree species. Hence, soil water limitations can occur on two levels, due to soil drought during water stress in the summer months and the water supply that is generally available for the whole season (Lexer and Seidl, in prep.).

Drought tolerance of a species can be determined by the soil moisture requirements of each species; the higher the species demands, the higher its sensitivity to water deficit (Steiner, 1998). In TSM, soil water availability can either be compensated by low atmospheric drought or intensified by high values of atmospheric drought (Steiner, 1998). The soil moisture index (SMI), derived according to Lexer and Hönninger (2001), is an indicator relating the amount of water supply to potential water demand during the growing season. In TSM, SMIs are considered both for the driest month of the summer as well as for the entire vegetation period (Lexer and Seidl, in prep.). Values for optimum of SMI (no limitation) and maximum of SMI (no plant activity due to complete water limitation, Table 1a), determine the response of a species to the soil moisture deficit. Responses range between 1, optimal water availability for species growth ($<SMI_{opt}$), and 0 for full soil water limitations ($>SMI_{max}$) (Lexer and Hönninger, 2001; Lexer and Seidl, in prep.; Steiner, 1998). These SMI values are species specific evaluated in a response function in TSM (Equation 4, Lexer and Seidl, in prep.).

Equation 4: SMI

$$f_w = \begin{cases} 0 & SMI > SMI_{max} \\ 1 - \left(\frac{SMI - SMI_{opt}}{SMI_{max} - SMI_{opt}} \right)^2 & SMI_{opt} < SMI < SMI_{max} \\ 1 & SMI < SMI_{opt} \end{cases}$$

Stagnant soil water

Due to changes in soil moisture interactions or water stagnation in gleyic soils, insufficient soil aeration can affect the development of flat root plats where species cannot exploit its growth potentials at a site (Steiner, 1998; Lexer and Seidl, in prep.). Hence, primary roots may not develop naturally to their full extension and tree growth may therefore be inhibited and stability impaired.

Further, primary roots may also struggle to reach for a deeper nutrition source as the gleization blocks root access.

The species suitability responses to gleyic soils are categorized in Table 1a for wet gleys as $SMI \leq 0.2$ or for dry gleys as $SMI > 0.2$ (Lexer and Seidl, in prep.). These two parameters are based on Steiner's (1998) suitability values of a range between 0 and 1 which either represent the absence of a tree species at 0 or are defined as the optimum of occurrence of a tree species at 1.

3.3.3 Soil limitations

Acidity/alkalinity

The pH-value represents the soil acidity (Figure 2) and allows conclusions about the general nutrient availability of a forest site (Steiner, 1998). The soil acidity has influence on physical, chemical and biotical soil properties and thus, direct and indirect influence on tree growth and regeneration (Schachtschabel *et al.*, 1992). The thresholds of tolerable minimum- and maximum pH in which a species can grow (Table 1b) are identified in TSM for every species (Steiner, 1998; Lexer and Seidl, in prep.). Within this range an optimum range for no limitations from soil pH is defined, usually in the range of moderately acidic soils (Lexer and Seidl, in prep.). A linear ramp function is used to estimate the effects of acidity or alkalinity on nutrient uptake in TSM (Equation 5, Lexer and Seidl, in prep.).

Equation 5: linear ramp function for pH value

$$f_A = \begin{cases} 0 & pH < pH_{\min} \\ \frac{pH - pH_{\min}}{pH_{opt1} - pH_{\min}} & pH_{\min} < pH < pH_{opt1} \\ 1 & pH_{opt1} < pH < pH_{opt2} \\ 1 - \frac{pH - pH_{opt2}}{pH_{\max} - pH_{opt2}} & pH_{opt2} < pH < pH_{\max} \\ 0 & pH > pH_{\max} \end{cases}$$

Nutrient availability

The Carbon-to-Nitrogen (C/N) ratio in the soil is a good indicator for the nutrient availability of a site: Lower C/N ratios indicate better nitrogen supply and decreasing nutrient limitations to forest growth (Lexer and Hönninger, 2001, Steiner, 1998). Hence, the C/N ratio is used to represent nutrient availability in the TSM. The different C/N ratios are arranged in five classes within the first centimeters of the upper soil layer (Table 1b) and demonstrate the species suitability for each class by indicating a suitability value as was explained in the parameter 'stagnant soil water' before (0 = complete limitation; 1 = no limitation)(Steiner, 1998). C/N values below 10 indicate optimal growing conditions for most species, whereas values exceeding 20 for some species indicate increasing nutrient limitations.

Root access and soil depth

The dimension of rooting access depends on the physical conditions of different soil groups, whereas the three levels of soil depth, categorized by Pichler (2000)(cf. Table 1b), depend in natural condition on the species specific response of their root systems to growth (Polomski and Kuhn, 1998; Steiner, 1998, Lexer and Seidl, in prep.). The soil groups for the rooting access that is described in Table 1b are based on the Austrian Forest Soil. Each soil group is associated with mean values as determined by the Austrian Forest Soil Survey (Lexer, 2001). Both, rooting access and soil depth, are indicators for a sound tree growth and can be a limiting factor to growth and survival where their suitability value ranges between 0 and 1, as described previously. All assigned suitability values of the parameters were either taken from Pichler (2000), Polomski and Kuhn (1998) or were adjusted in relative comparisons between species, based on ecological expectations.

3.3.4 Interconnection of limiting parameters

All individual parameters were further interconnected within their three regimes of energy, water and soil, where any limiting factor of these three regimes can limit the total aggregated species suitability. For almost all parameters in the set, the interconnections of the response functions are based on the multiplicative connection. Steiner (1998) already interconnected the parameters with an inductive approach by a mathematical operator to define the suitability, which was now further complemented with additional values in R:

(1) The minimum of GDD and winter frost is derived from Liebig's law of the minimum and can neither compensate nor intensify each other (energy regime).

(2) SMI can compensate the VPD if there is enough water in the soil. Otherwise, these two factors can intensify each other drastically if VPD is high due to atmospheric drought and SMI is high due to soil drought (water regime).

(3) The SMI can influence the effect of gleization as a limiting factor during the vegetation period in context to the general water supply. This may limit the occurrence of a sensitive reacting species, whereas a compensating effect can be excluded (water regime).

(4) C/N ration and pH-value limit each other (again Liebig's law), where either a low C/N ratio can limit nutrient availability or an acidic pH of a minimum value can limit the nutrient uptake from the soil (soil regime).

(5) Same counts for rooting access and soil depth. Unsuitable soil groups for low rooting access and low soil depth can limit each other (soil regime).

(6) Due to high temperatures in (1), there can be compensation by enough water supply, as well as an intensification due to drought or high SMI between energy regime (1 - temperature) and water regime (2).

(7) Also, there can be compensation between the soil regimes (4) and (5) (between available nutrients and soil access).

(8) An intensification of frost (1) and water deficit (2) does usually not happen in Austria as it is influenced more by maritime climate as that continental climate could have such a strong influence.

As mentioned before, the values for these limiting parameters in Table 1a and 1b for the ten most abundant tree species of Austria were compiled. For this parameter set below, empirical data was collected through literature research. In cases where no such data was available, descriptive data from phenomenological studies and general ecological understanding was used. For species with no existing data, parameter values were determined relative to well-defined species based on ecological knowledge.

Table 1a: Energy and water parameters (Lexer and Seidl, in prep.; Steiner, 1998; Lexer, 2001; Jochheim *et al.*, 2009; Lyr, 1996; Hölscher *et al.*, 2005).

Energy Parameter	Unit	P. abies	A. alba	L. decidua	P. sylvestris	F. sylvatica	Q. robur	A. pseudopl.	F. excelsior	C. betulus	B. pendula
GDD (min.)	Degree Day Sum	250	400	180	550	580	1050	490	840	880	390
GDD (opt.)	Degree Day Sum	1115	1200	1200	1584	1540	1900	1443	1443	1500	1443
Frost (max.)	°C	-Inf	-6.3	-Inf	-Inf	-5.8	-8	- Inf	-7	-9	-Inf
Temperature (opt.)	°C	16	18	17	20	24	24	15	21	25	18
Temperature (max.)	°C	43	43	43	43	35	39	31	31	35	35

Water Parameter	Unit	P. abies	A. alba	L. decidua	P. sylvestris	F. sylvatica	Q. robur	A. pseudopl.	F. excelsior	C. betulus	B. pendula
Vapor Pressure Deficit (opt.)	kPa	0.05	0.025	0.08	0.05	0.5	0.2	0.8	0.8	0.2	0.65
Vapor Pressure Deficit (max.)	kPa	1.5	1.4	3.2	2.5	2.7	2.55	2.8	2.2	2.55	3.3
Soil Moisture Index (opt.)	Dimensionless [0,1]	0.1	0.15	0.1	0.2	0.15	0.1	0.1	0.15	0.15	0.15
Soil Moisture Index (max.)	Dimensionless [0,1]	0.37	0.42	0.45	0.67	0.48	0.67	0.43	0.4	0.65	0.6
Gleysols wet (SMI ≤ 0.2)	Dimensionless [0,1]	0.5	1	0.6	0.7	0.5	0.85	0.6	0.5	0.7	0.5
Gleysols dry (SMI > 0.2)	Dimensionless [0,1]	0.7	1	0.8	0.9	0.7	1	0.8	0.7	0.9	1

Table 1b: Soil parameters (Lexer and Seidl, in prep.; Steiner, 1998; Jochheim *et al.*, 2009; Polomski and Kuhn, 1998).

Soil Parameter	Unit	<i>P. abies</i>	<i>A. alba</i>	<i>L. decidua</i>	<i>P. sylvestris</i>	<i>F. sylvatica</i>	<i>Q. robur</i>	<i>A. pseudopl.</i>	<i>F. excelsior</i>	<i>C. betulus</i>	<i>B. pendula</i>
pH (tolerable min.)	pH-value in H2O	3	3	2.85	2.7	3	2.85	2.9	3.8	2.85	2.5
pH (lowest opt.)	pH-value in H2O	4	4.2	4	4	4.5	4.2	4.2	5.25	4	4.25
pH (highest opt.)	pH-value in H2O	5.5	6	6	5.5	6.5	6	6.5	7	7	7.5
pH (tolerable max.)	pH-value in H2O	8	8	8	8	8	8	8	8	8	8
C/N ratios (0-10)	Dimensionless [0,1]	0.95	0.95	0.95	0.95	1	1	1	1	1	1
C/N ratios (10-15)	Dimensionless [0,1]	1	1	1	1	0.9	0.9	0.9	0.9	0.85	1
C/N ratios (15-20)	Dimensionless [0,1]	0.9	0.95	0.95	0.9	0.85	0.85	0.85	0.8	0.85	1
C/N ratios (20-26)	Dimensionless [0,1]	0.8	0.85	0.85	0.8	0.65	0.7	0.6	0.55	0.65	0.9
C/N ratios (>26)	Dimensionless [0,1]	0.7	0.65	0.65	0.8	0.45	0.5	0.4	0.35	0.45	0.7
Rooting – Braunerde	Dimensionless [0,1]	0.9	0.87	0.95	0.85	0.9	0.9	0.9	0.9	0.9	0.9
Rooting - Semipodsol_Podsol	Dimensionless [0,1]	0.89	0.85	0.94	0.85	0.89	0.89	0.89	0.89	0.89	0.85
Rooting - Lockersed.-Braunerde	Dimensionless [0,1]	0.95	0.92	0.97	0.87	0.95	0.95	0.95	0.95	0.95	0.87
Rooting – Pseudogley	Dimensionless [0,1]	0.94	0.83	0.85	0.95	0.74	0.86	0.74	0.74	0.83	0.85
Rooting – Rendsina	Dimensionless [0,1]	0.75	0.83	0.87	0.68	0.75	0.84	0.7	0.75	0.84	0.68
Rooting - Kalk-Braunlehm	Dimensionless [0,1]	0.95	0.98	0.82	0.83	0.92	0.99	0.92	0.92	0.99	0.83
Rooting - Other Soil Types	Dimensionless [0,1]	0.9	0.87	0.95	0.85	0.9	0.9	0.9	0.9	0.9	0.85
Soil Depth (0cm-15cm)	Dimensionless [0,1]	0.65	0.45	0.65	0.7	0.65	0.45	0.65	0.65	0.45	0.7
Soil Depth (15cm-70cm)	Dimensionless [0,1]	1	1	1	1	1	1	1	1	1	1
Soil Depth (>70cm)	Dimensionless [0,1]	0.95	0.75	0.95	0.95	0.9	0.75	0.85	0.85	0.85	0.9

3.4 Calibration of the parameter set

All statistical and spatial analyses of the methodology were performed with the R Software “R Studio version 0.95.265” for statistical computing (Bivand *et al.*, 2008).

The first mode of action was to compile a set of new parameters for the study (see Table 1a and 1b) and include the individual response functions of the TSM. Secondly, as previously explained in the section of the TSM description, these response functions were connected with each other to define the tree species suitability for each species individually.

3.5 Evaluation of species suitability

For evaluation purposes, each tree species' ecophysiological suitability was calculated in accordance with TSM for every inventory plot and every year of the 30 year climate period '1961-1990'. Subsequently, the 30 suitability scalars were aggregated to a central tendency for the site by means of a median function.

The main aim of TSM evaluation was to investigate whether the model is able to produce realistic suitability patterns for each of the ten tree species investigated. To that end, two independently observed datasets for the evaluation were used as reference. At first, the current distribution of the ten tree species in Austria was used. The second data set contained the natural tree species distribution of the PNV, which is assessed at each inventory plot by experts of the Federal Forest Office. TSM was used to predict species suitability for the AFI plots of these two data sets. In both tests, the expectation value (i.e. a correct prediction) was TSM predicting tree species occurrence at the sites where a species either can be found currently growing or is a dominant or co-dominant species of the PNV. A minimum suitability threshold of >0.25 was set as to determine suitability/occurrence in TSM, i.e. to determine if site conditions conform to a species, being able to occur on this site. The prediction success (percentage of currently classified AFI plots) of these two evaluation experiments was estimated for each tree species separately.

3.6 Development of climate scenarios

In this study, there was no use of climate change data neither from GCMs nor from RCMs. The present climate data served as a baseline from which self-defined generic climate scenarios were developed. The climate scenarios considered here, focused on changes in temperature and precipitation, whose variability range are based on predicted climate change data from literature mentioned in the introductory section 1.1 and was taken to build the generic climate scenarios. In

order to bracket a wide range of potential temperature changes, and reflecting a review of future predictions until 2100, temperature changes from 0°C to 6 °C were studied in 1°C increments (cf. Table 2, Solomon *et al.*, 2007; Niedermaier *et al.*, 2007; Matulla, 2009). With regard to precipitation changes, the analysis was focused on changes between -20% to +20% in 10% incremental steps (Strauss *et al.*, 2012; Eitzinger *et al.*, 2009). Consequently, the model was parameterized by these two climatic variables in order to generate 35 generic climate scenarios. All 35 combinations of different temperature and precipitation levels were analyzed. Furthermore five scenarios highlighted in grey in Table 2 are analyzed in greater detail in the results section.

