





# Stand-scale climate change impacts on forests over large areas: transient responses and projection uncertainties

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**Abstract.** The increasing impacts of climate change on forest ecosystems have triggered multiple model-based impact assessments for the future, which typically focused either on a small number of stand-scale case studies or on large scale analyses (i.e., continental to global). Therefore, substantial uncertainty remains regarding the local impacts over large areas (i.e., regions to countries), which is particularly problematic for forest management. We provide a comprehensive, high-resolution assessment of the climate change sensitivity of managed Swiss forests (~10,000 km<sup>2</sup>), which cover a wide range of environmental conditions. We used a dynamic vegetation model to project the development of typical forest stands derived from a stratification of the Third National Forest Inventory until the end of the 22nd century. Two types of simulations were conducted: one limited to using the extant local species, the other enabling immigration of potentially more climate-adapted species. Moreover, to assess the robustness of our projections, we quantified and decomposed the uncertainty in model projections resulting from the following sources: (1) climate change scenarios, (2) local site conditions, and (3) the dynamic vegetation model itself (i.e., represented by a set of model versions), an aspect hitherto rarely taken into account. The simulations showed substantial changes in basal area and species composition, with dissimilar sensitivity to climate change across and within elevation zones. Higher-elevation stands generally profited from increased temperature, but soil conditions strongly modulated this response. Low-elevation stands were increasingly subject to drought, with strong negative impacts on forest growth. Furthermore, current stand structure had a strong effect on the simulated response. The admixture of drought-tolerant species was found advisable across all elevations to mitigate future adverse climate-induced effects. The largest uncertainty in model projections was associated with climate change scenarios. Uncertainty induced by the model version was generally largest where overall simulated climate change impacts were small, thus corroborating the utility of the model for making projections into the future. Yet, the large influence of both site conditions and the model version on some of the projections indicates that uncertainty sources other than climate change scenarios need to be considered in climate change impact assessments.

*Key words:* adaptation; dynamic vegetation model; ForClim; forest gap model; forest model; management; mountain forest; species composition; Switzerland; tipping point; uncertainty.

## INTRODUCTION

Forest ecosystems and their sustainable management are of key importance for the provisioning of a broad range of ecosystem services such as biogeochemical cycling, terrestrial biodiversity, timber and food production, recreation and tourism, or protection from soil

erosion, rockfall, and snow avalanches (FAO 2010). Yet, changing temperature and precipitation patterns resulting from anthropogenic climate change and increased disturbance frequency and severity have already started reshaping forest ecosystems (Seidl et al. 2017a, Henne et al. 2018), i.e., by changes in stand productivity (Charru et al. 2010, Pretzsch et al. 2014), drought-induced tree mortality (Allen et al. 2010, Peng et al. 2011, Senf et al. 2018) or species range shifts (Walther 2003, Iversen and McKenzie 2013), and thus affecting the manifold ecosystem services they provide (Schröter et al.

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2005, Elkin et al. 2013). In the coming decades, the impacts of climate change are expected to strongly alter the species composition (Gonzalez et al. 2010, Hanewinkel et al. 2013, Clark et al. 2016), structure (Elkin et al. 2013, Clark et al. 2016) and productivity (Boisvenue and Running 2006, Gauthier et al. 2014) of today's forests.

Across large spatial extents, a number of consistent trends to global warming have been identified by empirical and model-based studies (IPCC 2019). First, greatest changes in productivity and biomass are expected for forests currently limited by water availability or low temperature (Bugmann et al. 2015, Mathys et al. 2017, Brecka et al. 2018). In Europe, for example, climate-induced negative impacts on forest productivity will thus occur predominantly at low elevations and in southern and continental areas, whereas temperature-limited forests at high elevations and latitudes are expected to feature increased productivity and biomass (Lindner et al. 2010, Hartl-Meier et al. 2014, Reyer et al. 2014, Schelhaas et al. 2015, Morin et al. 2018). Second, tree species are expected to shift their distributions poleward in latitude and upward in elevation, while being replaced by more drought- and warmth-adapted species at their low latitude and elevation range limit (Lexer et al. 2002, Walther et al. 2002, Peñuelas and Boada 2003, Morin et al. 2008, Hanewinkel et al. 2013, Takolander et al. 2019).

Yet, at the local to regional scale, factors other than general climatic trends strongly affect forest dynamics, thus likely resulting in more complex and heterogeneous transient responses of forests in time and space. Most importantly, topography can cause substantial regional and local climatic variation (CH 2000 2011, Engler et al. 2011) impacting forest dynamics (Johnstone et al. 2010). Furthermore, current stand structure and species composition, which is strongly influenced by past management legacies (Bürgi et al. 2013) and disturbances (Janda et al. 2019), determine the future development of these forests at the local scale, at least in the short- to mid-term (Pretzsch 2009, Ruiz-Benito et al. 2013, De Cáceres et al. 2015, Etzold et al. 2019). In addition, species interactions influence both species productivity (Mette et al. 2013, Forrester et al. 2017) and distributions (Bullock et al. 2000, Takolander et al. 2019) and may hamper the immigration of other species at a given site (Walther 2010, Takolander et al. 2019). Finally, soil properties contribute to differences in local and stand-specific growth patterns (De Cáceres et al. 2015) and tree species distributions (Walther and Meier 2017).

However, as most previous climate impact projections of change in forest structure and composition have either focused on a few sites only (e.g., Lasch et al. 2002, Hlásny et al. 2014, Mina et al. 2017a) or adopted a purely climate-based approach when conducting large-scale analyses (i.e., continental to global level; e.g., Hickler et al. 2012, Hanewinkel et al. 2013), substantial uncertainty remains regarding the complex local

responses over larger areas (i.e., regions to countries; Millar et al. 2007, Reyer et al. 2015). Even though some regional-scale studies do account for factors other than general climatic trends (e.g., Elkin et al. 2013, Xiao et al. 2017, Schuler et al. 2019), only few studies are based on actual stand structure and species composition (e.g., Temperli et al. 2013, Maroschek et al. 2015, Thom et al. 2017a). Current stand structure and composition are however strongly determining future forest response to climate change (e.g., Etzold et al. 2019), and thus highly relevant for forest management and planning in view of climate change adaptation (Lindner et al. 2014). Therefore, decision makers still lack essential knowledge at the level that is relevant for forest planning and management with regard to (1) the possible implications of climate change, especially concerning the fate of the extant species and the potential of substitute species that may arise due to migration or planting and (2) the temporal aspects of these changes.

In this context, forest gap models (FGMs) are suitable tools to project and assess the transient response of forests with a high level of detail (Snell et al. 2014, Larocque et al. 2016), as they simulate the regeneration, growth and mortality of individual trees or cohorts on small patches considering abiotic (e.g., climate) and biotic factors (e.g., competition; Bugmann 2001). Thus, they account not only for climate-induced direct effects, but also for indirect effects through changes in interspecific competition at the local scale (Snell et al. 2014). Hence, these models provide a suitable framework for exploring forest dynamics across elevation gradients (e.g., Shuman et al. 2014, Foster et al. 2016, Fyllas et al. 2017). Moreover, these models consider small-scale forest stand characteristics (Lindner et al. 1997), incorporate management functions (Rasche et al. 2011) and account for small-scale factors such as topography or soil properties (Shugart et al. 2018).

Yet, considerable uncertainty is inherent in the projections of FGMs (e.g., Bugmann et al. 2019) that originates from various sources. In the context of climate change impact assessments, typical sources of uncertainty include future greenhouse gas emissions (IPCC 2019), climate change projections (Knutti and Sedláček 2012, Lehner et al. 2020), uncertainties in climate input data (Wu et al. 2017, Snell et al. 2018), in the model structure and parameterization (e.g., Hlásny et al. 2014, Reyer et al. 2016, Snell et al. 2018, Bugmann et al. 2019), or in the societal demands for ecosystem goods and services (Alberdi Asensio et al. 2015, Fronzek et al. 2019). Although it has been emphasized that model projections should explore uncertainty ranges (Matott et al. 2009, Augusiak et al. 2014, Lindner et al. 2014), impact studies typically focus on the uncertainties arising from the choice of the climate change scenario alone (e.g., Fyllas and Troumbis 2009, Manusch et al. 2014) or compare projections across different models (e.g., Nishina et al. 2015, Ito et al. 2017). Hence, few climate change

impact studies for forests have simultaneously accounted for uncertainties arising from different sources and decomposed them systematically (but see Horemans et al. 2016, Kallikokoski et al. 2018).

