Climate is one of the major drivers of plant and tree distribution, while soil variables or interspecific competition are often considered to be primary drivers of their local abundance, with the latter still debated (Meier et al. 2010, 2011, 2012). Climate making up the primary constraining factors on species ranges is generally accepted (Woodward 1987). The debate on climate change impacts on biodiversity and ecosystems is of great relevance to long-lived plants such as trees or shrubs, as these take many years to reach maturity and fecundity, and given their sessile growth strategy they are especially vulnerable to rapid changes in climatic conditions. Also, forest management plans usually span many decades, some extending to the end of the 21st century, highlighting the challenges to managing such organisms successfully for such long planning horizons. This calls for careful and adaptive management strategies and for a good understanding of the uncertainties related to the expected changes and their impacts on trees and forest ecosystems.

Many approaches exist to project the impact of climate change on trees and forests. Yet, most of the approaches either can be applied only to comparably small regions, to few species only, or they need to be run at very coarse spatial resolutions in order to enable coverage of larger spatial extents. Here we will describe five basic approaches, and list their major advantages and disadvantages. We then explain how we have used the last of these five approaches to project how species might respond in their habitat preference at the scale of the European Alps as a result of projected climate change. Other approaches exist and often they borrow from the five approaches described below:

(1) Biogeochemistry-driven dynamic vegetation models (DVMs) are very mechanistic with regards to physiological processes, and therefore represent growth and the fluxes of water, carbon (Sitch et al. 2003), and – in some cases – nitrogen very well (Thornton et al. 2002). Demography or structural details, interspecific competition or stochastic disturbances are handled less well (for an exception, see Hickler et al. 2012), and these models are most often operated at very coarse spatial resolution such as 10’ to 0.5° Latitude/Longitude cells, and are therefore not easily applicable to forest management. This model family does not usually...
distinguish between individual trees or cohorts, but rather biomass pools and the translocation of carbon and energy between pools.

(2) Population dynamic models of vegetation such as forest gap models (Bugmann 2001) represent a model family that is highly suited for forest management applications at a regional spatial scale. These models are process-oriented — although they lack the physiological processes of DVMs — and include significant demographic and structural details originating from the simulation of individual trees or cohorts, as well as simulate interspecific competition. Many of these models are not spatially explicit, and thus operate at a stand level. Few versions exist that are spatially explicit, and thus allow for regional assessment of management and climate change impacts. The model LandClim (Schumacher et al. 2006) is an example of such a spatially explicit forest dynamics model, while TreeMig (Lischke et al. 2006) is another. The latter additionally includes seed maturity and seed dispersal processes, as well as modelling the full regeneration processes that are often lacking in most other models. It therefore facilitates the simulation of natural tree migration in a landscape following climate change. The model can be run at a comparably fine spatial resolution; however, regions such as the Alps or Europe in its entirety cannot easily be simulated due to computational demand. While the forest gap models were the first such model type, new versions of such vegetation models incorporating other plant functional types are currently being developed. While stand structural details are often well simulated, NPP, LAI and other ecosystem properties are less well simulated.

(3) Demographic range models (DRMs; Schurr et al. 2012) operate in a similar fashion as population dynamic models in that they also simulate the demography of species. They do so in a spatially explicit manner, but they lack inter-specific competition, and only model one species at a time. This model type is thus best suited to dominant species. Habitat suitability is taken from species distribution models (see the fifth model family below), while demographic processes and spatial migration is modelled explicitly. These models can be applied to larger spatial scales, but are moderately demanding in calibrating new species, as the models are very data hungry.

(4) Phenological (partly physiological) models such as PhenoFit (Chuine & Beaubien 2001, Chuine 2010) and conceptually similar models (Huey et al.) attempt to calibrate those processes that directly affect — and moreover — constrain the demographic processes and life history, such as leaf unfolding, seed maturity, juvenile survival, etc. Such models have been designed to calibrate significant elements of the fundamental niche (Hutchinson 1957), while interspecific competition or demographic processes are not modelled. This model family can easily be applied to large spatial extents, but the calibration is very demanding for each species, resulting in very few tree species having been calibrated to date.

(5) Species distribution models (SDMs) are a simple but very efficient statistics-based method to map the spatial range of species and to project climate change impacts on species ranges (Zimmermann et al. 2010). The method is mature from a statistical and conceptual perspective (Guisan & Thuiller 2005, Elith et al. 2006), and it is used for many different purposes including conservation management, theory testing in biogeography and ecology, species management, and climate change impact assessment (Guisan & Zimmermann 2000). The method is based on calibrating statistical relationships between the observed spatial distribution and climate and other spatial predictor variables. Sampling design is therefore very important, and the fitted spatial patterns represent the realized, not the fundamental niche. The method does not include processes or details on transient responses following change; neither does it provide structural information. This method simply — but efficiently —
provides an assessment of the suitability of any region for a species under current or projected future climate, and under the assumption that roughly the same species are available as potential competitors. SDMs are thus often used to assess whether a given species has a future in a specific region or not, while the question of whether it can reach a certain region and how long it would take a species to get there are not handled by this method. SDMs, therefore, are best suited to assess habitat suitability and whether certain management options concerning species preference/selection are likely sustainable in the long run.