Table 2: Selection of the climate scenarios based on change in temperature- and precipitation variables.

Temperature (C°)	0	1	2	3	4	5	6
Precipitation (%)							
-20	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5	Scenario 6	Scenario 7
-10	Scenario 8	Scenario 9	Scenario 10	Scenario 11	Scenario 12	Scenario 13	Scenario 14
0	Scenario 15	Scenario 16	Scenario 17	Scenario 18	Scenario 19	Scenario 20	Scenario 21
10	Scenario 22	Scenario 23	Scenario 24	Scenario 25	Scenario 26	Scenario 27	Scenario 28
20	Scenario 29	Scenario 30	Scenario 31	Scenario 32	Scenario 33	Scenario 34	Scenario 35

As baseline to these scenarios, serves the climate data for the period 1961-1990, which was explained in section 3.1.3. All scenarios assumptions were applied instantaneously and uniformly to all years of the baseline climate, i.e. no transient climate changes were simulated. Thus it has to be noted that the inter- and intra-annual variability in climate remains constant in these scenarios. One has to mention that the inter-annual variability in climate remains constant in these scenarios.

3.7 Calculation of tree species sensitivity to climate

Based on these 35 climate scenarios, the sensitivity of each tree species to changes in climate was analyzed on two levels: First, climate sensitivity was assessed separately for each individual species at their current distribution. Second, focusing at potential species loss at the stand level, all ten species were assessed in combination at each inventory plot, weighted by their respective basal area shares.

3.7.1 Tree species sensitivity at species level

For the calculation of the individual species sensitivity at their current locations, all AFI plots were used that currently hold a species. For each tree species, all 35 generic climate scenarios were applied to derive species sensitivity from TSM.

With the individual species data of the calculated species suitability for each of the climate scenarios, the relative and absolute risk of species change of the current tree species distribution was estimated, addressing hypothesis 1. In this context, the relative risk of species loss is defined by the number of plots with TSM predictions <0.25 to the total share of plots where the species occurs under current climate. The absolute risk of species change is defined by the absolute number of inventory plots for which species loss (TSM predictions <0.25) is estimated. Hypothesis 2 was addressed by investigating the effect of both climate variables on orthogonal axes using contour plots.

3.7.2 Risk of species loss at plot level

Wiens *et al.* (2009) states that the probability of species occurrences may shift with the high variability of climate change and can be made visible in high-resolution maps of niche based species distribution models. Based on the relative share of the basal area of the current tree species distribution, it is demonstrated where the risk of species loss is likely to occur in space, using five indicative climate scenarios that were selected from the 35 studied (cf. Table 2). Potential species loss at the plot level was estimated based on a basal-area weighted aggregation of suitability in three categories for each inventory plot, again using a suitability of <0.25 as threshold for species loss. Three risk categories were used in the analysis at the inventory plot level, i.e., low ($<33\%$ of basal area at risk), moderate ($33\% - 66\%$ of basal area at risk), and high ($>66\%$ of basal area at risk). This analysis was subsequently used to investigate variation in the risk of species loss over elevation (hypothesis 3.1), in the ecoregions (hypothesis 3.2), as well as with species diversity (hypothesis 4).

In regards to hypotheses 3.1 and 3.2, the spatial distribution of species loss in elevation (Figure 3) and main ecoregions was analyzed (Figure 4). Based on climatic- and plant-sociologic aspects, Kilian *et al.* (1994) categorized individual elevation levels with their approximate elevation bands at average as follows (exact elevation differs in each ecoregion):

<u>Low elevations:</u>	colline	100m/200m – 300m/400m
	submontane	150m/750m – 500m/1000m
<u>Central elevation:</u>	lower montane	500m/900m – 750m/1300m
	montane	600m/1100m – 1000m/1450m
	upper montane	950m/1400m – 1060m/1850m
<u>High elevation:</u>	subalpine	1100m/1700m – 1400m/2100m
	upper alpine	1600m/2000m – 1750m/2300m

Kilian *et.al.* (1994) defined the ecoregions (Figure 4) according to following aspects: Ecoregions are natural landscapes with uniform climatic characteristics and geomorphic basic units which define different compositions of forest communities. This study focused on the main ecoregions that are categorized with regards to Figure 4 as follows (Kilian *et.al.*, 1994, cf. Seidl *et al.*, 2009):

- (1) Inner Alps
- (2) Northern intermediate Alps
- (3) Eastern intermediate Alps
- (4) Northern Alpine rim
- (5) Eastern Alpine rim
- (6) Southern Alpine rim
- (7) Northern pre-alpine area
- (8) Pannonic area
- (9) Bohemian Massif

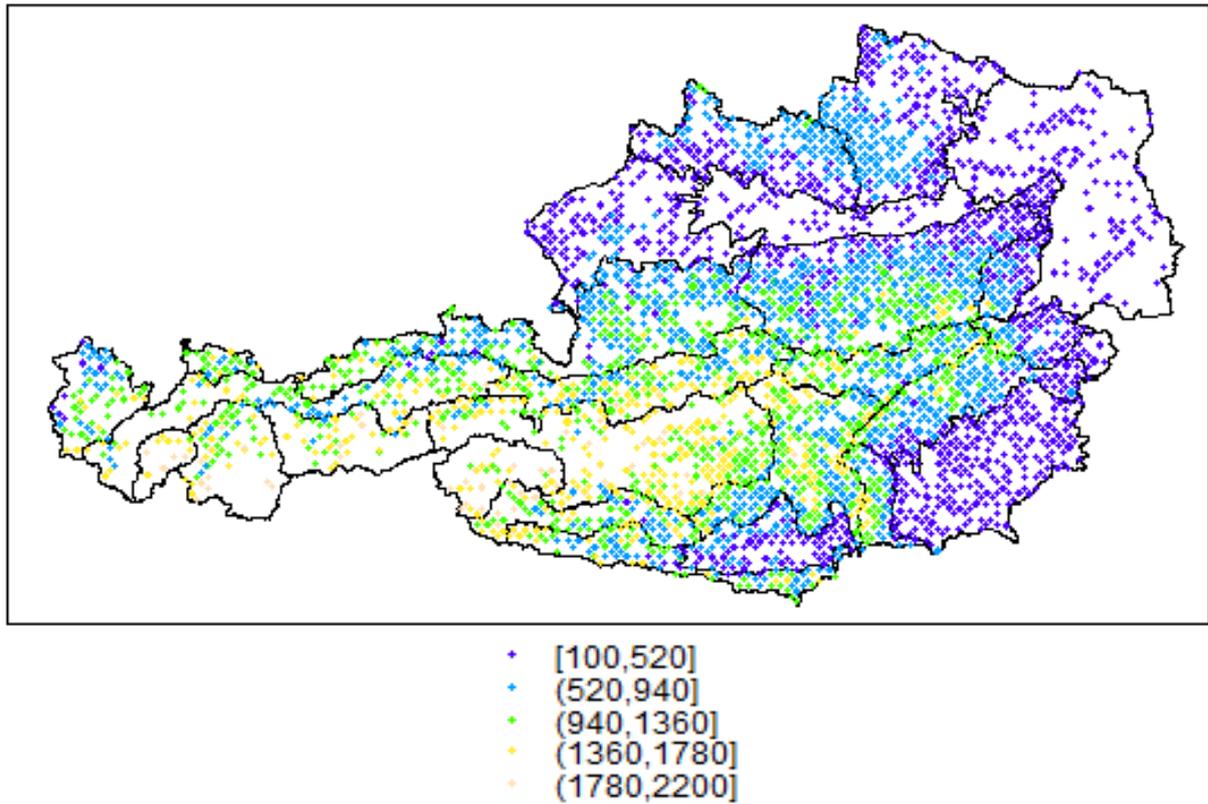


Figure 3: Elevation levels (unit in meter (m) above sea level) of Austria.

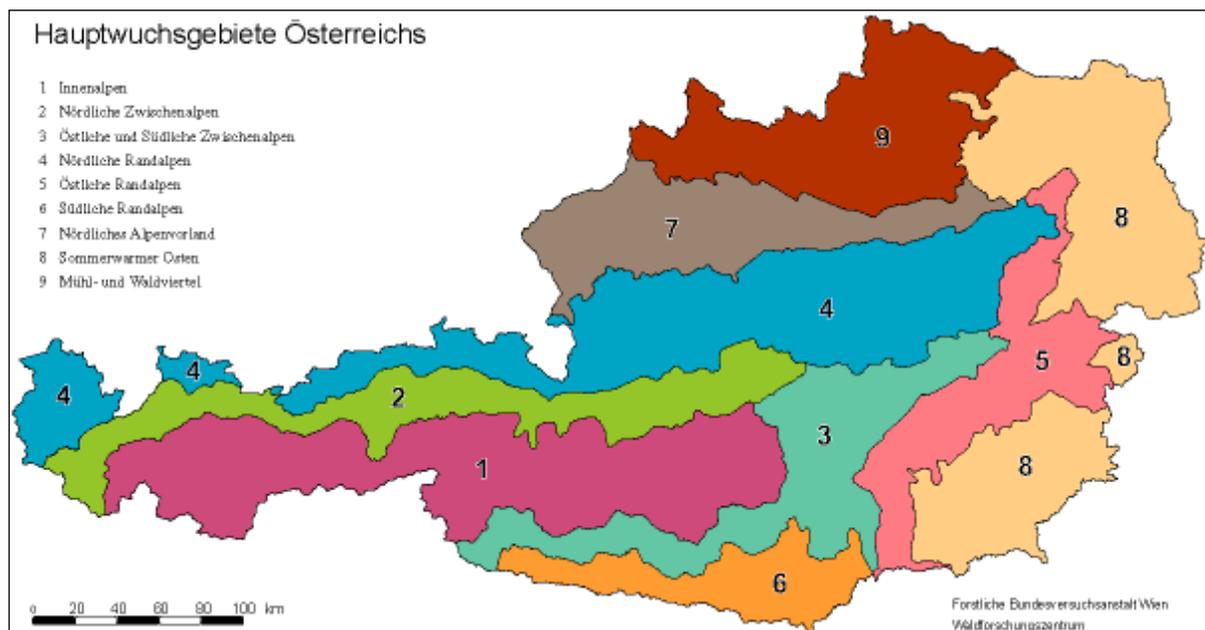


Figure 4: Main ecoregions of Austria based on Kilian *et al.* (1994), reference source of BFW (2000).

For the fourth and last hypothesis, which tests whether higher species diversity and evenness reduces the risk of species loss, the Shannon equitability index (Eq. 6) was calculated. It is assumed that species diversity can positively affect the forest stands stability against risk of species loss. According to Magurran (1988), the formula for the Shannon diversity index determines the quantity (p_i) of the proportional abundance of individuals found in the i th species:

Equation 6: Shannon diversity index

$$H = - \sum_{i=1}^S p_i \ln p_i$$

This index for species richness addresses the evenness of species diversity. However, not all existing species in each inventory plot are included in this analysis; rather, the focus was set on the ten most abundant species (i.e. the maximum number of species per plot in this investigation is ten). Therefore, the index of Shannon's equitability (relative Shannon index) was applied, which relates H to the maximum diversity (H_{max}) which could occur with 10 equally distributed tree species per inventory point, explaining how equally abundant the species are at each point (Eq. 7, Magurran, 1988).

Equation 7: Shannon's equitability (E_H)

$$E_H = H / H_{max} = H / \ln S$$

This measure of evenness has a scale ranging from 0 to 1, where 0 describes the situation where species diversity and evenness is low, with only one species dominating the plot. A value of 1, on the other hand would be the case where species diversity and evenness is at its maximum, i.e. with all ten species considered here occurring equally abundant.

4 Results

4.1 Evaluation of the TSM model

As shown in Table 3, the prediction success confirms that TSM predictions are generally in line with observed and PNV species presence. The evaluation against the current tree species distribution shows a minimum prediction success of at least 90% at the level of sample plots over all species, whereas the results compared of the PNV indicate an even slightly higher success. These two evaluating measurements ascertain that the model approach of the TSM as well as the parameters compiled for this study conform to the biological realism for the ten selected species. Hence, it can be assumed that TSM can be applied for the main study question of this thesis, i.e. determine the climate sensitivity of major Austrian tree species at their current location.

Table 3: Prediction success of TSM. A successful prediction is one where a species either occurs currently or is expected to occur as dominant species in the PNV and where TSM predicts a suitability scalar of >0.25.

Tree species	<i>Picea abies</i>	<i>Abies alba</i>	<i>Larix decidua</i>	<i>Pinus sylvestris</i>	<i>Fagus sylvatica</i>	<i>Quercus robur</i>	<i>Acer pseudopl</i>	<i>Fraxinus excelsior</i>	<i>Carpinus betulus</i>	<i>Betula pendula</i>
Prediction success of observations (%)	99.43 (n=1776)	98.56 (n=472)	99.74 (n=158)	99.64 (n=396)	94.94 (n=151)	99.74 (n=42)	93.72 (n=151)	90.64 (n=86)	100 (n=9)	99.75 (n=60)
Prediction success of PNV (%)	99.17 (n=1744)	98.78 (n=60)	99.85 (n=51)	99.96 (n=709)	96.3 (n=55)	99.95 (n=41)	99.72 (n=55)	99.18 (n=59)	99.97 (n=22)	100 (n=4)

4.2 Tree species sensitivity at species level

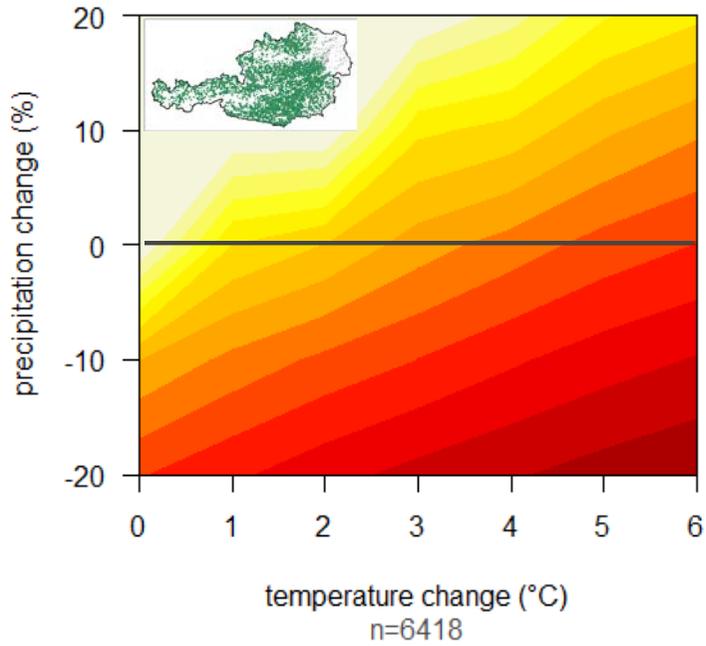
The climate sensitivity of tree species was investigated individually at the level of AFI plots considering their current distribution. Figures 5a to 6b show the relative (AFI plots currently occupied by a species which have a suitability <0.25 under a given climate scenario, relative to all AFI plots currently occupied by the species) and absolute (number of AFI plots currently occupied by a species with suitability <0.25) risk of species loss by means of basal area. Contour lines depict the degree of risk of species loss and illustrate species sensitivity of each tree species related to changes in temperature and precipitation.