The aim of this study was to analyze the transient response of forests to climate change, at a scale relevant to forest management planning, while considering relevant uncertainty sources. We used ForClim, a state-of-the-art FGM that has been evaluated under a wide range of environmental conditions in Europe (e.g., Rasche et al. 2011, Mina et al. 2017b). Recent studies have systematically assessed the model's parameter (Huber et al. 2018) and structural (Huber et al. 2020) sensitivity for a broad range of applications (e.g., for long- and short-term simulations, managed and unmanaged as well as monospecific and mixed-species stands). These studies revealed that ForClim is particularly sensitive to assumptions regarding climate, soil conditions and the three core processes establishment, growth and mortality (Huber et al. 2018, Huber et al. 2020), all of which are thus relevant uncertainty sources to consider in simulation studies.

To assess the climate sensitivity of actual forests, we projected the development, until the end of the next century (i.e., 2200 AD), of 71 stands typical of Swiss forests in terms of stand structure and species composition that were derived from a stratification (Bircher 2015) of the Third Swiss National Forest Inventory (Keller 2011). Switzerland was selected as study region because it features a large elevation gradient resulting in a high diversity of forest ecosystems ranging from Mediterranean-type Scots-pine-oak forests to temperate spruce-fir-beech forest and subalpinelarch-Stone-pine forests (Frehner et al. 2005, Bircher 2015), thus covering a bioclimatic gradient representative for large parts of Europe. To investigate the effect of the enrichment of the local species pools (e.g., species' upward shifts in mountain forests due to natural dispersal or to plantation), two types of simulations were run, where one was limited to using the extant local species of the typical stands, whereas the other considered immigration. Finally, to assess the robustness of our model projections, we quantified and decomposed the uncertainty in projected stand basal area (BA) resulting from three downscaled climate change scenarios, two assumptions about local soil conditions, and eight FGM versions featuring different ecological assumptions regarding establishment, growth and mortality. Thereby, the eight model versions account for the uncertainty of different processes within *one* single model, an aspect rarely taken into account in FGMs.

In particular, we addressed the following questions: (1) Which stands are expected to be subject to adverse impacts of climate change? (2) Can adverse impacts be mitigated by enriching the local species pool? (3) How large are the uncertainties in model projections resulting from the choice of the climate change scenario, of the local soil conditions, and of the FGM version?

## METHODS

### *The ForClim model*

ForClim is a climate-sensitive FGM that simulates the establishment, growth and mortality of trees at yearly time steps based on biotic and abiotic conditions (Bugmann 1996). To project the development of a forest stand, the simulations of  $n$  independent forest patches (usually  $n = 200$  and patch size = 500–1,000 m<sup>2</sup>) are aggregated to account for stochasticity in tree establishment and mortality as well as site conditions (i.e., weather conditions or stand properties; Bugmann 1996, 1997). The model is parameterized for >30 central European tree species that establish as saplings with an average dbh (diameter at breast height) of 1.27 cm. A random experiment determines whether establishment occurs in a given year based on a site-specific establishment probability parameter (Huber et al. 2020). If establishment takes place, the overall number of new saplings is deduced from site and stand characteristics and subsequently distributed across the species that passed several species-specific requirements (referred to as establishment flags EFs; Huber et al. 2020). The following EFs are considered: available light at the forest floor, soil moisture, winter temperature, growing-season degree-days, and browsing (Bugmann 1996, Risch et al. 2005, Didion et al. 2009).

ForClim's tree growth equation is based on a modified version of the carbon budget model by Moore (1989), where annual growth is derived by reducing optimum growth according to morphological (crown length) and environmental constraints, i.e., available light, soil moisture, growing-season degree-days, and soil nitrogen (Bugmann 1996, Didion et al. 2009). Annual growth is allocated to diameter and height growth taking account of competition and site-specific climatic conditions (Bugmann 1996, Rasche et al. 2012).

Individual-tree mortality is modeled as a stochastic process derived from the combination of three mortality rates: background, stress-induced, and disturbance-related mortality. The "background" mortality accounts for processes not considered explicitly in the model, such as individual tree death due to small-scale disturbances (e.g., lightning or fungal attacks; Bugmann 1994). The stress-induced mortality is acting when annual diameter increment falls below an absolute or relative minimum for at least three consecutive years (Solomon 1986, Bircher et al. 2015). The disturbance-related mortality (exogenous mortality) represents major landscape-level disturbances such as fire or pest outbreaks (Busing and Solomon 2005). In addition, management interventions can be simulated explicitly by applying a wide range of planting, cutting, and thinning techniques (Rasche et al. 2011).

For each forest patch, a stochastic weather generator derives random series of weather data from observed or projected monthly long-term characteristics of

temperature and precipitation (Bugmann 1996). Based on these weather series, bioclimatic indices, i.e., minimum winter temperature and degree-days, and drought indices are derived. The latter are calculated from a modified version of the monthly soil water balance model by Thornthwaite and Mather (1957) with one soil layer and a snow accumulation-and-melt module (Bugmann and Cramer 1998, Bugmann and Solomon 2000, McCabe and Wolock 2009). For evergreen species, the monthly drought indices are aggregated to an annual drought index, while for deciduous trees, the monthly indices are aggregated to a seasonal drought index by considering all months between April and October with a mean monthly temperature exceeding 5.5°C (Bugmann and Solomon 2000). In combination with the species-specific drought tolerance parameter (Appendix S1: Table S1), these drought indices were used to simulate species-specific drought responses with regard to establishment and growth (Bugmann 1996).

We used ForClim v4.0.1, which corresponds to ForClim v4.0 (Huber et al. 2020) but includes a revised snow-melt function (Huber et al. 2019) and revised species-specific parameters (Appendix S1: Table S1).

#### Forest strata

A large elevation gradient inducing strong ecological differences is the main feature of Swiss forests (Frehner et al. 2005, Rigling and Schaffer 2015, Fig. 1). At low

elevations, European beech (*Fagus sylvatica*) represents the naturally dominant species in the sub- and low montane elevation zone. In the superjacent upper montane elevation zone, beech co-dominates with silver fir (*Abies alba*), and is gradually replaced by Norway spruce (*Picea abies*) in the high montane elevation zone (Brändli 2010). The subalpine elevation zone is mainly stocked by Norway spruce, while European larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) are the prevailing tree species in the upper subalpine zone (Frehner et al. 2005). Due to past management practices, Norway spruce is also widespread in the lowland regions of the Northern Alps (Bürgi and Schuler 2003). Furthermore, in the Southern part of Switzerland, sweet chestnut (*Castanea sativa*) is an abundant species due to traditional chestnut cultivation (Conedera et al. 2010).

To study the future development of typical forest stands in Switzerland across these elevation zones (Fig. 1), we used the 71 strata derived from 6,838 forested plots of the Third Swiss National Forest Inventory (NFI; Keller 2011) by Bircher (2015). For this stratification, the forested NFI plots were first grouped into eco-regions and elevation zones (Frehner et al. 2005) and subsequently segregated according to their vertical stand structure and developmental stage (Bircher 2015). Thus, these strata are representative stands in terms of structure and tree species composition for the particular eco-region and elevation zone (Bircher 2015, Appendix S1: Table S3).

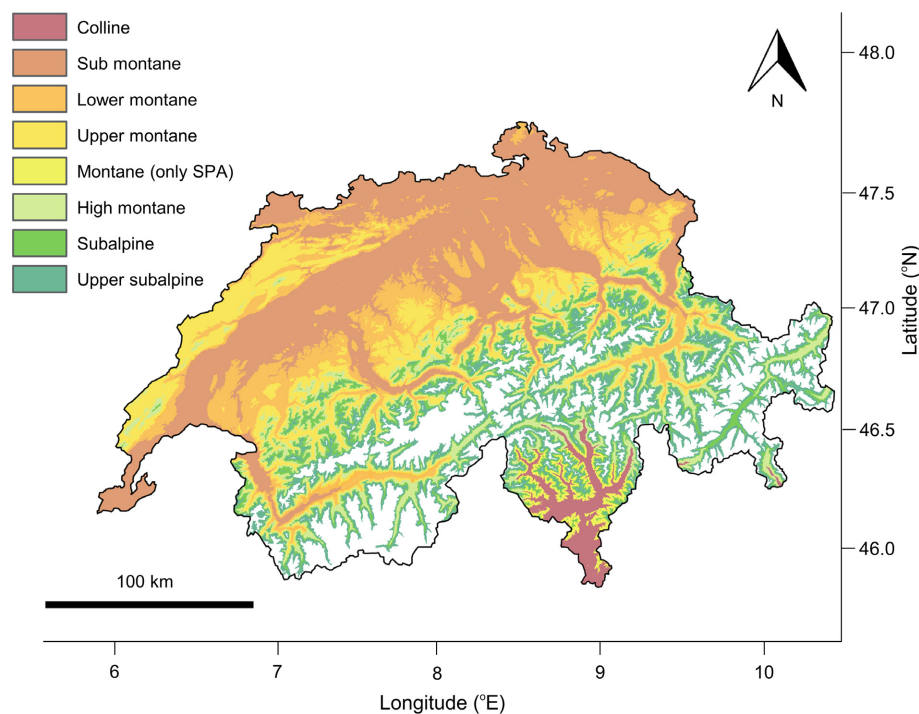


FIG. 1. Elevation zones of Switzerland (modified from Bircher 2015). White patches represent areas beyond the upper tree line. SPA, Southern Pre-Alps.