In the following paragraphs, we present the SDM simulations performed, often also termed climate envelope models (CEM), for major tree species of the European Alps in order to assess the consequences of climate change on the habitat suitability of these tree species. We used presence/absence information from forest inventories of France (Alps only), Northern Italy, Austria, Southern Germany Slovenia and Switzerland in order to build a database of tree species presences and absences across the Alps. We compiled data for ca. 50 tree species for a total of >80 000 inventory plots, although some countries did not distinguish all species at the same taxonomic level (i.e. some countries did not distinguish between different oak and maple species). We then compiled a series of climate maps under current and potential future climate from downscaled RCM models for future climates. Additionally, we compiled some topographic variables that may influence the spatial patterns of trees. Finally, we used the following variables as predictors of species distribution in our models: (1) degree days with a 5.5°C threshold, (2) temperature seasonality (standard deviation of monthly values), (3) summer precipitation (sum of April to September monthly values), (4) winter precipitation (October to March), (5) potential yearly global radiation, (6) slope angle (in degree), (7) topographic position (difference between the average elevation in a circular moving window applied to a 100m digital elevation model and the centre cell of the window (Zimmermann et al. 2007), (8) aspect value (ranging from 0(south) to 100(north), and (9) distance to flowing water.

Potential future climate was taken from six different RCMs (see previous chapter), providing a range of potential climate futures. The use of several RCM models is meant to provide the mean trend that can be expected from climate change impacts on trees balanced with some measure of uncertainty associated with the projection of these trends (Araujo & New 2007, Thuiller et al. 2009). Several statistical models were used, since the choice of a statistical model has been shown to significantly contribute to uncertainty in projections (Buisson et al. 2010). More specifically, we used the following statistical models: (1) Classification and regression trees (CART), (2) Flexible discriminant analysis (FDA), (3) Generalized linear models (GLM), (4) Generalized additive models (GAM), (5) Artificial neural networks (ANN), and (6) Generalized boosted regression trees (GBM). Using six statistical models along with six future climate model runs, we modelled 36 different possible futures per species and time slice. This facilitates a reduction in uncertainty by including both the variability in climate models and the variability originating from the choice of statistical methods.

We optimized each statistical model following procedures described in Thuiller et al. (2003, 2009) and where feasible, we maximized kappa to select thresholds to split probabilistic projections of species presence into simulated presence and absence values. We then produced one presence/absence map per climate model/statistical model combination available. Following, we built ensembles of these model projections and classified them as follows: (1) a species is unlikely to find a suitable habitat if less than 30% of the projections indicated presence of a species; (2) a species is moderately likely, associated with high uncertainty, if 30-60% of the projections suggested that the species is there; (3) a species is
most likely present, with rather low uncertainty, under projected climates if in >60% of the 36 model projections presence of a species is simulated. This simple classification avoids an over-interpretation of the results from the simple model approach used.

Figure 3 illustrates the potential future range shift in two species *Fagus sylvatica* L. (European beech) and *Picea abies* (L.) Karst. (Norway spruce) in eight panels, indicating the areas that are suitable for the two species under current and future climate conditions in three different time steps towards the end of the 21st century. Both species are expected to lose much terrain at low altitudes, and will retract to higher altitudes following climate change. Currently, Norway spruce is planted at lower altitudes than it occurs naturally. These lower altitudes are still within the fundamental niche of the species, which is taken into consideration in the simulated maps; the maps also capture the extended range of the species to lower altitudes under both current and future climates. However, compared to beech, it extends to higher altitudes, reaching treeline in many parts of the Alps. This is specifically visible for the simulations for the 2051-2080 time period where occurrences of Norway spruce are projected to be at visibly higher elevations than those suitable for beech. Larger areas at lower altitudes become unsuitable for both species in the future, while the habitat suitability in large areas in Southern Germany is projected to be highly uncertain for both species. This uncertainty arises from highly contradicting projections on the part of both climate and SDM model combinations.
Figure 1: Projected future habitat suitability from ensemble SDM modeling of Fagus sylvatica and Picea abies for current and projected future climate in three time periods. Dark red colors represent high confidence of agreement of high habitat suitability from all six statistical and six climate models, while orange colors indicate high uncertainty in projected habitat suitability per time period.
More than 50 tree species possibility of occurrence have been simulated for the Alpine region, while only two species are displayed here. A more complete set of species data can be viewed at the following link: http://www.wsl.ch/lud/motive. From our results, it becomes evident that species with a higher drought tolerance, such as *Quercus petraea* and *Quercus pubescens* can be expected to become more abundant at lower altitudes throughout the Alps, while other species such as *Acer pseudoplatanus*, *Tilia spp.*, *Ulmus spp.* or *Abies alba* are likely to further reduce their ranges in a manner similar to beech and spruce. Species from (Sub-) Mediterranean regions such as *Quercus ilex*, *Ostrya carpinifolia* or *Q. suber* are expected to extend their ranges to the North, but these species will not reach the areas of formerly suitable for beech by the end of the 21st century. Several pine species are also expected to extend their ranges quite considerably. However, they will be unlikely to extend their ranges to very fertile soils either, and some of the species such as *P. sylvestris* could face indirect threats through insects and other pests, rather than direct threats from climate change alone.

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

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