In absolute terms, Norway spruce is the most threatened tree species, predicted to have the highest number of plots at risk of species loss (589 AFI plots) under the worst case climate scenario 7 (i.e. at 6°C temperature increase and -20% precipitation decline). However, it has to be considered that this

coniferous species has the by far widest occurrence of all species considered here, currently appearing on 6418 sample plots. In comparison, for the other nine species the total number of inventory plots that they occur on varies between 129 (silver birch) and 1219 (European beech). According to the first hypothesis, one can conclude that in absolute terms, Norway spruce is likely to be most sensitive species to climatic change at its current forest distribution. Considering relative risk, on the other hand, yields a different result. Under the worst case climate scenario 7, hornbeam (risk of loss at 28.3% of its current occurrence) and pendunculate oak (risk of loss at 26.7% of its current occurrence) have the highest risk of species loss relative to the total number of plots that they currently occur on. This can be explained due to the two species high share in basal area in the pannonic area, which is considered to be highly at risk to drought. In comparison, the relative risk of Norway spruce in scenario 7 is only 8.9%.

Regarding the second hypothesis, the assumption that tree species in general react more sensitive to changes in precipitation than to temperature has been supported. From Figure 5a, 5b, 6a and 6b it can be seen that most species are particularly sensitive to precipitation declines, but that the highest loss can be expected from the interaction of increasing temperatures and decreasing precipitation. Where the contour lines are $<45^\circ$ from the horizontal alignment, precipitation has a greater impact than temperature, while at $>45^\circ$, temperature would have a greater impact on species sensitivity. One exception to the finding of higher sensitivity to precipitation changes is mountain maple which - above a certain threshold temperature - is more strongly driven by temperature change both with regard to absolute (7b) and relative (8b) risk of species loss. One reason might be that mountain maple is a species adapted to cool montane conditions and canyons, frequently found on well water-supplied sites, and thus more sensitive to changes in temperature than to precipitation. Similar behavior can be seen also for some species particularly with regard to the absolute risk of species loss, where species react more sensitive to low temperature changes as long as they have ample water supply (by additional precipitation). But this pattern levels off once temperature increases strongly (above 4°C). However, for all species, intensified warming with reduced water availability intensifies the risk of species loss.

Picea abies



Abies alba

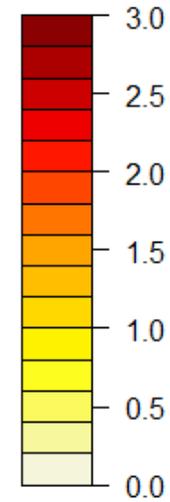
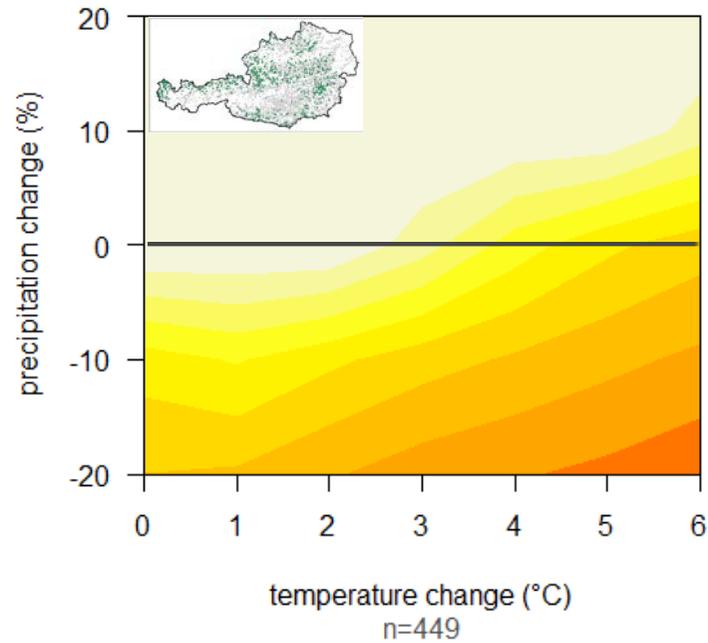
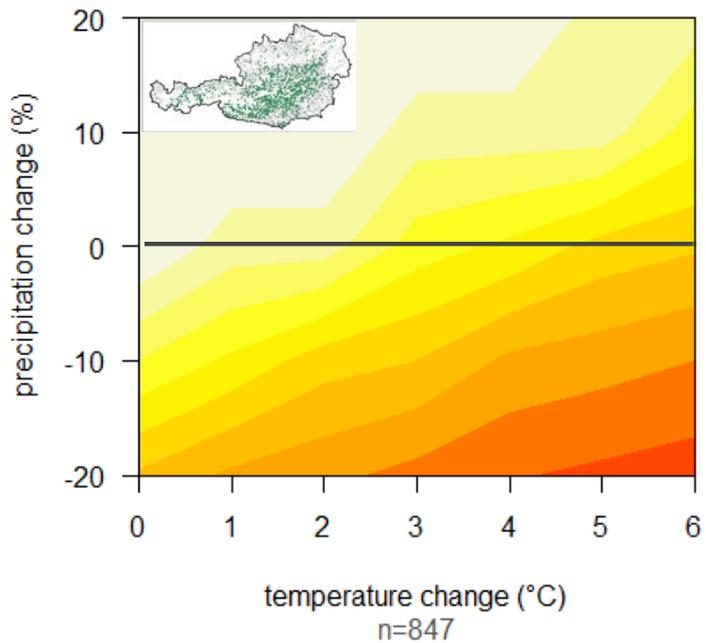
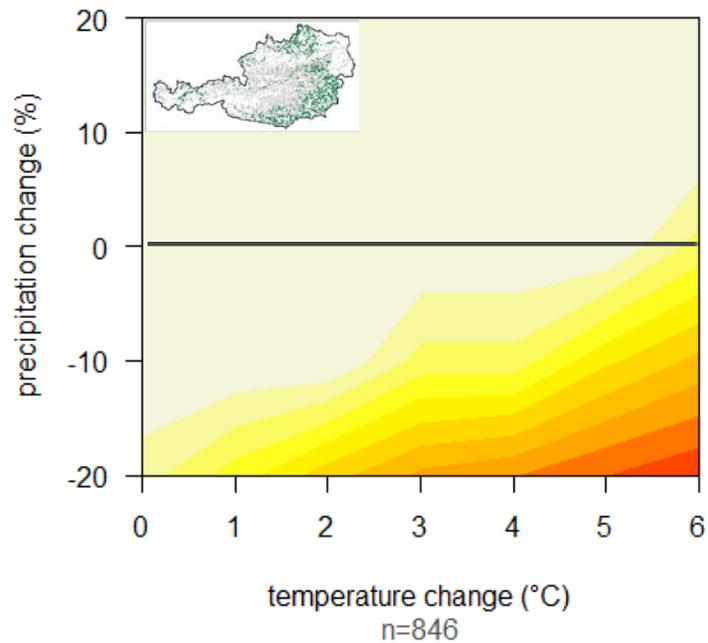


Figure 5a: The absolute risk of species loss (number of AFI plots on log-scale currently occupied by the species with low suitability under changed climate) for each species under changing temperature and precipitation regimes, given its current distribution. The map insert shows the current distribution for each species and n is the number of inventory points with the species present.

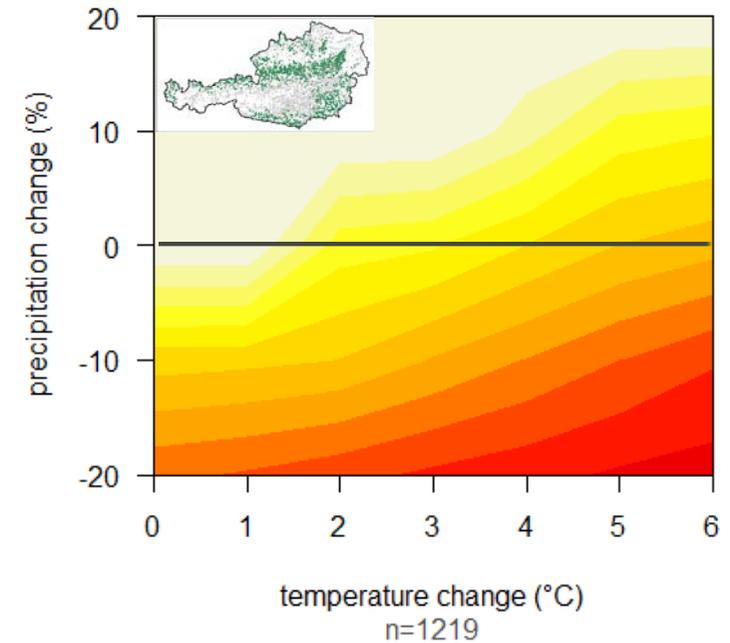
Larix decidua



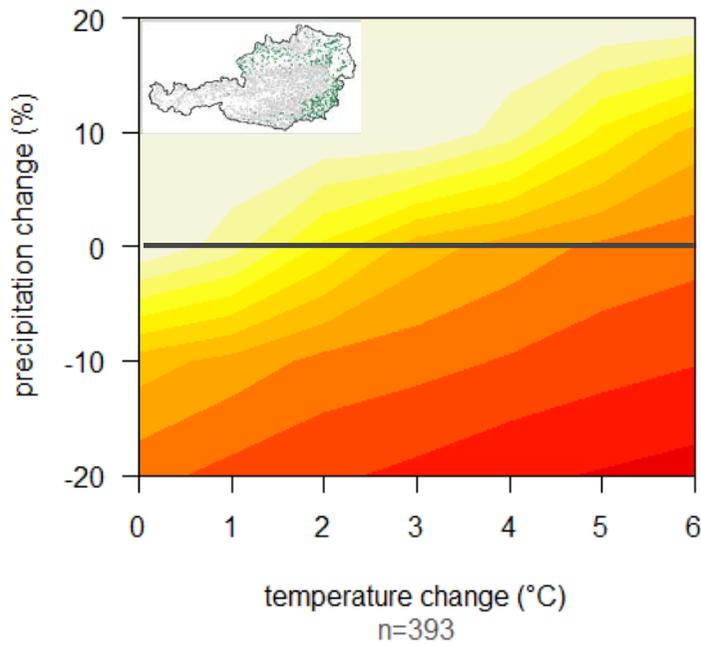
Pinus sylvestris



Fagus sylvatica



Quercus robur



Acer pseudoplatanus

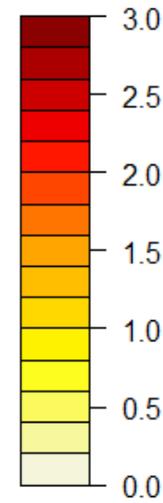
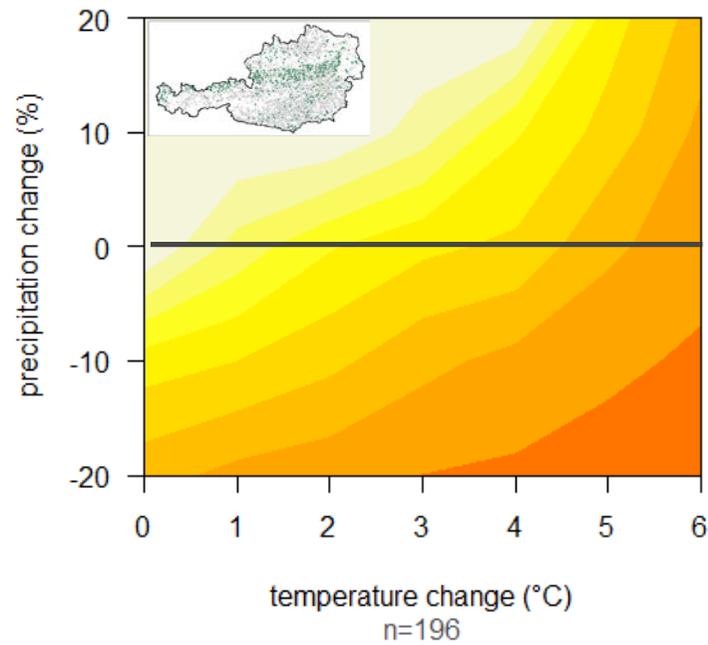
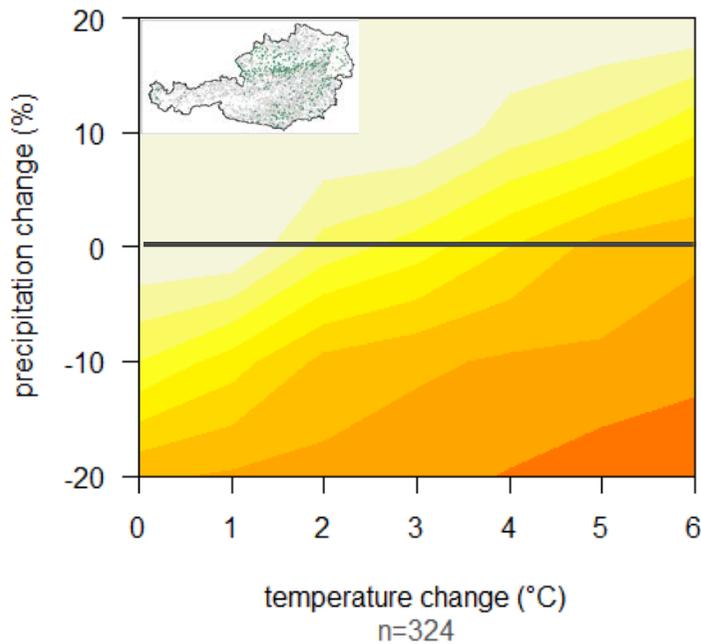
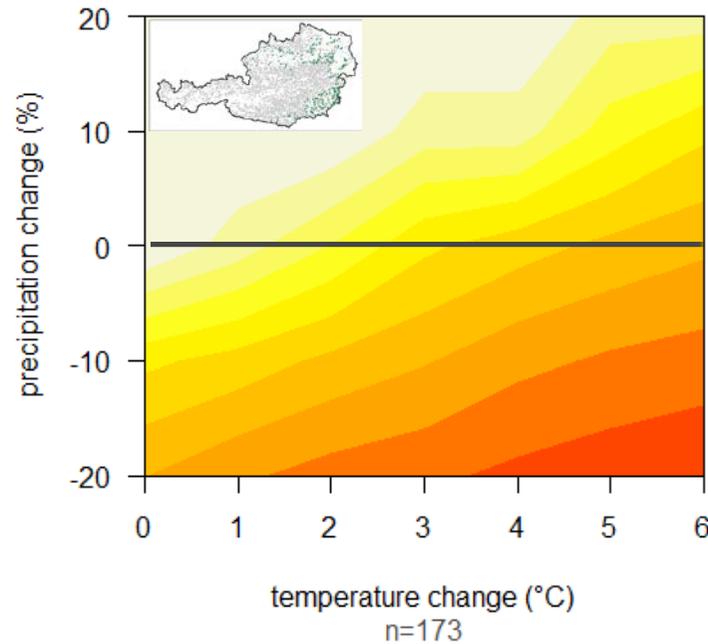


Figure 5b: The absolute risk of species loss (number of AFI plots on log-scale currently occupied by the species with low suitability under changed climate) for each species under changing temperature and precipitation regimes, given its current distribution. The map insert shows the current distribution for each species and n is the number of inventory points with the species present.