To assess the future development of these strata, the model was initialized for the year 2006 with the single-tree data of the stratification by Bircher (2015). For each stratum, the model was run for 200 forest patches, whereby each of these patches was initialized with the inventory data of one associated NFI plot. Using this approach reduces the influence of the initialization as well as the stochastic processes (e.g., mortality) on model outputs (Bugmann 1997, Wehrli et al. 2005). Further, a slope and aspect correction factor (kSIAsp) was considered in the simulations to account for topographic effects on potential evapotranspiration (Bugmann and Cramer 1998). We used the most frequent values of slope and aspect of the associated NFI plots for each stratum.

#### *Forest management*

Management interventions were defined to reproduce “best practice” management in Switzerland (Bircher 2015) per elevation zone and stand type (i.e., even-aged vs. uneven-aged). Even-aged stands were thinned and harvested from above (Rasche et al. 2011; further details are provided in Appendix S1). Uneven-aged stands were managed in two different ways depending on elevation. For strata located at high elevations (i.e., within or above the high-montane elevation zone), a mountain forest plentering was applied (group selection; cf. Thrippleton et al. 2020a). At lower elevations, uneven-aged strata were managed according to an individual tree plentering (single-tree selection; Rasche et al. 2011). The management interventions were applied to all tree species present on a forest patch. All simulations assumed natural regeneration, thus no planting was simulated. Major landscape-level disturbances were not considered.

To assess whether adverse climate impacts can be mitigated by enriching the local species pool, we ran two types of simulations, i.e., “base species pool” (BP) and “immigration” (IM). For the BP simulations, the local species pool was restricted to the “extant species” of the respective stratum, i.e., all species that contributed at

least 5% to stand BA in 2006 (Appendix S1: Table S3). This allows focusing on the fate of the individual strata, especially with regard to the response of the individual tree species, without potentially confounding effects arising from a possible replacement of the already present “extant species” by other immigrant species. To analyze the latter, we allowed the establishment of all parameterized central European species in the IM simulations (in addition to the extant species) after a lag phase of 50 yr, to account for the fact that immigrant species need to become available locally, i.e., in a given stand. This can be either due to upward natural migration with climate change, or due to changing management strategies such as fostering of nearby seed trees or active planting (assisted migration). Both extant and immigrant species establish as saplings only if the species-specific abiotic and biotic requirements are fulfilled.

#### *Sensitivity to selected sources of uncertainty*

In addition, we assessed the uncertainties in model projections due to the following sources of uncertainty: climate change scenarios, local soil conditions and model assumptions. These uncertainty sources do not cover the whole range of uncertainty inherent in model projections, yet they were selected based on insights from recent ForClim-related studies (Huber et al. 2018, 2020) in order to focus on the most relevant sources of uncertainty for the questions addressed in this study. Specifically, the model versions used here represent a subset of those evaluated in detail by Huber et al. (2020). Hence, we ran simulations for historic climate and three downscaled climate change scenarios, two soil types, and eight model versions featuring different ecological assumptions regarding establishment, growth, and mortality (Table 1).

*Historic climate and climate change scenarios.*—For the historic climate, we used data for the reference period 1980 to 2009. For each stratum, we used long-term monthly mean temperatures and precipitation sums as

TABLE 1. Overview of the simulation runs per stratum.

Characteristic and levels	Abbreviation	No. simulations	Further details
Local species pool		2	Appendix S1: Table S3
Base species pool	BP		
Immigration	IM		
Climate		4	Fig. 2
Historic climate	Hist		
Three CC scenarios	A2.1, A2.2, A2.3		
Soil type		2	Appendix S1: Table S3
Rich soil	R		
Poor soil	P		
Model version		8	Appendix S1: Table S2
Different process formulations	11–14; 21–24		

well as the respective standard deviations and cross-correlations from spatially interpolated weather data (Remund et al. 2016; provided by the Federal Office of Meteorology and Climatology MeteoSwiss) of all associated NFI plots (Bircher 2015). For the climate change simulations, we used the emission scenario A2, anticipating strong increases of global greenhouse gas emissions (CH2011 2011). The CH2011 climate scenarios provide seasonal estimates (lower, medium and upper estimates) of temperature and precipitation changes derived from several global and regional climate models (van der Linden and Mitchell 2009) for three future 30-yr periods. Spatially aggregated estimates are available for five regions (Zubler et al. 2014). We applied the delta change method to derive monthly mean temperatures and precipitation sums over time, i.e., by linearly interpolating the differences between the values of the historic climate and the estimates of the central years of the three 30-yr periods. To account for the uncertainty inherent in the climate change projections of the A2 scenario, we applied three combinations of the seasonal lower, medium and upper estimates of temperature and precipitation change, resulting in three climate change (CC) scenarios (A2.1–A2.3, Fig. 2 and Appendix S1: Fig. S1). In spite of being based on one single emission scenario, these combinations span a very wide range of possible outcomes of future climate and consider positive inter-seasonal relationships for temperatures and a negative temperature–precipitation relationship during summer (Fischer et al. 2016).

**Local soil conditions.**—For each stratum, soil water holding capacity (WHC, cm) and available nitrogen ( $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ ) were derived (Appendix S1: Table S3). Since estimating WHC is a major challenge for all large-scale applications of vegetation models (De Cáceres et al. 2015) and ForClim outputs have been shown to be highly sensitive to this parameter (Huber et al. 2018), we derived two values per stratum

representing rather deep and shallow soils, respectively. For the former, WHC was derived from spatially explicit METEOTEST data (Bircher 2015). For the latter, these values were reduced depending on elevation (Schwörer et al. 2014, Wohlgemuth and Moser 2018), i.e., by 50% for the highest elevation zones (subalpine and upper subalpine) and by 25% for the other zones. Due to the lack of site information on available nitrogen, this parameter was varied in concert with WHC, with values ranging from 40 to  $100 \text{ kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ , resulting in two soil types (i.e., rich and poor).

**Model versions.**—Two recent studies systematically assessed the behavior and parameter sensitivity (ForClim v3.3; Huber et al. 2018) as well as the representation of ForClim’s core processes (ForClim v4.0; Huber et al. 2020). Both analyses were conducted over a wide gradient of ecological conditions in Europe and highlighted the sensitivity of model projections to assumptions regarding regeneration, growth, and mortality. In particular, assumptions on sapling densities have shown to be of key importance for model output but are associated with high uncertainty (Huber et al. 2018, 2020). Moreover, there is considerable uncertainty with a large influence on model projections regarding the formulations of mortality and of the allocation of volume increment to height vs. diameter growth (see also Rasche et al. 2012, Hülsmann et al. 2018, Bugmann et al. 2019, Thrippleton et al. 2020b). Hence, we applied eight model versions (Appendix S1: Table S2) that represent a factorial combination of different formulations introduced by Huber et al. (2020) with respect to the establishment probability, the allocation to height vs. diameter growth, and the background mortality. With these model versions, we account for uncertainties in the model formulations but do not provide a parameter uncertainty analysis, where parameters are varied within their ranges of uncertainty (as e.g., done by Reyer et al. 2016; but see

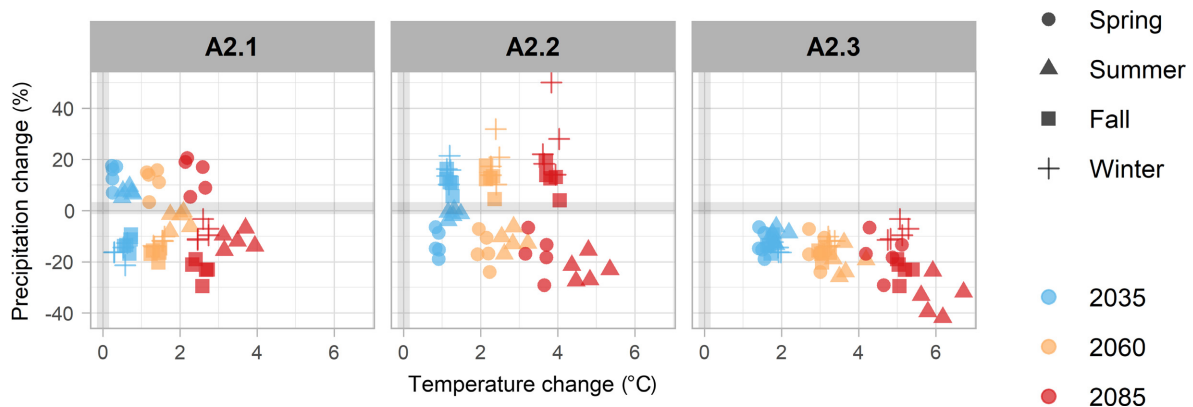


FIG. 2. Climate change delta values for temperature and precipitation for the three climate change scenarios (A2.1–A2.3) based on an A2 emission scenario (CH2011 2011) for the five regions of Switzerland relative to the reference period 1980–2009. For details on the region-specific values, see Appendix S1: Fig. S1.

Huber et al. 2018). More details of the model formulations are provided in Appendix S1.

### Analysis

We compared stand BA, harvested BA and species composition projected for the three CC scenarios to the “reference” projections, i.e., the projections obtained under the historic climate of the reference period 1980–2009. Since residual stand BA and harvested BA were strongly correlated (Appendix S2: Fig. S1), we focus on residual stand BA (Data S1 and Data S2). Due to the large number of simulations (128 per stratum, see Table 1), results are presented for one particular model version (i.e., model version 22, Appendix S1: Table S2), which has been evaluated and shown to provide accurate results when applied to a wide range of situations (Isler 2019, Huber et al. 2020, Thrippleton et al. 2020b). In addition, we assessed the robustness of the projected BA changes across the eight model versions by estimating the inter-model variability of the responses for the different forest strata under different climatic and site conditions (i.e., standard deviation of the share of strata falling into a given impact category; for details, see caption of Appendix S2: Fig. S19).

To investigate the role of potential explanatory variables for the relative change in stand BA caused by CC, we applied linear mixed effects models. Models were fitted separately for BP and IM simulations with the R package nlme (Pinheiro et al. 2018). Explanatory variables included as fixed effects were the stratum-specific WHC, kSIAsp, elevation, the number of species at initialization, and BA at initialization. Further, we considered the initial shares of European beech, Norway spruce, and silver fir. These explanatory variables were standardized (mean = 0, standard deviation = 1) prior to analyses. Finally, the CC scenario and the stratum were included as categorical variable and as a random effect for the intercept, respectively. Strata managed according to the individual tree planting (Appendix S1: Table S3) were excluded from the analysis because the corresponding management aims at a constant BA, which is a distinct difference to the other strata and precludes a statistical analysis of the drivers of the changes in BA (Appendix S2: Fig. S1).

To analyze changes in species composition, we calculated a percentage similarity coefficient (PS; Eq. 1; Bugmann 1997)

$$PS = 1 - \frac{\sum_{i=1}^n |x_{CC} - x_{RP}|}{\sum_{i=1}^n (|x_{CC} + x_{RP}|)} \quad (1)$$

where  $x_{CC}$  and  $x_{RP}$  denote the relative share of a species under the CC scenario and the historic climate of the reference period 1980–2009, respectively.

Further, we calculated the relative climate-induced BA change by species of all strata within one elevation zone

$$BA\ change_{Species} = 1 - \frac{x_{CC} - x_{RP}}{\sum_{i=1}^n (|x_{CC} + x_{RP}|) \times n} \quad (2)$$

where  $x_{CC}$  and  $x_{RP}$  denote the absolute species BA under the CC scenario and the historic climate of the reference period 1980–2009, respectively, and  $n$  is the number of strata in the respective elevation zone. Change values >0 and <0 indicate increases and decreases in absolute species BA under CC compared to the reference climate, respectively. The absolute values of species BA change sum up to 1 per elevation zone.

Moreover, we determined the influence of the selected sources of uncertainty on model projections, i.e., CC scenario, soil type and model version. For each stratum, we calculated the fraction of variance in projected stand BA that was attributed to each uncertainty source with an analysis of variance (ANOVA) using the R package vca (Schuetzenmeister and Dufey 2018).

All analyses were performed in the statistical software R (v3.4.3; R Core Team 2018).

## RESULTS

### Climate change impacts on stand BA across elevation zones

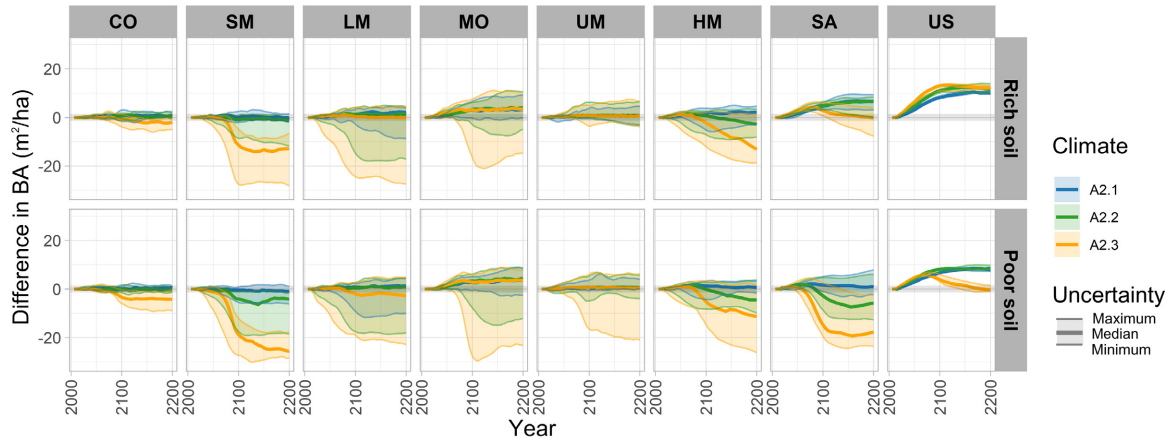
The model projected mainly small climate change effects for the lowest (i.e., colline) and positive effects for the highest elevation zone (i.e., upper subalpine; Figs. 3, 4). In the other zones, projected BA changes depended strongly on the climate change scenario, the local soil conditions, species pool, and the strata.

For the BP simulations, the share of strata showing negative effects increased with the magnitude of climate change, i.e., from scenario A2.1 (“low impact”) to A2.3 (“high impact”; Figs. 3a and 4a). Climate-induced abrupt changes were projected to occur in most elevation zones before the end of this century and were usually followed by a period of stabilization during the next century (Fig. 3a). By 2200, more than one-third of the strata in the sub-, low, and high montane zones featured pronounced negative effects relative to the historic climate (>25% decrease of BA) under the high impact (A2.3) scenario for both rich and poor soils (Fig. 4a). Substantial increases in BA ( $\geq +15\%$ ) relative to the historic climate were simulated only for some strata at higher elevations (upper montane, subalpine and upper subalpine) and in the montane zone of the Southern Pre-Alps (Fig. 4a). The strata of the subalpine zone were highly sensitive to the assumption on local soil conditions showing a shift from generally positive to mostly negative responses to climate change from rich to poor soils, respectively (Figs. 3a and 4a).