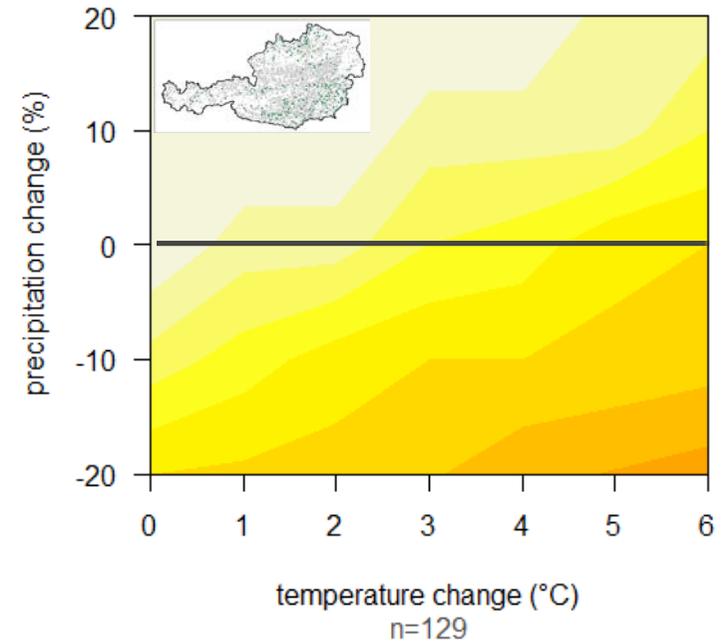
Fraxinus excelsior



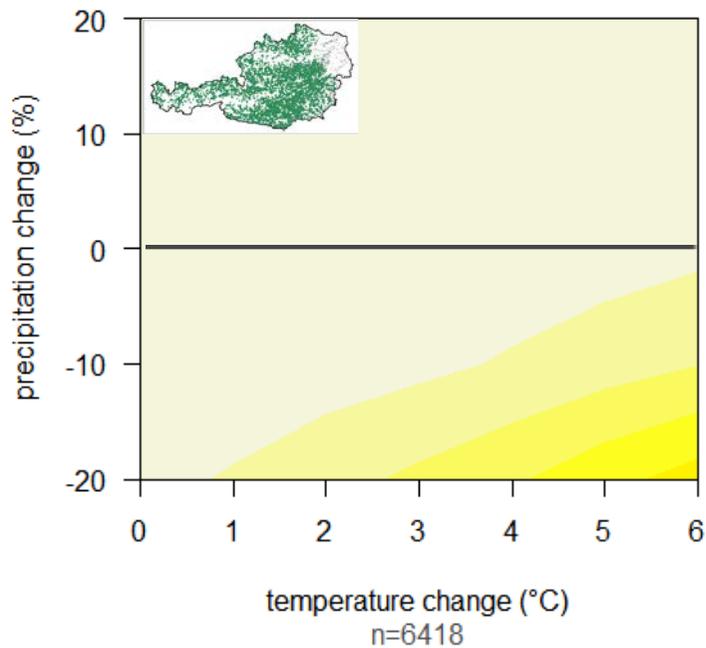
Carpinus betulus



Betula pendula



Picea abies



Abies alba

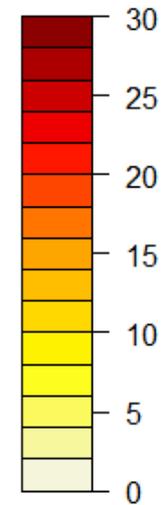
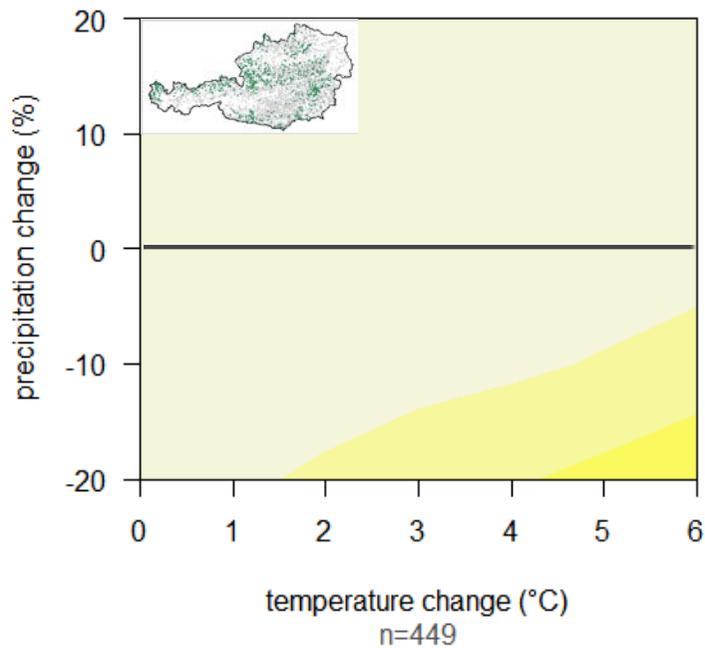
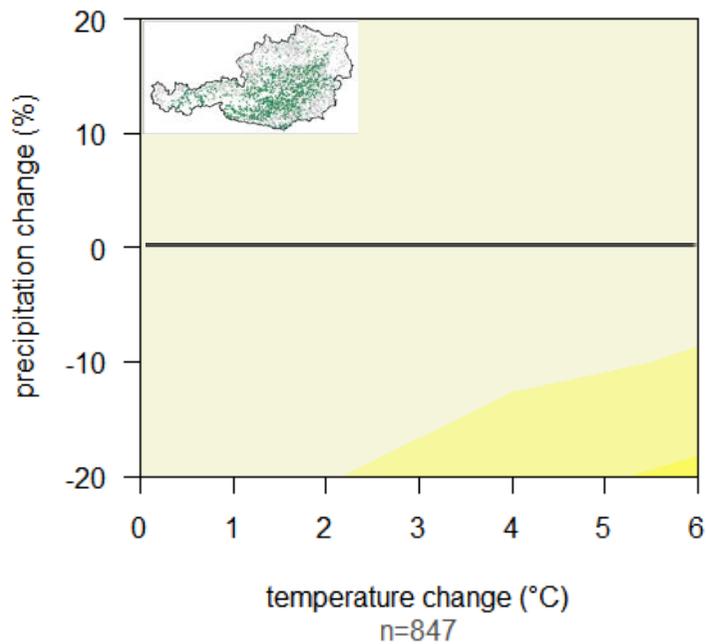
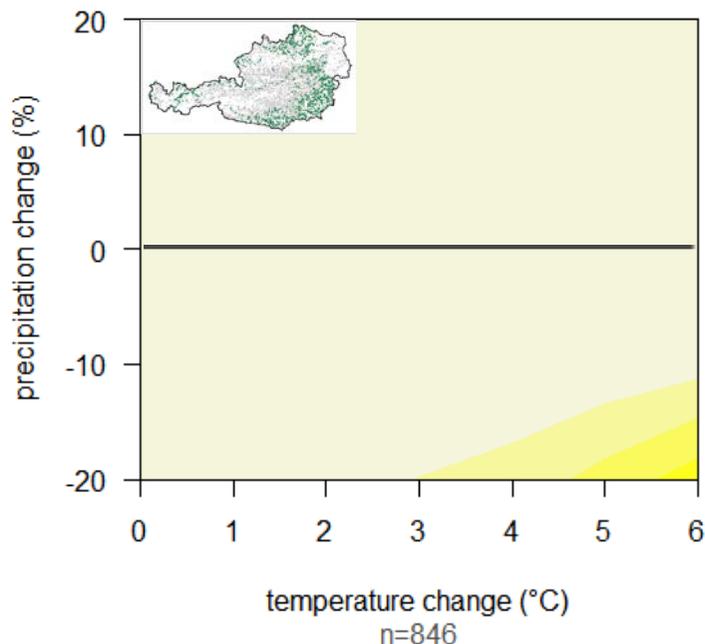


Figure 6a: The relative risk of species loss (percent of AFI plots currently occupied by the species with low suitability under changed climate conditions) under changing temperature and precipitation regimes. The map insert shows the current distribution for each species and n is the number of inventory points with the species present.