For the IM simulations, fewer strata were negatively affected by climate change compared to the BP



## a) BP



## b) IM

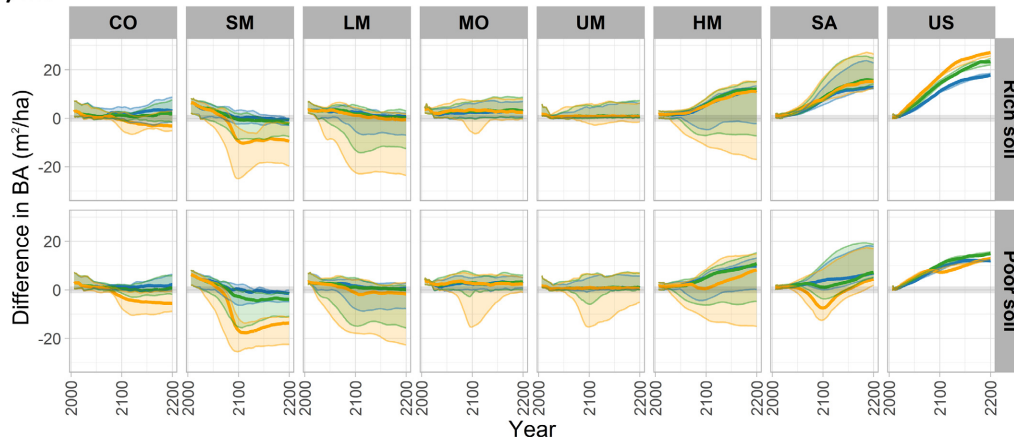


FIG. 3. Absolute differences in basal area (BA) over time for the three climate change scenarios (A2.1–A2.3) with respect to the base species pool (BP) simulations under the historic climate of the reference period 1980–2009 for (a) BP and (b) immigration (IM). Colored lines represent the median value of the differences for all strata within the respective elevation zone. The shaded colored areas show the uncertainty bounds among all strata (maximum and minimum value). For better visualization, a running mean was applied, which corresponded to the management interval. Results are shown for model version 22. The number of strata per elevation zone are CO (colline), 6; SM (sub montane), 8; LM (low montane), 12; MO (montane zone of the Southern Pre-Alps), 4; UM (upper montane), 16; HM (high montane), 14; SA (subalpine), 8; US (upper subalpine), 3. For BA at initialization and simulated absolute BA (and species composition) per stratum, see Appendix S1: Table S3 and Appendix S2: Figs. S3–S18, respectively.

simulations (Fig. 4b vs. 4a). Decreases in absolute stand BA were less pronounced and projected to be at least partly compensated by species immigration, especially in the upper montane zone and the montane zone of the Southern Pre-Alps (cf., Fig. 3a vs. 3b). At higher elevations (i.e., high montane, subalpine, and upper subalpine zone), IM led to a larger increase of projected BA compared to BP (Figs. 3a vs. 3b and 4a vs. 4b). Yet, IM did not prevent the large negative differences in stand BA in the sub-montane zone under the high impact (A2.3) scenario.

These patterns were generally robust across the eight model versions, as depicted by the inter-model variability of projected impacts (Appendix S2: Fig. S19). Different allocations of strata to impact categories were usually observed for neighboring categories, indicating

that the projected trends tended to be consistent for the model versions and suggesting that these differences were at least partly due to the categorization into discrete impact categories. Moreover, the projections of the eight model versions were generally robust when the strata within one elevation zone featured consistent climate-change responses based on model version 22 (indicated by an asterisk in Appendix S2: Fig. S19; cf. Figs. 3 and 4).

As shown by the mixed-effects models (Appendix S2: Table S1), negative effects of climate change were associated with (1) increasing magnitude of climate change relative to the historic climate, (2) both low and high values of WHC and available nitrogen, (3) south-facing steep slopes and (4) low elevations. Moreover, projected BA was negatively related to a high initial proportion of



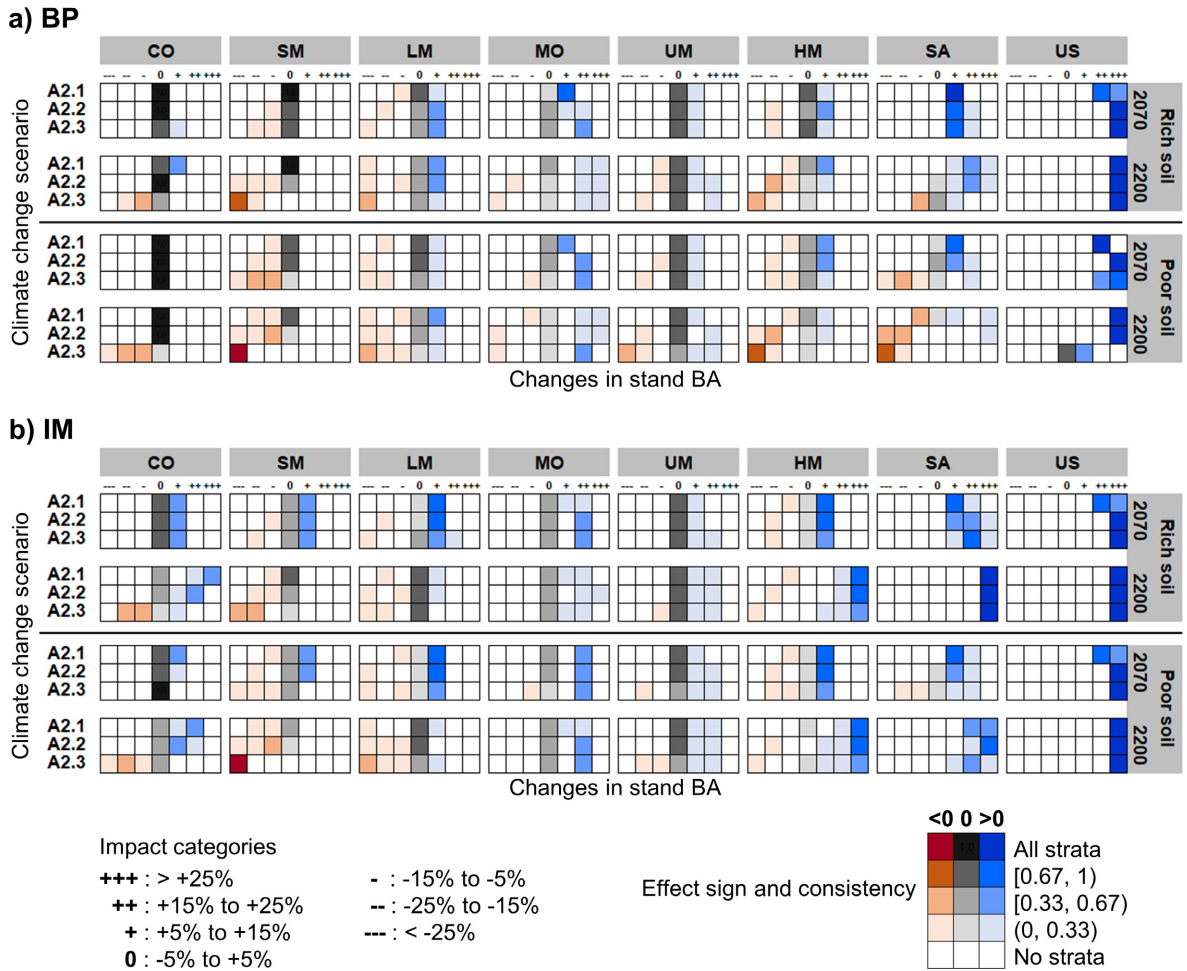


Fig. 4. Changes in stand basal area (BA) per elevation zone (column groups) for the three climate change scenarios (rows, A2.1–A2.3) with respect to the BP simulations under the historic climate of the reference period 1980–2009 for (a) BP and (b) IM. The different impact categories (---,--,0,+,++,++) indicate the magnitude of change, from strong decrease to strong increase, and are defined by percentage deviation from the reference. The color code indicates the effect sign and color shading indicates effect consistency across the strata expressed as the fraction of strata falling into a given impact category. Results are shown for two points in time, i.e., 2070 and 2200, where model outputs per stratum were averaged across one intervention period with the years 2070 and 2200 as the central years, respectively. Results are further displayed for rich and poor soils. For number of strata, cf. caption of Fig. 3. Results are shown for model version 22. For raw data, see Appendix S2: Fig. S2.

Norway spruce for the BP simulations, while it was positively related to a high initial proportion of silver fir for both the BP and IM simulations.

*Projected changes in species composition and mitigation effects*

By the end of the next century, projected changes in species composition relative to the reference species composition showed consistent trends across all elevations (Fig. 5 and Appendix S2: Fig. S20).

First, species composition tended to become increasingly dissimilar to the reference composition with increasing magnitude of climate change, especially when immigration was considered (Fig. 5 and Appendix S2: Fig. S20). This was not the case for strata located in the

colline zone, however. There, sweet chestnut, an important species in two-thirds of the strata (Appendix S1: Table S3), was projected to become subject to strong interspecific competition by other species (i.e., European beech, oak, or linden). However, under the high impact (A2.3) scenario, it was most competitive, resulting in a species composition that was similar to the reference (Appendix S2: Figs. S3, S11).

Second, as immigration allowed species substitution to occur, species composition was more dissimilar to the reference composition for the IM than for the BP simulations for most strata (Fig. 5 and Appendix S2: Fig. S20). Under the high impact (A2.3) scenario, some strata even featured PSI values close to zero, indicating an almost complete replacement of the extant species by a different set of species due to the direct and indirect

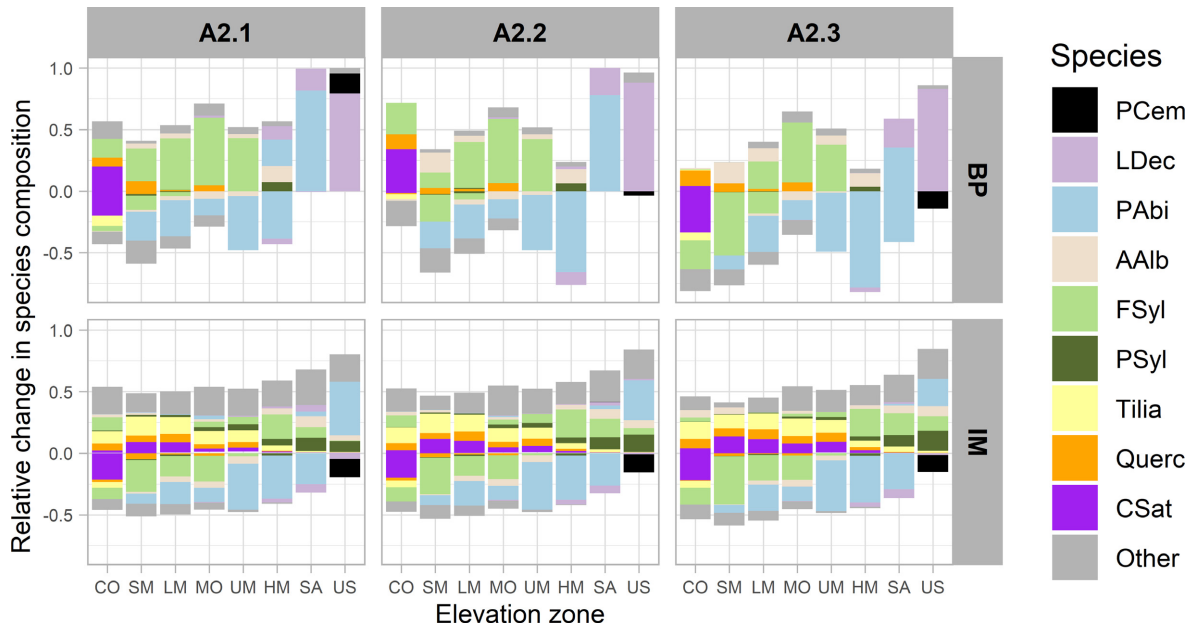


FIG. 5. Species change (Eq. 2) per elevation zone for the three CC scenarios with respect to the reference species composition. The reference composition is derived from BP simulations under the historic climate of the reference period (RP) 1980–2009. Values  $>0$  represent an increase in BA of the respective species, while values  $<0$  represent a decrease in BA of the respective species. Note that the same species can show changes in both directions, thus indicating an increase in some strata and a decrease in others within the same elevation zone. Results are shown for rich soils in the year 2200 and model version 22. For poor soils, see Appendix S2: Fig. S21. Values of absolute species BA were averaged across one management interval with the year 2200 representing the central year. For an explanation of the abbreviations and number of strata per elevation zone, cf. caption of Fig. 3. Species are PCem, *Pinus cembra*; LDec, *Larix decidua*; PAbi, *Picea abies*; AAAlb, *Abies alba*; FSyl, *Fagus sylvatica*; PSyl, *Pinus sylvestris*; Tilia, *Tilia* sp.; Querc, *Quercus* sp.; CSat, *Castanea sativa*; other, other species.

effects of CC (Appendix S2: Fig. S20). The immigrating species were either drought-tolerant, such as sweet chestnut, Scots pine (*Pinus sylvestris*), oak, or linden, or dominant tree species from lower elevations that expanded their range upslope (e.g., European beech or silver fir; Fig. 5). The latter was most pronounced for the high montane zone, where European beech, which was not present at all in the extant species pool (Appendix S1: Table S3), immigrated and thus strongly altered species composition (Fig. 5 and Appendix S2: Fig. S20).

Third, the shift toward more drought-adapted species was generally more pronounced for poor than rich soils (Fig. 5 and Appendix S2: Fig. S21).

Apart from these general trends, changes in species composition varied substantially with elevation, particularly for the BP simulations (Fig. 5 and Appendix S2: Fig. S20). Strata featuring rather small changes in the relative shares of the local species for all CC scenarios were mainly located in the montane zone of the Southern Pre-Alps and in the colline, subalpine and upper subalpine zones. While strata in the sub-montane zone also featured rather small changes under the A2.1 and A2.2 CC scenarios, they exhibited distinct differences to the reference composition under the high impact (A2.3) scenario (Appendix S2: Fig. S20). Specifically, the dominant European beech became prone to dieback and progressive replacement by silver fir and oak species, and

Norway spruce disappeared completely (Fig. 5: upper panel). The climate response of the strata in the low montane zone was variable (Appendix S2: Fig. S20) and depended mostly on the share of Norway spruce, which was generally replaced by European beech and silver fir (Fig. 5: upper panel, Appendix S2: Figs. S5 and S13). In the upper montane zone, species composition was projected to be distinctly different from the reference composition for all CC scenarios (Appendix S2: Fig. S20) due to a decrease of Norway spruce in all strata, which was accompanied by a relative increase of European beech (Fig. 5: upper panel, Appendix S2: Figs. S7, S15). In the high montane zone, Norway spruce became prone to dieback and gradually replaced by European larch, silver fir and Scots pine (Fig. 5: upper panel, Appendix S2: Figs. S8, S16).

#### Sensitivity to selected sources of uncertainty

The uncertainty in projected stand BA varied among elevation zones and was larger for 2200 than for 2070 (Fig. 6a, c). The BP and IM simulations featured similar uncertainty ranges in 2070, while they were generally smaller for IM than BP in 2200 (Fig. 6a, c), as explained below.

In 2070, the sensitivity of projected stand BA to the uncertainty sources was almost identical for the BP and