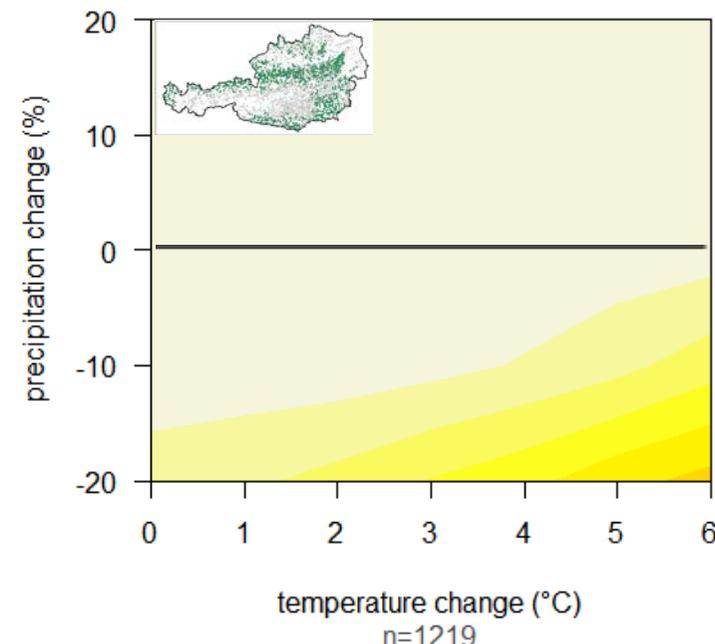
Larix decidua



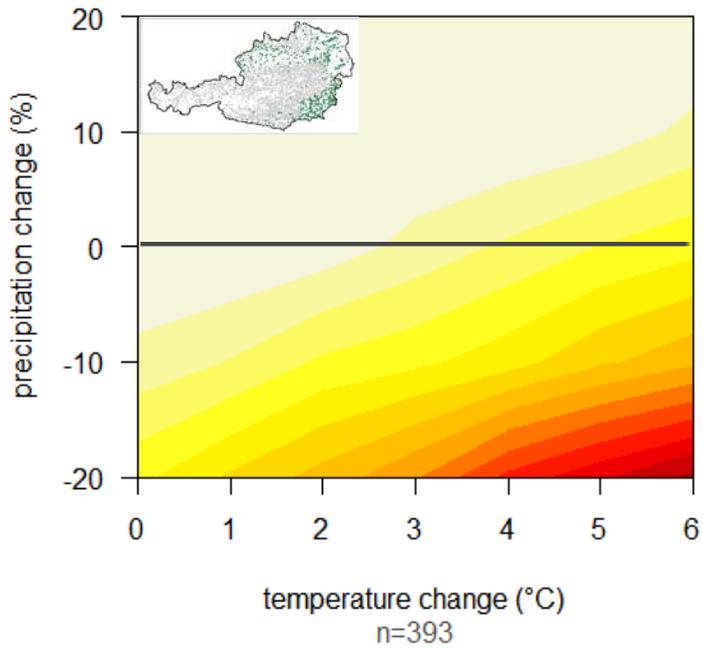
Pinus sylvestris



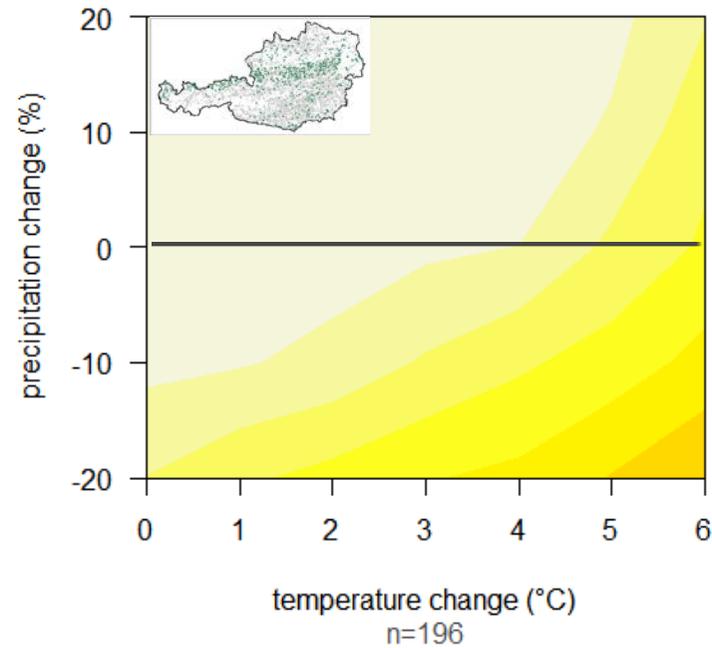
Fagus sylvatica



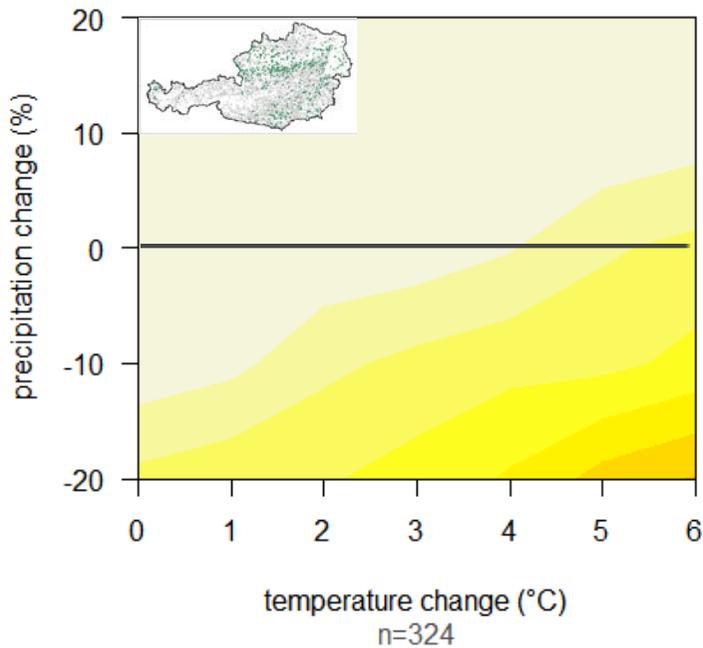
Quercus robur



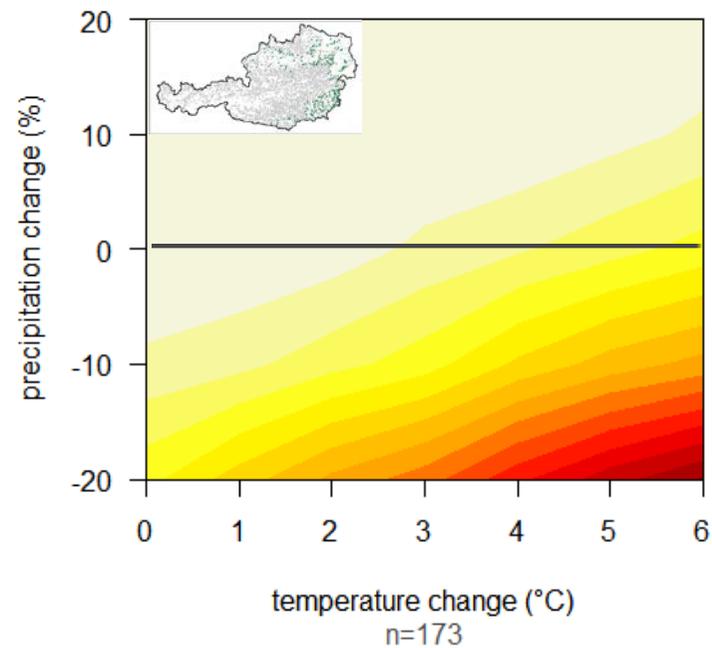
Acer pseudoplatanus



Fraxinus excelsior



Carpinus betulus



Betula pendula

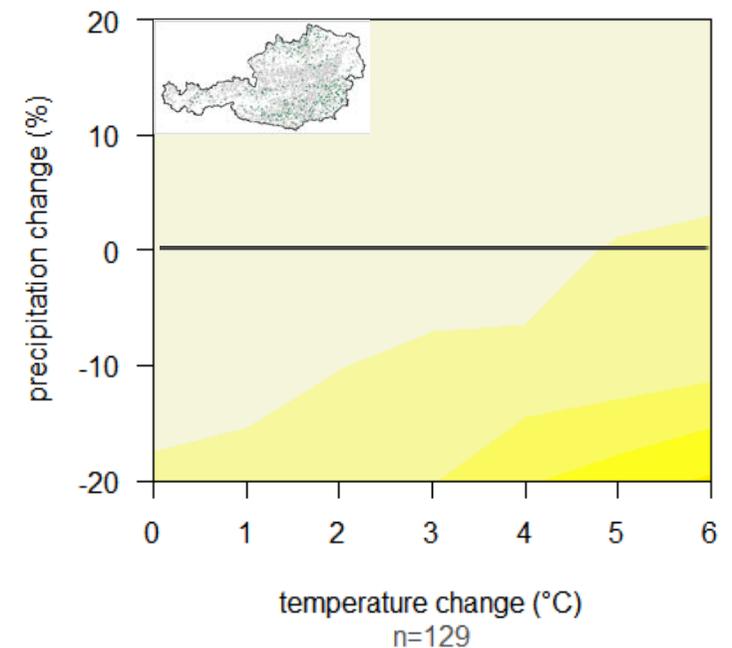


Figure 6b: The relative risk of species loss (percent of AFI plots currently occupied by the species with low suitability under changed climatic conditions) under changing temperature and precipitation regimes. The map insert shows the current distribution for each species and n is the number of inventory points with the species present.

4.3 Risk of species loss at plot level

After analyzing each tree species individually with regard to its sensitivity, the risk of species loss for all of the ten dominant tree species jointly at plot level was investigated, quantifying the relative share of basal area that might be lost in response to climate change. The shares of inventory plots at risk are shown in Table 4 in three risk classes.

Table 4: Degree of risk of species loss at the level of inventory plots.

Percentage of inventory plots at low risk (i.e. climate-change induced basal area loss of $\leq 33\%$)

Temperature (C°)							
Precipitation (%)	0	1	2	3	4	5	6
-20	98.1	97.2	96.2	95.1	93.8	92.4	91.4
-10	99.5	99.2	98.7	98.3	97.4	96.6	95.6
0	100	99.9	99.8	99.5	99.1	98.7	98.3
10	100	100	100	99.9	99.9	99.7	99.4
20	100	100	100	100	100	100	99.8

Percentage of inventory plots at moderate risk (i.e. climate-change induced basal area loss of $>33\%$ and $\leq 66\%$).

Temperature (C°)							
Precipitation (%)	0	1	2	3	4	5	6
-20	0.5	0.8	1.1	1.4	1.7	2.0	2.1
-10	0.2	0.2	0.4	0.5	0.8	1.1	1.3
0	0	0	0.1	0.2	0.2	0.5	0.6
10	0	0	0	0	0	0.1	0.2
20	0	0	0	0	0	0	0.1

Percentage of inventory plots at high risk (i.e. climate-change induced basal area loss of $>66\%$).

Temperature (C°)							
Precipitation (%)	0	1	2	3	4	5	6
-20	1.4	1.9	2.7	3.6	4.6	5.7	6.9
-10	0.3	0.6	0.9	1.2	1.7	2.3	3.1
0	0	0.1	0.1	0.4	0.6	0.9	1.2
10	0	0	0	0.1	0.1	0.2	0.4
20	0	0	0	0	0	0	0.1

Next, Figure 7 visualizes the hotspots of risk for species loss in Austria. Henceforward, the bracketing climate scenarios highlighted in grey in Table 2 and 4 are analyzed in more detail (scenario 1 = (a), scenario 5 = (b), scenario 7 = (c), scenario 19 = (d) and scenario 21 = (e)).

Also the analysis of the spatial pattern of risk in Figure 7 underlines the findings regarding the second hypothesis: As precipitation has more influence on species sensitivity than temperature, scenario (a) with no change in temperature but a precipitation change of -20% has more plots at high risk than the two scenarios (d) and (e), with no change in precipitation but change of temperature of 4°C and 6°C, respectively. In all scenarios, the highest loss is expected for sites in northeastern Austria, which is currently already the warmest and driest part of the country. In the worst case scenario (c) a high number of inventory plots along the Alpine rim and foothills of the Alps as well as the lowlands of the northeast, east up to the south east would be threatened to risk of species loss. According to the analysis, changes in climate could exceed the ecophysiological thresholds of many important species currently occurring in this area. This climate scenario data were subsequently also used to investigate the last three hypotheses on elevation (3.1), ecoregions (3.2), and diversity (4) in more detail.

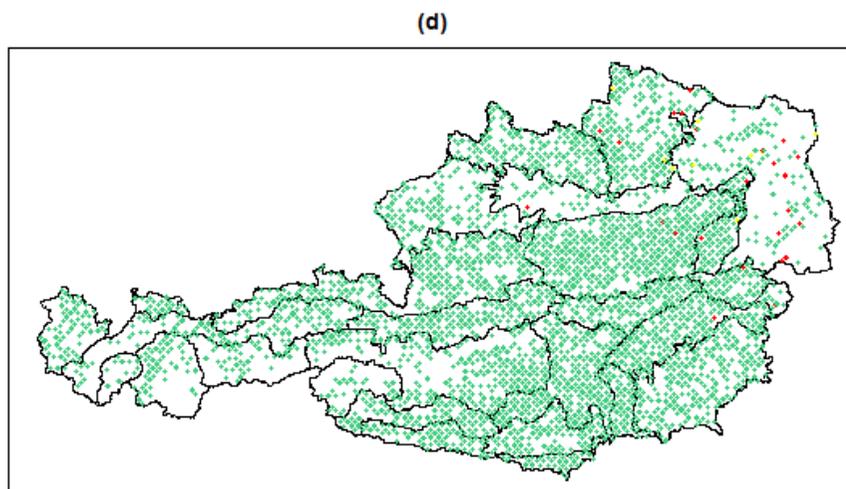
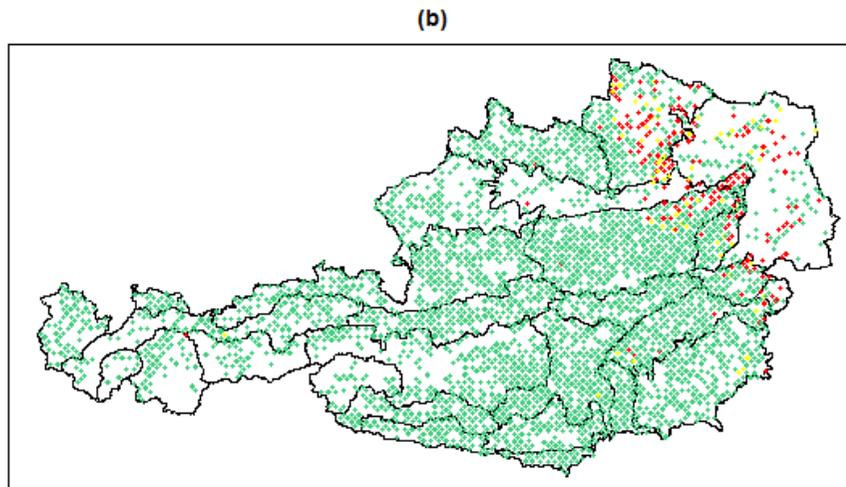
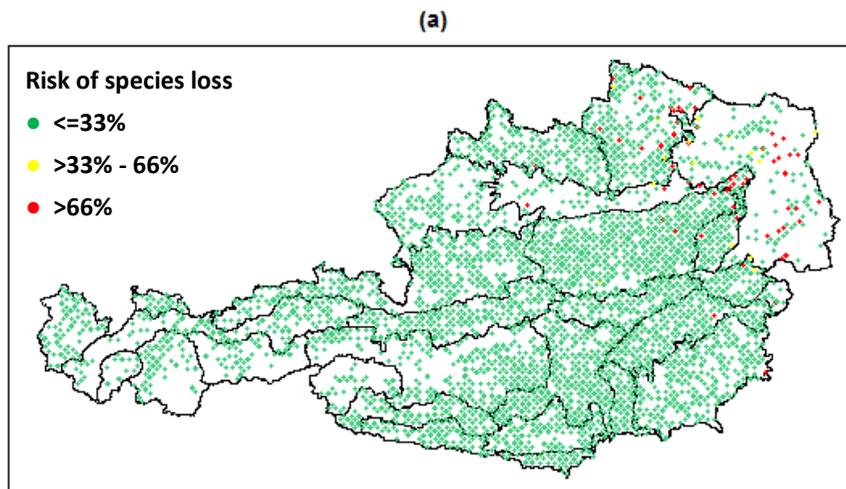
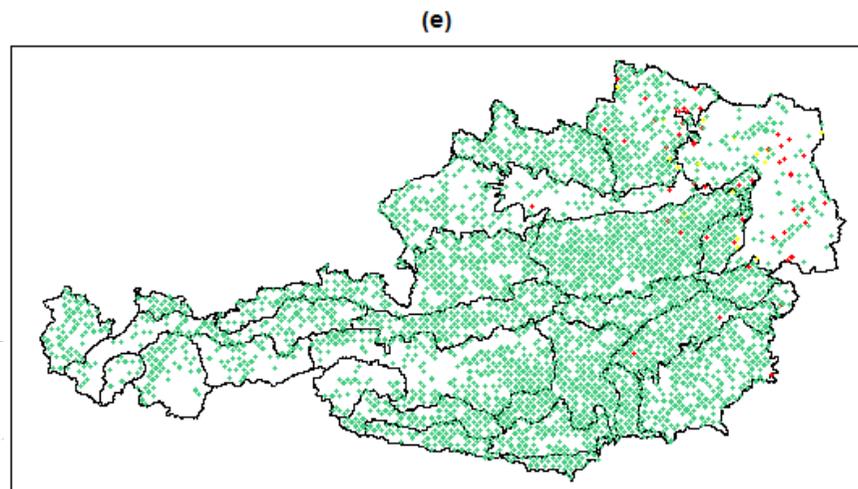
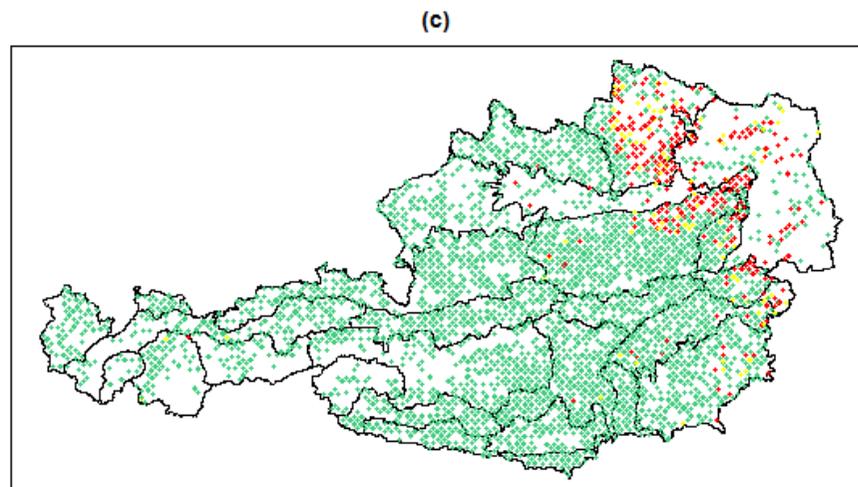


Figure 7: Spatial distribution of risk of species loss (relative to total basal area) at the level of forest inventory plots in Austria. Panels represent different levels and combinations of temperature increase (°C) and precipitation change (%); (a) 0°C / -20%, (b) 4°C / -20%, (c) 6°C / -20%, (d) 4°C / 0%, (e) 6°C / 0%. Green = low risk (≤33% of the current species share lost); yellow = medium risk (>33% - 66% of the current species share lost); red = high risk (>66% of the current species share lost).