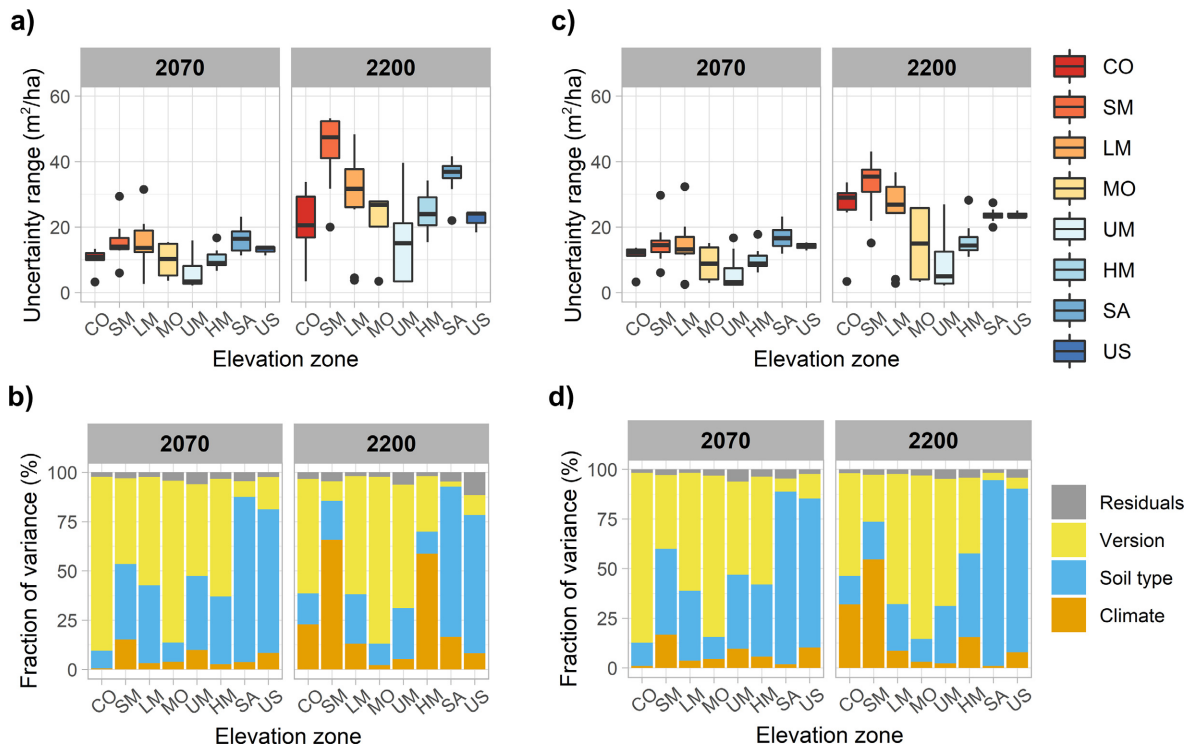


Fig. 6. Range and origin of uncertainty on model projections for (a, b) BP and (c, d) IM for 2070 (left panels) and 2200 (right panels). The upper panels (a, c) show the extent of uncertainty in projected stand BA. The uncertainty range represents the difference between the maximum and minimum value of projected BA out of 48 simulations per stratum (3 climate change scenarios  $\times$  2 soil types  $\times$  8 model versions). The lower panels (b, d) show the proportion of variability caused by the choice of the climate change scenario, the local soil conditions and the model version per elevation zone. Thereby, the relative proportions of the median values of the variability caused by the selected uncertainty sources across the strata in the respective elevation zone are shown. For details on the strata-specific values, see Appendix S2: Fig. S22. For all panels, BA was averaged across one management interval with the years 2070 and 2200 representing the central years, respectively. For an explanation of the abbreviations and number of strata per elevation zone, cf. caption of Fig. 3.

IM simulations. Strata in the sub-montane (SM), low montane (LM) and subalpine (SA) zones featured the highest uncertainty ranges (Fig. 6a, c). For most strata in the sub-montane and low montane zones, the soil type and model version accounted for the majority of the variation in projected stand BA (Fig. 6b, d and Appendix S2: Fig. S22). Yet, the two highest BA uncertainty ranges in these zones (approximately 30 m<sup>2</sup>/ha; Fig. 6a, c) resulted from the variability induced by both the CC scenarios and the soil types (CC scenarios 42% and 50%, soil type 50% and 44%, for both BP and IM), not from the model versions. At high elevations (sub-alpine and upper subalpine [US]), the variability induced by the soil type was the largest source of systematic uncertainty, accounting for at least 71% of the variability (Fig. 6b and d). For strata in the colline (CO), upper montane (UM), and high montane (HM) zones as well in the montane zone of the Southern Pre-Alps (MO), the model versions generally caused the largest variability in stand BA (Fig. 6b and d).

In 2200, the sensitivity of projected stand BA to the selected uncertainty sources was higher than in 2070 in both types of simulation, but the uncertainty was higher

and featured higher variability for BP than IM simulations (Fig. 6a and c). In both cases, the strata of the sub-montane zone featured the largest uncertainty in stand BA (Fig. 6a, c), which originated mainly from the CC scenarios for both the BP and IM simulations (Fig. 6b, d). Generally and not surprisingly, the strata were more sensitive to the CC scenarios in the year 2200 than in 2070 in most elevation zones. As in 2070, soil type was the largest source of systematic uncertainty at high elevations, whereas the model versions were more important at lower elevations. While the BP and IM simulations generally featured similar patterns, strata in the high montane zone were more sensitive to CC for the BP than IM simulations because climate-induced diebacks of Norway spruce stands could not be compensated by other species (see *Projected changes in species composition and mitigation effects*).

## DISCUSSION

We provide a comprehensive assessment of the climate sensitivity of stand BA and species composition of typical managed Swiss forests under different assumptions

of climate change, local soil conditions, species pool (with and without immigration), and model version. Our strata-based approach provides a template for upscaling stand-scale impact assessment data to the national level while maintaining local accuracy. Furthermore, our approach accounted for various uncertainty sources, including model-related uncertainty, which has previously not been assessed in a similarly comprehensive way.

Overall, our results are in line with the two general climate-induced trends identified by many empirical and model-based studies from Switzerland and over Europe: (1) negative climate-induced impacts on forest productivity at low elevations and positive effects at high elevations (e.g., Linares et al. 2009, Bugmann et al. 2015); and (2) an increase in drought-adapted species proportion at the local scale and an upward (or northward) shift of current species ranges (e.g., Peñuelas and Boada 2003, Hanewinkel et al. 2013, Rigling et al. 2013). Yet, our results reveal highly variable climate sensitivity across elevation zones, highlighting the relevance of small-scale mediating effects, as discussed in detail in the following section.

#### *Climate change impacts on stand BA across elevation zones*

Unexpectedly, the strata at the lowest elevations, i.e., in the colline zone, did not generally show high sensitivity to CC. In this zone, adverse effects of CC on stand BA were projected by the end of the next century only under the high impact CC scenario. This surprising pattern can be explained by a combination of regional climatic conditions and historic management. First, all strata of the colline zone were located in the Southern Pre-Alps, featuring an insubric climate (i.e., dry mild winters and warm summers with short, heavy spells of precipitation) and thus comparably high annual precipitation sum (1,600–2,100 mm; Telesca et al. 2010). Second, the stratification did not include forest stands located at extreme site conditions (Bircher 2015), e.g., rock debris or forest edges (Conedera et al. 2010). Third, most of the strata located in the colline zone are mainly composed of drought-adapted species such as sweet chestnut (i.e., artificial chestnut orchards and coppices; Conedera et al. 2001), oak or linden, hence leading to a comparably low sensitivity of the current strata to CC. Overall, our results indicate that the regional climate regime and the current species composition resulting from past forest management and land use (Conedera et al. 2004) likely mitigate the direct climate-induced effect of CC on forest stands. Yet, further processes may affect these strata, which were not accounted for in this study, e.g., diseases (Robin and Heiniger 2001, Vannini and Vettrano 2001), the immigration of exotic species (Knüsel et al. 2017), extreme events and their lag effects (Conedera et al. 2010, Ogle et al. 2015), or interactions among these (Sallé et al. 2014).

In contrast, adverse climate-induced effects were projected already under the low impact CC scenario by 2070 for several strata in the sub-montane, low montane, and high montane zones. Forest stands at these elevations were generally most sensitive to adverse CC impacts in the long term (i.e., by 2200) compared to other zones, even under good soil conditions. Interestingly, these zones represent today's rear edges (i.e., dry, warm range limits; Lenoir and Svenning 2013) of the two currently most important late-successional species, i.e., European beech and Norway spruce (Frehner et al. 2005). Due to widespread planting of Norway spruce (Bürgi and Schuler 2003), this species is important in many strata below its natural distribution limit, even in the sub-montane zone (Appendix S1: Table S3). In the Swiss lowlands, a marked decrease of Norway spruce was reported by the NFI, which is at least partly due to climate-related changes (Rigling and Schaffer 2015). Our simulation results indicate that the drought-related dieback of Norway spruce and European beech at low elevations is unlikely to be compensated by more drought-tolerant species, such as Scots pine, sweet chestnut, oak, or linden, due to their comparably lower productivity (Schelhaas et al. 2015). Yet, in the conifer-dominated high montane and subalpine zones, the projected declines of Norway spruce were compensated by the warming-promoted immigration of European beech. Such temperature-driven upward shift of beech has been observed already in the recent past and are expected to increase significantly in the future (Peñuelas and Boada 2003, Peñuelas et al. 2007). Overall, our results indicate that strata in the sub-montane and low montane zones are likely to be most prone to climate-induced losses of stand BA, even under mesic conditions (Martin-Benito et al. 2018), due to the drought-related vulnerability of European beech and Norway spruce (Vanoni et al. 2016).

Strata in the subalpine zone featured mostly positive effects but were most sensitive to the assumption on soil conditions. Thus, our results suggest a heterogeneous response of these strata to CC depending on site-specific water and nitrogen availability, particularly in dry inner-alpine environments. Therefore, the general expectation of positive CC induced effects on forests at higher elevations due to increasing temperature (e.g., Lexer et al. 2002, Harsch et al. 2009, Bugmann et al. 2015, Jochner et al. 2018) should be considered with caution. This is supported by recent empirical evidence (van der Maaten-Theunissen et al. 2012, Charru et al. 2013, Martin-Benito et al. 2018) and model-based studies (Henne et al. 2011) showing regional and local variations in growth responses to CC suggesting an interplay of warming with local water and nutrient limitations.