4.3.1 Risk of species loss over elevation

To test hypothesis 3.1, the risk of species loss at different elevations for the climate scenarios (a) to (e) have been analyzed (Figure 8). The plots support the a priori formulated hypothesis that low-lying elevations below <400m (approximately corresponding to the colline elevation belt) and areas between 400m and 700m (approximately corresponding to the submontane elevation belt) are less buffered to climatic changes as investigated here compared to higher elevations. More than 90% of the plots that show a high risk are below 700m in the worst case scenario (c). This distribution of risks in elevation can also be seen from the maps in Figure 7. This risk pattern over elevation mainly results from lower precipitation and higher temperatures at low elevation sites. There are, however, individual inventory plots for which a considerable risk was calculated also at higher elevations (up to 1400m in elevation) particularly in climate scenario (c).

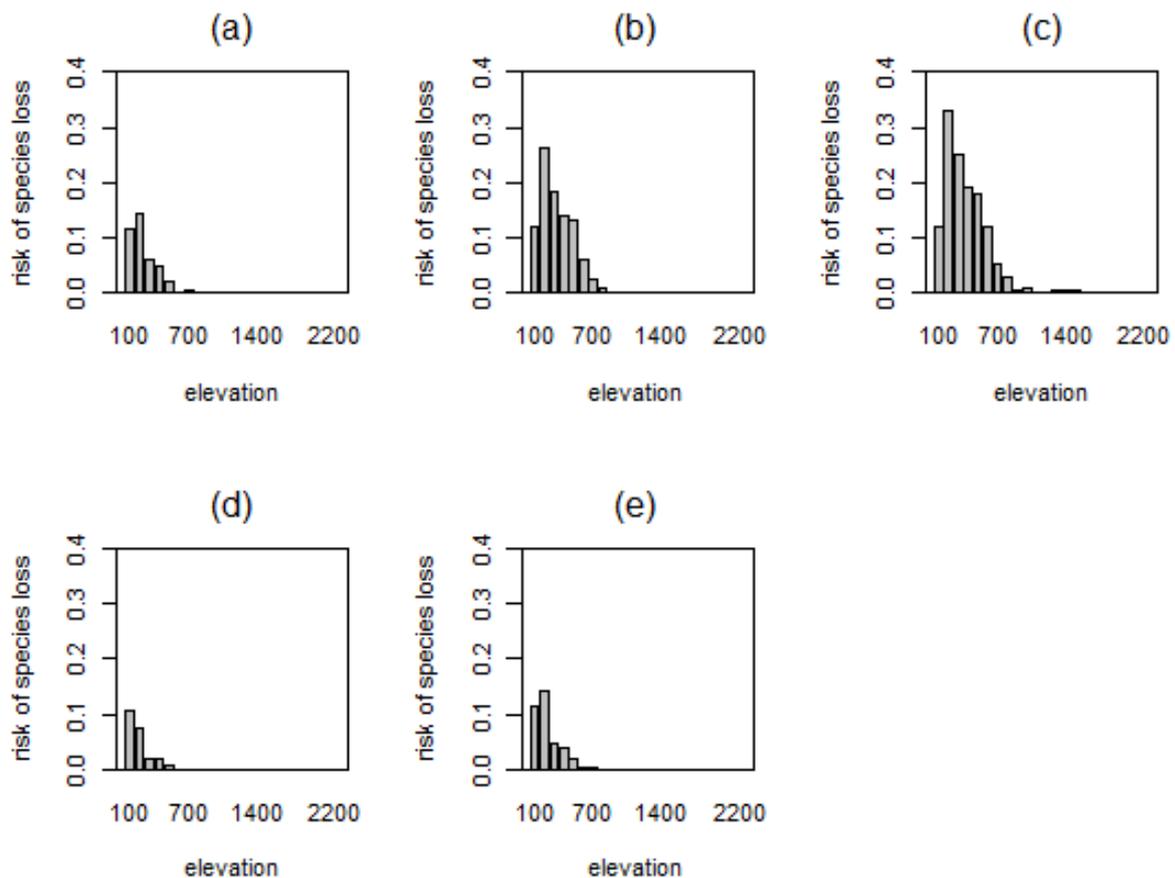


Figure 8: Distribution of risk of species loss (relative to total basal area) over elevation for different scenarios of temperature increase (°C) and precipitation change (%): (a) 0°C/-20%, (b) 4°C/-20%, (c) 6°C/-20%, (d) 4°C/0%, (e) 6°C/0%. Values are means over all inventory plots per elevation band. The risk of species loss (y-axis) ranging from 0 (no loss) to 1 (complete loss).

4.3.2 Risk of species loss at the main ecoregions

Furthermore, the spatial pattern of risk with regard to the main ecoregions according to Kilian *et al.* (1994) has been analyzed. From this analysis, ecoregions particularly at risk are ecoregions 5, 8 and 9, particularly in climate scenarios (b) and (c), i.e. those in which changes in temperature and in precipitation intensify. However, risk of species loss is expected to be happening under all five climate scenarios in ecoregions 8 and 9.

Here it is important to note that the ecoregion 5 (Eastern Alpine rim) is characterized by less precipitation (700mm to 1250mm) in comparison to the Northern and Southern Alpine rim, and is therefore at higher risk compared to the other pre-alpine areas. Ecoregion 8 comprises the pannonic area characterized by sub continental dry warm summers with frequent drought periods and poor snow cover during moderate cold winters. With only 450mm to 700mm it is the ecoregion with lowest annual precipitation in Austria (Kilian *et al.*, 1994), and further changes in precipitation could thus result in exceeding a critical threshold for many tree species. Although ecoregion 9, the Bohemian Massif, has a short vegetation period (Kilian *et al.*, 1994) and features higher precipitation levels (500mm to 1100mm) than ecoregion 8, it is still predicted to have one of the highest risks of species loss, inter alia due to its high share of the sensitive species Norway spruce.

Also the eastern parts of bordering ecoregions show a considerable amount of areas at risk from species loss, although they are generally less sensitive due to higher precipitation levels. For ecoregion 4, for instance, a transition zone in its eastern part appears to have the same high level of risk as ecoregions 5, 8 and 9. The same was found for ecoregion 7, which borders ecoregion 8 and 9 and has a drier eastern part in which precipitation levels vary between 600mm and 1000mm (Kilian *et al.*, 1994). Overall, the a priori hypothesis that the pannonic area and foothills are the most threatened areas to experience species loss from climate change found support by the results. However, the findings further specify hypothesis 3.2 insofar as not the entire northern and eastern foothills of the Alps were found sensitive, but rather specifically the eastern parts of the Bohemian Massif (ecoregion 9) as well as eastern parts of the Northern Alpine rim (ecoregion 4) and the north of the Eastern Alpine rim (ecoregion 5) were particularly at risk in the scenario analysis of Figure 7 (cf. Figure 9).

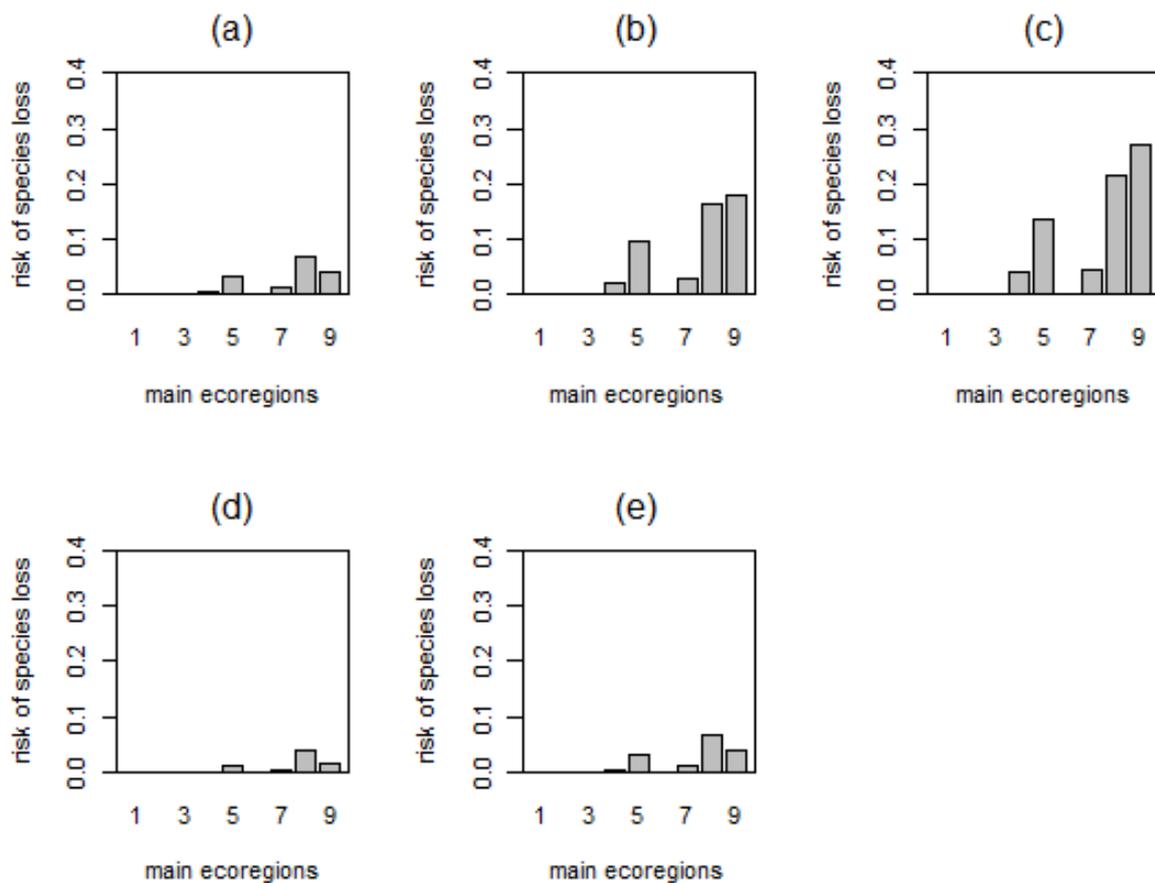


Figure 9: Distribution of risk of species loss (relative to total basal area) over the ecoregions according to Kilian *et al.* (1994), for different scenarios of temperature increase (°C) and precipitation change (%): (a) 0°C/-20%, (b) 4°C/-20%, (c) 6°C/-20%, (d) 4°C/0%,(e) 6°C/0%. Values are means over all inventory plots per ecoregion. The risk of species loss (y-axis) ranging from 0 (no loss) to 1 (complete loss).

4.3.3 Impact of species diversity on the plot level risk of species loss

A further aim of this work was to investigate to what extent the evenness in species diversity could reduce the risk to species loss at the level of inventory plots. It was hypothesized (hypothesis 4) that if species diversity and evenness are high, the risk for substantial species loss is smaller as with one or only a few species dominating an inventory plot. To test this hypothesis the Shannon equitability index was calculated at each inventory plot. Figure 10 shows that evenness has no significant influence on risk of species loss. The reasons for this unexpected finding might be twofold: The eastern provinces and low elevation sites are most sensitive to risk of species loss due to their already higher temperature and lower precipitation levels, but are at the same time also the most diverse sites and forest types with regard to species distribution (compared to the relatively species-poor high elevation forests). Overall, this concludes that there is no significant difference for the risk

of species with species diversity, and the last hypothesis has to be rejected based on the material and analyses conducted here.

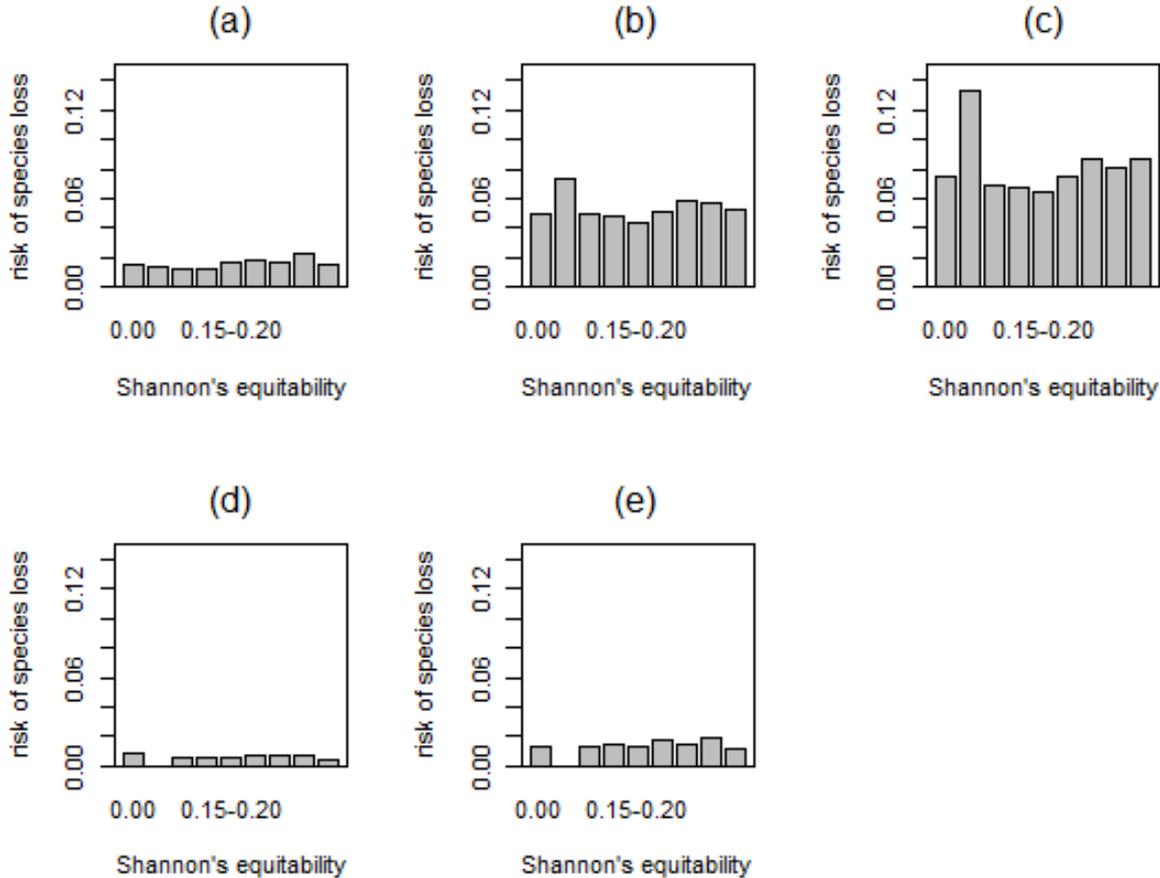


Figure 10: Distribution of risk of species loss (relative to total basal area) over tree species diversity for different scenarios of temperature increase (°C) and precipitation change (%): (a) 0°C/-20%, (b) 4°C/-20%, (c) 6°C/-20%, (d) 4°C/0%, (e) 6°C/0%. Values are means over all inventory plots per diversity level. The risk of species loss (y-axis) ranging from 0 (no loss) to 1 (complete loss).