Knowledge on the temporal dynamics of climate-induced structural changes of forest stands is of utmost interest for practitioners (Ammer et al. 2018). Yet, few studies have addressed such trajectories although they are highly relevant for forest management (Temperli

et al. 2012). Our simulations show that climate-induced abrupt changes in absolute BA are likely to occur mainly toward the end of this century. Yet, for the high impact CC scenario, abrupt declines were projected already before, particularly for some strata in the sub-montane and low montane zones. When taking immigration of drought-adapted species into account, the decreases in stand BA were generally less pronounced and projected to be at least partly compensated by the introduction of new species. However, these results should be considered with caution because they primarily account for long-term climatic trends, i.e., gradual increases of the average of the monthly mean temperatures and directed relative changes of monthly precipitation. Other factors can strongly drive abrupt changes in stand BA, particularly extreme events and disturbances (i.e., fire, drought, wind, snow and ice, insects, and pathogens; Lindner et al. 2010, Barros et al. 2017, Seidl et al. 2017a, Janda et al. 2019), whose temporal occurrence is quite difficult to predict (but see Thom et al. 2017a, b). Still, the expected changes in species composition provide key information on strata that are most prone to abrupt declines of stand BA (Morin et al. 2018).

#### *Projected changes in species composition and mitigation effects*

We found a number of consistent trends regarding changes in species composition across elevation. On the one hand, CC generally led to an increase of drought-tolerant species, such as Scots pine, sweet chestnut, oak, or linden, at all elevations, which is in agreement with trends observed under the ongoing CC in Switzerland (Rigling et al. 2013) and elsewhere (Peñuelas and Boada 2003). The shift toward more drought-adapted species was generally more pronounced on poor soils and south-facing slopes, which again agrees well with initial trends from the studies mentioned above. On the other hand, a general upward shift of species ranges was projected, especially for the main species European beech, silver fir, and Norway spruce. Although reported evidence for such climate-induced upward shifts of forest biomes remain scarce (Harsch et al. 2009) or are restricted to a few quite extreme regions, i.e., the dry inner-Alpine zone (Rigling et al. 2013), some studies report a progressive vegetation shift along elevation (Peñuelas and Boada 2003, Lenoir et al. 2008).

Yet, apart from these general trends, the strata of the different elevation zones featured dissimilar and sometimes rather abrupt responses to CC (see discussion in the following subsection), with the latter indicating tipping point dynamics (i.e., the system exhibits a sharp transition between contrasting stable states instead of a smooth response; Scheffler and Carpenter 2003, Hirota et al. 2011). The identification of alternative states is of high interest because distinct abrupt changes in species composition are associated with fundamental changes in

ecosystem functioning and thus forest ecosystem services (Temperli et al. 2012).

Strata in the upper montane zone were the closest to a tipping point because Norway spruce was facing increasing interspecific competition by European beech and, to a lesser extent, silver fir. This resulted in a climate-induced rank-reversal in species dominance in these strata. The same applied to strata in the high montane zone. Substantial changes in species composition were expected due to the immigration of European beech even for the “low impact” CC scenario. Yet, due to its sensitivity to late frost, European beech may have a comparably lower capacity to migrate to higher elevations than silver fir (Cailleret and Davi 2011), a factor not fully considered in ForClim. Strata in the sub-montane elevation zone featured distinct changes in species composition only for the high impact CC scenario. Thus, apart from the disappearance of the silviculturally favored Norway spruce (Seidl et al. 2017b), our results suggest that current species composition is relatively robust to slight and even moderate CC. Yet, under high impact CC, the currently dominant European beech became prone to progressive replacement by more drought tolerant species, as observed already today for drought-affected areas in other parts of Europe (Bontemps et al. 2010, Mette et al. 2013).

Overall, our results suggest that the admixture of more drought-tolerant species, such as silver fir (Baumbach et al. 2019), European larch (Wolfslehner et al. 2011), Scots pine, sweet chestnut, oak, or linden, is highly advisable across all elevations to mitigate future adverse climate-induced changes of basal area and thus aboveground carbon storage. To derive more precise recommendations for forest management, further analyses of adaptive management scenarios would be an important next step (e.g., Temperli et al. 2012).

#### *Sensitivity to selected sources of uncertainty*

The largest uncertainty regarding future BA was generally associated with the CC scenarios. Yet, the large influence of soil conditions and model versions for some elevation zones indicates that uncertainty other than the CC scenarios are highly relevant for future projections.

This is in line with findings of other impact studies (Nishina et al. 2015, Horemans et al. 2016, Kalliokoski et al. 2018, Snell et al. 2018) emphasizing that other uncertainty sources than climate can be highly relevant, but their importance depends considerably on the biogeographical and environmental context. Unfortunately, further comparisons of the uncertainty decomposition between these studies and our results are not feasible due to differences in study design, model output and the selection of uncertainty sources.

At high elevations, soil conditions were the dominant source of uncertainty, leading to substantial uncertainty ranges of BA. This was mostly due to the comparably higher underlying uncertainty on soil conditions (WHC

and nitrogen availability) at high elevations combined with the low drought tolerance of Norway spruce, the dominant species at this elevation (Büntgen et al. 2005, Hartl-Meier et al. 2014). Hence, the assumption on local soil conditions strongly determines the climate signal of the model projections. Reliable site-specific soil information is thus of utmost importance for robust projections of future forest dynamics (De Cáceres et al. 2015, Huber et al. 2018), especially in the context of mountain forests (Seidl et al. 2005, Henne et al. 2011, Schwörer et al. 2014, Wohlgemuth and Moser 2018).

At low elevations, the model versions were a relevant source of uncertainty in addition to the CC scenario, reflecting strongly different simulated species responses to the underlying model assumptions. For instance, different assumptions on the regeneration process (i.e., assumptions on sapling densities) have long-lasting effects on BA, particularly for shade-tolerant species. This effect is the key cause underlying the differential relative contribution of the model versions to uncertainty across the elevation gradient: at low elevations, the highly shade-tolerant European beech is dominant under current climatic conditions, and thus these strata are particularly sensitive to the model assumptions. By contrast, the much less shade-tolerant Norway spruce is currently dominant at higher elevations, and therefore these strata are more sensitive to other factors including drought, i.e., the assumptions on local soil conditions. Thus, the (further) reduction of model uncertainty represents an essential factor to better constrain the uncertainties of climate assessments and to increase the robustness of the projections for practical decision support. Yet, although the assumptions on model structure led to differences in BA projections, the model versions featured consistent patterns in response to the CC scenarios, pointing at robust trajectories of forest dynamics.

## CONCLUSIONS

We investigated the climate sensitivity of stand basal area and species composition of typical managed Swiss forests using a state-of-the-art model of forest dynamics. We simultaneously accounted for uncertainties arising from the climate change scenarios, soil conditions and model structure, and systematically decomposed their relative importance.

We identified the following stands as being most prone to negative climate-induced impacts: (1) stands in the sub-montane and low montane elevations zones and (2) stands located on poor soils in the high montane and subalpine elevation zones. However, species immigration partly mitigated the negative impacts of climate change. Thus, admixing drought-tolerant species is advisable to increase the resistance and resilience of forest stands to climate change.

The uncertainty ranges of projected basal area were substantial, being primarily associated with the climate change scenarios. Yet, the high importance of soil

conditions at high elevations and the relevance of the choice of the model version at lower elevations point at uncertainty sources other than climate change scenarios that need to be considered in impact assessments. We thus recommend accounting for model-related uncertainty not only by comparing projections across different models but also by explicitly considering parameter and/or structural uncertainty within one single model.

The results of this study are likely to be relevant for (1) other dynamic vegetation models as well, because these models feature strong structural similarities, and (2) other regions because Switzerland covers an exceptionally wide range of environmental conditions. Ultimately, our study demonstrates a systematic approach for (1) providing locally accurate climate impact assessments over large areas, a scale that has not previously been accessible, and (2) considering explicitly the uncertainties arising from model assumptions in addition to other sources of uncertainty. This is highly relevant information toward better, evidence-based decision support in forest management under climate change.

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## SUPPORTING INFORMATION

Additional supporting information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/eap.2313/full>