5 Discussion

5.1 Species sensitivity and risk of species loss

5.1.1 Predicted changes in species distribution

Climate change has either a positive or negative impact on individual species behavior depending on regional climate changes and site conditions of a forest stand (Lindner *et al.*, 2010). In this study, the focus was on the negative effect of species loss relative to its current occurrence due to increasingly unsuitable conditions from climate change. It has to be noted that the risks of species loss reported here do not necessarily mean that a species will disappear from a given area but rather indicates where climate change impacts are likely to exceed important species-specific thresholds and affect the current forest vegetation the most. Such changes are also likely to strongly affect the competitive relationships between species, which were, however, not considered in this study. In many areas where precipitation gets increasingly limiting while temperatures are increasing, thermophile species such as hornbeam, pendunculate oak and Scots pine could be gaining competitiveness relative to other species. Below the findings were discussed with regard to climate sensitivity individually for each species.

Conifers

(1) Norway spruce (*Picea abies*)

Hanewinkel *et al.* (2012) states that Norway spruce is predicted to shift northwards, losing its tree species suitability in large part of its current distribution in central Europe, and becoming increasingly restricted to higher elevation sites. With a share of over 50% of forest cover in Austria (based on basal area), Norway spruce is economically the most important forest tree species, and will – according to the predictions of this study - have the biggest absolute loss from climate change in Austria (see also Niedermair *et al.*, 2007). Hence, with increasing temperatures and decreasing mean annual precipitation, Norway spruce may become unsuitable at lower elevations, where it might have been cultivated previously due to its high economic revenues (Leitgeb *et al.*, 2013; Spiecker, 2000). This is in line with Lexer *et al.* (2001), who state that current forest sites of this tree species might become soon unsuitable in the submontane and montane elevation zones, if exposed to declining precipitation levels during the vegetation period. This would, on the other hand, open up niches and could also increase forest diversity when these niches are occupied by other migrating tree species (Niedermair *et al.*, 2007). Norway spruce is in many aspects not ecologically fit to the ongoing climate change at the lower elevations of its current range distribution. In areas with

sufficient precipitation, however, and considering adapted silvicultural activities (e.g. admixture of other species to improve soil conditions), it could still be a suitable species for management even under changing climate conditions (Leitgeb *et al.*, 2013).

(2) Silver fir (*Abies alba*)

Silver fir has the ability to use deeper-lying water reservoirs in the soil by its tap-root system in order to saturate its high water demand (Leitgeb and Reiter, 2009). This can be an inherent physical limitation, but the species can develop an extraordinary deep rooting system that can reach far into the deeper soil layers, thus accessing available soil water sources - an ability that could give this species an advantage to persist in an increasing struggle for water (Leitgeb and Reiter, 2009; Hartmann, 2011). On siliceous and heavy soils it can be more resistant to drought in the lowlands than Norway spruce (Diaci, 2011). It is likely to become more vulnerable to species loss in the eastern parts of Austria, but will likely be able to adapt to climate change under cooler forest-microclimate in suitable forests, which are able to cope with atmospheric droughts for a longer time of period.

(3) European larch (*Larix decidua*)

European larch is a typical alpine tree species of the higher elevations and might be at slight changes of temperature, still be suitable at the lower elevations (Falk *et al.*, 2012). This species strongly differs genetically within its provenances and is generally well adapted to warmer conditions. Where European larches' bioclimatic envelope exceeds mean annual temperature above 10°C, however, it might become quite vulnerable to climatic changes (Falk *et al.*, 2012; Kölling, 2007). This pioneer has a lower relative risk of species loss in basal area compared to Norway spruce, but reacts at its current forest distribution more sensitive to changes in temperature than silver fir and Scots pine. It is, however, also at risk in the low elevation forests of eastern Austria due to changing climate conditions.

(4) Scots pine (*Pinus sylvestris*)

Although Scots pine occurs widely in lower elevation areas, according to the results, it has the lowest risk to species loss and it is least sensitive to temperature as well as precipitation change among all ten tree species studied here. Therefore, this deep rooting species could play a key ecological role in climate change adaptation, particularly as it has been found to be one of the most stress-tolerant tree species regarding drought events previously (Leitgeb and Reiter, 2009; Jackson *et al.*, 1995; Roloff *et al.*, 2008). Due to its ability to cope with low precipitation rates and be resistant to drought periods, Scots pine is widely expected to be a tree species expanding its relative importance under

climate change (Niedermair *et al.*, 2007; Roloff *et al.*, 2008). Although it has the lowest risk to species loss, it is still sensitive to climate changes, particularly in the colline and submontane elevation belts of eastern Austria. The species Austrian Black pine (*Pinus nigra*) that is at its most northern natural distribution in Europe located in Lower Austria (Isajev *et al.*, 2004), could be a substitution in those areas. Its populations have survived untroubled in the lower valleys and whose today's natural distribution was shaped by the ice ages (Isajev *et al.*, 2004) and have after Kölling (2007), a much greater bioclimatic envelope, tolerating temperatures of up to 5°C more than Scots pine. Hence, Austrian Black pine is genetically well adapted to climate change and could be an asset for silviculture, when Scots pine will be out of its bioclimatic range (Isajev *et al.*, 2004, Kölling, 2007).

Broadleaved trees

(5) European beech (*Fagus sylvatica*)

Although found to be threatened by considerable area loss in eastern Austria, European beech is also expected to occupy new niches by migrating to higher elevation areas in the future (Niedermair *et al.*, 2007). Current European beech stands in the eastern parts of ecoregions 4 and 9 as well as in the north of ecoregion 5 appear to be most at risk from the analysis. As it is currently widely present along the Alpine rims in Austria, the species might successfully migrate to higher elevations under climate change. Due to it being the second most abundant species, it also has under the worst case scenario (c), the second highest absolute risk of species loss from all the species studied in this thesis. This finding is supported by a study by Hanewinkel *et al.* (2012), simulating tree species distribution for Europe until the 2100. Due to a climate-mediated succession in coniferous forest stands and a migration to higher elevation areas, at first hand, the share of European beech will likely increase for the short term within the next twenty years - but is then predicted to drastically decrease its distribution in the second half of this century due to increasing drought-stress, especially in the lower elevations (Hanewinkel *et al.*, 2012; Jandl *et al.*, 2012).

(6) Pendunculate oak (*Quercus robur*)

Judged by the relative risk of species loss, pendunculate oak - is besides hornbeam - the most threatened species considering its current location and ecophysiological sensitivity. It is the species that showed in both, relative- and absolute risk, a quite high risk of species loss. A large number of current oak stands at risk are located in the pannonic area (ecoregion 8), which is considered to be the driest region of Austria (Kilian *et al.*, 1994). Yet, pendunculate oak like silver fir has a tap-root system that can access reservoirs in deeper soil layers (Leitgeb and Reiter, 2009). In addition, this

species is quite drought tolerant and might be a favored tree species for the forestry sector in increasingly dry and warm parts of Austria (Seidl *et al.*, 2011). However, as shown by this study, extreme climate scenarios might in some areas also exceed ecophysiological limits for oak, and silvicultural measures such as admixture of endemic species such as Scots pine, field maple (*Acer campestre*), wild service tree (*Sorbus torminalis*) or other drought-adapted tree species might need to be considered (Kölling, 2012; Roloff *et al.*, 2008). According to Kölling (2012) and Kölling (2007), these latter two species showed a greater tolerance to higher temperatures than pendunculate- or sessile oak (*Quercus robur*). Therefore, they could be considered as admixed species on forest sites (mainly in pannonic area), where pendunculate oak might become more sensitive to temperature changes in the future. However, Kölling (2012) and Kölling (2007) also state that pendunculate oak, like European ash, is the species that is most capable to sustain low mean annual precipitation rates. Consequently, pendunculate oak and other drought-adapted oak species (*Quercus* spp.) are predicted to have an increasing trend in forest growth in Europe (Hanewinkel *et al.*, 2012). In Austria, this might be the case for today's colline and submontane areas currently occupied by Norway spruce and other species that will not be longer suitable in those areas in the second half of the century. Consequently, in those low-elevation areas where less drought tolerant species such as Norway spruce, European beech and silver fir still dominate, the propagation of pendunculate oak could be an option for adapting to climate change (Seidl *et al.*, 2011).

(7) Mountain maple (*Acer pseudoplatanus*)

As European beech, mountain maple is a species occurring mainly along the Alpine rims currently, and is a native species to Austria (Weidema and Buchwald, 2010), but also native to some higher elevation areas. The highest risk for current maple populations were found for the eastern part of ecoregion 4 and in the north of ecoregion 5. Mountain maple has a quite similar bioclimatic envelope as European beech (Kölling *et al.*, 2007) and has to realize its niche mainly in areas where beech occurs or can occur too, but thus is there also outperformed by the more dominant beech in warmer and less moist conditions (Schmidt, 2009). This is also supported by the results of this study, finding that mountain maple is more sensitive to temperature changes. In general, this species is known to have a quite good adaptation capacity to warmer and drier conditions, as its current distribution reaches southern and eastern Europe (Aas, 2009; Brosinger and Schmidt, 2009). It is thus expected to play an important role for stable mixed forests, especially in mountainous terrain (Brosinger and Schmidt, 2009).

(8) European ash (*Fraxinus excelsior*)

European ash has two realized niches of occurrence, either on wet soils close to river banks or on more dry and aerated soils with calcareous soil characteristics (Aas, 2002). It thus has a wide ecological amplitude with regard to water demand, which could be benefiting especially under changing climate conditions. This amplitude is not a genetic fixation, but rather a result of flexibility with regard to ecophysiological responses (Aas, 2002). Its current tree species distribution focuses on the Alpine rims, where its sensitivity is like for most other tree species more strongly driven by change in precipitation and water availability than by temperature. European ash might be a vital species in mixed forests along the Alpine rims, as it is expected to be more resilient and less vulnerable to biotic disturbances under increasing temperatures (Schmidt, 2007). European ash is, like pendunculate oak, a species with a high potential for forest management in the future, as it can resist longer drought periods (Scherrer *et al.*, 2011, Kölling, 2007).

(9) Hornbeam (*Carpinus betulus*)

Hornbeam was found to have the highest relative risk of species loss in this study, i.e. given its current distribution it is the species with the highest relative risk from climate change. As it basically occurs in close association with pendunculate oak, the same areas as for this latter species are of concern for hornbeam. These in particular are the drier eastern part of Austria and especially in the pannonic area. While in these regions the ecophysiological thresholds for hornbeam are exceeded in many climate scenarios, the species can endure high temperatures under a changing climate (Kölling, 2012) and might be, when admixed with pendunculate oak, silviculturally attractive on sites where Norway spruce is threatened from species loss. Although it is predicted to have the highest relative risk in this study, hornbeam was found to persist climate change in riparian areas and on heavy soils of warm and dry site conditions (Schmidt, 1996; Türk, 1996).

(10) Silver birch (*Betula pendula*)

This pioneer species is current distributed quite evenly over the Austrian forest area, even though it is relatively low in abundance and plays only a minor role in forestry (0.6% of total forest stock in Austria (BFW, 2013)). As a quite light-demanding broadleaved pioneer it generally occurs at a quite small realized niche at forest edges, but has a wide bioclimatic range and is able to colonize distributed areas quickly. Its ecological amplitude to suitable sites is very wide, ranging from quite wet sites to very dry sites, as long as enough light is available (Wegmann, 2009; Roloff *et al.*, 2008). Therefore, silver birch will not only play an important role as pioneer species after disturbances, but

might also play an important ecological role in forests that are exposed to higher frequency of summer droughts (Wegmann, 2009).

5.1.2 General trend for tree species in Austria

That increasing water limitations coupled with continuous temperature increases are problematic for many Austrian tree species, particularly in lower elevation areas, was previously reported by Lexer *et al.* (2002). The possible response mechanisms of trees to such changes are adaptation or migration (Jandl *et al.*, 2012). Many coniferous tree species that favor cooler conditions for growth are predicted to decline with climate change in this century and give space to thermophile broadleaved tree species (Hanewinkel *et al.*, 2012). Kapeller *et al.* (2012) states that favorable soil moisture conditions for Norway spruce in Austria have not yet reached the upper limits of the species' thresholds and Norway spruce currently still seems to tolerate the continuous increase in temperature. Tree species always have their own bioclimatic range due to their physiological thresholds and cope with stresses individually. Even though some Norway spruce populations, due to their provenances, are better adapted to drier climate conditions, Norway spruce will suffer from continuous temperature increase (Kapeller *et al.*, 2012; Schüller *et al.*, 2013). The results show that the risk of species loss due to declining precipitation declines combined with rising temperatures is particularly high for eastern Austria and Norway spruce (Ledermann and Kindermann, 2013; Schüller *et al.*, 2013). There, insufficient water supply and drought events will limit its growth and outweigh the positive effect of longer vegetation periods, higher photosynthetic activity or late- and early frost events.

Many major broadleaved tree species in Austria are also likely to face problems from climate change. Although many broadleaved tree species generally favor warmer climate conditions, some species might react more sensitively than drought tolerant oak or pine species (*Quercus/Pinus* spp.) to increased water stress (Jandl *et al.*, 2012), exceeding their thresholds and not being able to cope with extreme drought events. Like European ash and Scots pine, pendunculate oak is better adapted for warmer and drier conditions, outperforming other species with regard to its ecophysiological properties, as it can persist higher temperatures and recover rapidly after drought events (Scherrer *et al.*, 2011; Beck, 2010). European beech may face several problems from increasing temperatures or extreme rain fall, as it may suffer from drought at shallow soils with low water holding capacity, as well as at floodplains or soils with low drainage capacity (Gesler *et al.*, 2007). Also it is known to be affected by frost events, where milder winters reduce winter hardening in trees and increase sensitivity to early or late seasonal frost not only for European beech, but also for many other

broadleaf trees (Hänninen, 2006). European beech has the highest share of the broadleaf species in Austria and is expected to increase its range into higher elevation areas, but generally decrease its forest cover at the second half of the 21st century (Jandl *et al.*, 2012).

5.1.3 The role of diversity and PNV in the context of risk from climate change

“Forests that are located at the domain boundaries and in areas with limited dispersal capacity, stressed state, low diversity are the most vulnerable to climate change” (Roberts, 2008). Also forests stands of poor diversity that have a limited genetic pool at isolated patches on mountain tops are considered to have less resilience towards climatic variation (Roberts, 2008). Although species diversity plays an important role for stand stability, e.g. against disturbances such as insect outbreaks, it was not found to mitigate risk of species loss in this study, considering the current distribution of species and the ecophysiological limits. There was no evidence that plots with higher species diversity and evenness might have a lower risk of species loss when species are exposed to changing conditions. An explanation might be that more diverse stands are found in low elevation stands and eastern Austria, which are at the same time the areas that already now experience warmer and drier conditions and are thus likely to exceed their ecophysiological limits under climate change.

A related assumption is that the PNV would be more stable in the face of climate change than the current species distribution, which is strongly skewed towards susceptible species such as Norway spruce (Leitgeb *et al.*, 2013; Lexer *et al.*, 2001). If one examines the similarity of current forest composition with the PNV (Figure 1) and compares it to the spatial distribution of risk of species loss (Figure 7), one can see that that areas where the current distribution differs more strongly from the PNV have a higher risk of species loss than areas which have a higher congruence of the current species distribution with the PNV. Gschwanter and Prskawetz (2005) mentioned that 45% of the secondary Norway spruce forests in Austria are below a 500m elevation and are thus likely to be more susceptible to climate change. One can conclude that forests strongly differing from their natural vegetation range are at particular risk from climate change. This does not mean that forests that show congruence with the PNV are not at risk, but rather indicates that they might have a higher adaptation capacity and are less sensitive to climate change than those forests outside their PNV range. Consequently, it is suggested that secondary forest stands of coniferous tree species should be converted to more natural forest stands in order to better prepare forests for climate change (Gschwanter and Prskawetz, 2005).

5.2 Methodological issues

5.2.1 Climate data

As a reference for studying climatic changes, data on present climate from regional weather stations was essential for the investigation of the effects of possible changes in ecophysiological suitability of trees species. Firstly, this data was applied in the evaluation of TSM to see if simulation results under current climate would yield realistic results. Secondly, present climate data was used as baseline scenario for temperature and precipitation changes for the generic climate change scenarios used here. There were no climate change predictions from General Circulation Models (GCM) applied. Downscaling of climate change predictions from GCMs is a quite difficult matter, as the poor spatial resolution of GCMs allows high fidelity only at the continental scale (Matulla *et al.*, 2002; Strauss *et al.*, 2012). GCMs, for instance, do not consider the complex terrain of the Alps (Strauss *et al.*, 2012). Thus climate data are frequently downscaled to a finer spatial resolution for improved regional climate change predictions (MPI-M, 2006). But even RCMs are inflicted with uncertainties due to strong topographic gradients in mountainous regions, and prediction success can vary greatly between locations (Strauss *et al.*, 2012). For this analysis, generic climate scenarios relative to high resolution climate data for the recent past were defined, thus circumventing problems with scale in climate models. A further advantage of this approach was that these generic scenarios allowed to cover the full climate gradient of plausible changes for the future equally. When developing the climate scenarios, the focus was set on changes of annual means of the most important climate variables, i.e. seasonal values were considered to change equally in the scenarios. A major shortcoming of this approach is that only annual changes relative to the past observations were considered, while possible changes in the inter- and intra-annual variability were neglected. Analyses with inter- and intra-annual variability would require the use of climate model output, but could be insightful particularly with regard to tree species sensitivity to extreme events, such as summer droughts. Also, the scenarios analyzed here are not transient scenario of climate change, but rather test the sensitivity to possible future levels of climate change. It has also been noted that one cannot make a statement as to which of the climate scenarios is more plausible.

For the detailed analysis of hypotheses 2-4, the 35 combinations of temperature and precipitation changes were narrowed down to five scenarios. Here, the five bracketing scenarios at the lower and upper end of the scenario range were selected, i.e. scenario 1 (a), scenario 7 (c) and scenario 21 (e). Furthermore, the two scenarios 5 (b) and 19 (d) were selected at a 4°C temperature increase, as they conform what is currently considered realistic scenarios of temperature increase for the Alps until the end of the 21st century (Matulla, 2009; UBA, 2006; Roberts; 2008).

5.2.2 Model parameterization

Coops and Waring (2011) illustrated that the main drawback with mechanistic models is that detailed knowledge of a species is required in order to identify the physiological response of a species to climate variation in the model. Here, literature was collected to amend the dataset of previous TSM applications (Lexer and Seidl, in prep.; Steiner, 1998; Lexer, 2001; Jochheim *et al.*, 2009; Lyr, 1996; Hölscher *et al.*, 2005; Jochheim *et al.*, 2009; Polomski and Kuhn, 1998). The exact definition of the physiological amplitude of the tree species remains uncertain; however, as literature sources often report different values or classifications for particular parameters. For some energy-, water- and soil parameters of the ten tree species, no explicit quantitative values were found in the literature and descriptive data from phenomenological studies had to be used. If there was no existing data available, parameter values had to be determined by interpolation relative to well-defined species. While a process-based model might have advantages over purely statistical models, uncertainties with regard to species responses and thresholds remain.

5.2.3 Model evaluation

The independent evaluation of prediction success showed that TSM predictions generally conform to the currently observed tree species distribution as well as to the PNV. However, these evaluation data sets are presence-only data, limiting the evaluation exercise with regard to assessing the ability of the model to correctly predict species absence. In general, however, the evaluation results underline the utility of current calibration and model structure of the TSM for this study. However, the relatively small number (*n*) of inventory plots available for evaluation for some of the species has to be kept in mind when interpreting the results of the evaluation exercise. Nonetheless, the general pattern of all ten species in both evaluation data sets showed satisfactory success.

5.3 Considerations for further analyses

5.3.1 Realized niche - approaches

This study is a study on the fundamental niche of tree species considering only environmental factors on individual tree species that can limit the suitability of a species under changing climate conditions. Zimmermann and Kienast (1999) state that each species adapts and migrates to the changing climate individually, and that it is therefore preferable to simulate species individually under altered climate conditions. An alternative approach to the study here conducted would be to consider climate change effects in the context of the realized niche of species (Zimmermann and Kienast, 1999). Such

an approach was taken by Lexer and Hönninger (2001), where species composition of forests was simulated dynamically. Using a similar approach Lexer *et al.* (2002) PNV would be less threatened to species loss from climate change than under the current species distribution until 2050.

5.3.2 Adding disturbance and dispersal

In this study no aspects of changing disturbance regimes have been considered. However, a risk of increased summer drought, more heavy storms with extreme wind speed and biotic pests is widely expected for central Europe (Seidl *et al.*, 2011; Meier *et al.*, 2011; Lindner *et al.*, 2010). Especially at very dry site conditions, Norway spruce might be threatened from insects and forest pests (Seidl *et al.*, 2007; Kapeller *et al.*, 2012; Hoch, 2013). Since disturbances strongly facilitate species change, a combined analysis of the effects of ecophysiological stress and disturbances on tree species distribution might be of interest.

An appropriate model approach, called iLand (the individual-based landscape and disturbance model), was developed by Seidl including physiological parameters and disturbances in the modeling that would be suitable as an addition to this study conducted here. Here one could conduct an analysis of the synecology between the tree species after disturbances at their current tree species composition for Austria. This multifunctional model demonstrates how species would be composed after natural disturbance regimes and investigates how dispersal limitations of species affect species change when competing with each other during succession. The variables applied for regeneration analyses could consider the shade tolerance of each tree species, preferences for north or south orientation due to Austria's very heterogeneous topography, distance of seed dispersion to the mother tree or seed distribution to the mother tree. As we will experience more natural disturbances on a larger scale, the facilitation of a species to growth is more likely to occur by new established niches (Seidl *et al.*, 2011). There arises the question of the role disturbances towards a change in species composition and what would actually change when such events occur at vast changing areas to a larger extension. Where tree species of the current forest distribution might be due to climate change at higher risk of species loss in the future (cf. results), there could result a regime change of tree species for long term. Especially Norway spruce stands that show a high sensitive to changing climate variables and represent the dominant status of tree species in the Austrian Alps could be further investigated to see how their management in combination with disturbances is influenced.

As mentioned in the beginning, the model approach always depends on the aim of the study. The study of Zimmermann and Kienast (1999) demonstrated that both types of models, individual and

community approach, showed satisfying results in their respective domains. Nitschke and Innes (2008), for instance, give an example of successful application of a process-oriented niche model structurally similar to the one presented in the current study. They modeled the probability of presence or absence of species over a landscape by phenological and biophysical variables that control the establishment, growth or persistence of a tree species. Hence, such complementary approaches could be an additional consideration for further investigations and further extend the analysis of species sensitivity presented here.

5.4 Relevance of the study for forest ecosystem management

5.4.1 Adaptation capacity

Trees adapt to a changing climate with physiological acclimatization, changing their genetic properties is a result over longer period of time, and happens at the population level (Geburek, 2006). Populations only have the ability to increase their genetic adaptation capacity under a changing climate to some extent, which depends on the genetic variance of species (Geburek, 2006). Valladares (2008) states that on a global scale the more low-latitudinal populations are usually very important key species for evolution and survival of species in changing environments, as they carry highly diverse ecological features that differ from populations at other ranges. Generally, forest tree species are highly capable to acclimatize due to their high genetic traits that allow different breeds from different provenances to survive and grow at different sites apart from their origin (Geburek, 2006). They have the genetic ability to tolerate and resist stress situations, such as droughts (Geburek, 2006). Nitschke and Innes (2008) state that a species' niche can be used as a measure of its resilience to climate change; meaning that a species that is well within its fundamental niche is likely to be well able to adapt to climatic changes. Analogies can be drawn to the occurrence of Norway spruce that has been predicted to face risk in many northern and eastern parts of Austria. This species has high genetic diversity due to its high differentiations among population provenances (Kapeller *et al.*, 2012). Norway spruce populations have been survived during the ice age at the transition between Bohemian Massif and the northern pre-alpine area as well as in the Southeastern Alpine rims (Tollefsrud *et al.*, 2008; Schiessl *et al.*, 2010). One would consider that their propagation material has a high adaptation capacity to changing climate conditions, but on the other hand, Norway spruce has a quite different bioclimatic envelope than for example European black pine (Kölling, 2007). One can conclude that species with higher genetic diversity have a greater resilience to changing climate conditions (Geburek, 2006).

5.4.2 Uncertainties and species choice

The whole Greater Alpine Region (GAR) has to be prepared for increase of drought periods within the 21st century, whereas the east of Austria will have a much higher number of days without precipitation during the growing season (Schüler *et al.*, 2012). On regional, local as well as on site levels, large-scale climatic changes affect the vegetation cover and thus silvicultural decision making for the long-term (Leitgeb and Englisch, 2006). Managers and scientists have to recognize that the achieved level of certainty in scientific studies is due to incomplete knowledge often not attainable in practice of current forest management (Wiens, 2008; Wiens *et al.*, 2009) - and although there is an uncertain knowledge about the future, one still can use the available information to arrive at relevant decisions in forestry (Kölling, 2012). It is almost inevitable that Europe's forests will face negative effects of climate change. However, climate change and the sensitivity of tree species are still associated with uncertainties (Lindner *et al.*, 2010; Kölling, 2011). Forest managers have to be flexible and retain as many adaptation options as possible in order to being able to react to unexpected situations. Furthermore, climate change suggests increasing importance of risk spreading, for example, the admixture of more species for higher diversity to reduce impacts of climate change (Kölling, 2012). Recommendation for forest managers about knowledge of best provenances of tree species to forest sites that are highly exposed to changing climate conditions in Austria are limited, but locally and regionally information on adapted breeds is available (Geburek, 2006). Therefore, provenance research and tests for adaptation strategies, which is widely known in forestry in Europe, should be prospectively emphasized (Kölling, 2011; Geburek, 2006). Forestry has the task to adapt the current forests by converting forest sites of not very suitable species compositions gradually to more suitable species that could be silviculturally an option. The question addressed here, is which of the analyzed species is most likely viable to grow and survive in precipitation and temperature regimes of the future. Hence, this study helped to identify the degree of sensitivity of the ten most common tree species in Austria under a changing climate, in order to support silvicultural actions, particularly with regard to identifying adaptation priorities.

6 Conclusion

The master thesis addressed the sensitivity of Austria's tree species to climate change in a two-step analysis: First, the tree species sensitivity at species level and secondly, the risk of species loss at plot level. The analysis at species level showed that Norway spruce had in number of inventory plots the highest absolute risk to species loss. Hence, Norway spruce was found to be the species that is most sensitive to climatic change at its current forest distribution. On the other, hand hornbeam and pendunculate oak had the highest relative risk to species loss relative to the total number of inventory plots. Precipitation change had an overall greater importance for climate sensitivity of tree species than temperature changes. Only mountain maple, at sufficient water availability, responded more sensitive to changes in temperature. However, tree species sensitivity was basically driven by already slight changes in precipitation, which was increased drastically with coupled increase in temperature.

The results of risk of species loss at plot level indicated a high risk of species loss at the colline and submontane elevation zones below 700 meters elevation. There, species especially in the Bohemian Massif (ecoregion 9) and the pannonic area (ecoregion 8) were most threatened. The Eastern Alpine rim (ecoregion 5) had a moderately high risk compared to the previous two ecoregions. Whereas the Northern Alpine rim (ecoregion 4) and the northern pre-alpine area (ecoregion 7) showed a higher risk to species loss only under conditions of worst case scenario (c). This explains also the high relative risk of hornbeam and pendunculate oak, a high share of basal area at risk of these latter two species is located in the colline and submontane elevation areas, especially in the pannonic area. Also plots of Norway spruce were predicted to be at risk at these elevations, but especially in the Bohemian Massif. Yet, the assumption that species diversity and evenness would mitigate the risk to species loss could not be verified, as species diverse forests occurred mainly at those forest sites that were threatened to be at risk of species loss by climate change.

Tree species respond individually to climate changes, not only as an individual but also genetically as population. Conversion of current forest stands at risk, to more suitable species provenances are a potential means for forest management in order to keep pace with the unpredictable climate change.

7 References

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