INTRODUCTION

Climate change is increasingly leading to climatic mismatches between the requirements of the tree species which are currently present and their environment (Bertrand et al., 2011). As a consequence, trees may suffer from climatic stress, grow less, be more vulnerable to disturbance and pathogen attacks and eventually die. This puts forest ecosystem services at risk (Moos et al., 2018). The
long time horizon of adaptation of forests to climatic changes requires an early and proactive reaction by forest managers (Klooster, 2002; Seidl & Lexer, 2013; Sousa-Silva et al., 2018). To plan for early adaptation measures, accurate, reliable and localized information about how forest communities will respond to those climatic changes is required. In general, climatic changes are expected to cause tree species to move poleward and in mountains upwards (Lenoir et al., 2008; Rumpf et al., 2018). In mountain regions such as Switzerland, this will lead to upward migration shifts of altitudinal vegetation belts. This implies changes in forest site types and tree species composition and thus results in a need for adaptation of forest management to climate changes, e.g., the selection of tree species that will find favourable conditions during their lifetime.

Current approaches for tree species selection, which are widely used in Swiss forestry, are based on a characterization of site conditions in terms of moisture and nutrient availability displayed in ecograms. A different ecogram is valid in each altitudinal vegetation belt (AVB), due to the fact that important growth factors change with altitude (von Humboldt & Bonpland, 1805). Within each ecogram, forest site types (ST) have been described to capture site variability due to factors like substrate, aspect and slope. As this ST classification generates reliable species recommendations and is relatively easy to use and well accepted among forest managers, initiatives to quantify the need for climate change adaptation in Swiss forestry and to communicate with forest managers should ideally rely on it.

The adaptation to climatic changes in forest management requires sound decision bases. Thus, an early involvement of experts and practitioners in the elaboration of climate change adaptation and transdisciplinary approaches or even post-normal science approaches are needed (Ravetz, 2004). Post-normal science approaches extend classical scientific approaches and professional consultancy with community knowledge and with participatory modelling approaches. This is especially required in situations where societally relevant decisions are to be made under deep uncertainties and the decision stakes are high (Ravetz, 1999). Several studies have shown that knowledge-engineering approaches, expert elicitation, and transdisciplinary co-production of knowledge can support decision-making in an uncertain world (Zischg et al., 2005; Refsgaard et al., 2007; Lenton et al., 2008; Staffler et al., 2008; Butts et al., 2014; Gharari et al., 2014; Chen et al., 2016; Lamb et al., 2017; Schneider et al., 2019). For example, Ross et al. (2015) showed that participatory modelling approaches research on social-ecological systems and water resources management help to understand climate adaptation needs. Participatory modelling is an interactive and iterative process in which stakeholder involvement is supported by modelling (Hedelin et al., 2017). The modelling approaches can be implemented by means of expert elicitation. Expert knowledge is often processed with the help of expert systems. These are computer programs that distill the experts’ problem-solving logic in a knowledge base that non-expert users or experts in other disciplines can apply to similar problems with data related to those problems and their context (Rodriguez-Bachiller & Glasson, 2004). Hence, expert systems simulate human reasoning about a problem domain, rather than simulating the domain itself (Jackson, 1999). Fundamental topics in expert systems are the transfer and the transformation of potential problem-solving expertise from a knowledge source to a program, the representation of knowledge, the modelling of the reasoning process, and the explanation of the computed solutions.

Modelling the effects of climate changes on forests in a territory with high variability in altitude, topography, geology, and local climate requires considering regional particularities. Thus, the involvement of experts from different regions in a participatory approach is advisable. The aim of this study was to develop a method for assessing changes of forest STs due to climate change in Swiss forests. To classify a ST, the AVB of the site must be known. Until now, these AVBs were not systematically mapped. Most ST maps in Switzerland rely on the Swiss classification scheme (NaiS, Nachhaltigkeit im Schutzwald, i.e., Sustainability in Protection Forests; Frehner et al., 2005/2009; Frey et al., 2021) and forest managers are basing silvicultural decisions, in particular species selection, on it. The widespread application of this ST classification scheme and the lack of alternatives which can take soil factors into account (in the absence of meaningful soil maps) motivated us to base our modelling framework on it. To assess the transformation of STs under changing climate conditions, the current and future AVB of the forest site location must be known. Thus, the main goal of this study is to map the current AVBs and to model the changes of the AVBs due to their upward shifts in a warmer climate. This information provides the basis for identifying forest areas that are particularly sensitive to climatic changes. To involve the main decision makers from the beginning in the development process and to include region-specific knowledge, we developed an expert system for enabling participatory modelling of the range shifts in the AVBs for assessing climate change impacts on STs.

2 | METHODS

In the following, we describe the overall structure of the participatory modelling approach, the Swiss classification scheme of STs, the details of the models for analyzing the impacts of climate changes on the AVBs and forest STs, and the data. The used taxon names correspond to the taxon nomenclature of Flora Helvetica (Lauber et al., 2018).

2.1 | Participatory modelling approach

The core of our modelling approach is a simulation of the AVBs under current and future climate conditions. The upward shifts in the AVBs provide the input for an inference engine to process expert knowledge to choose the suitable tree species for forest STs under a changing climate. We used expert elicitation and participatory modelling approaches for both the development and the quality assessment of the models. Specifically, experts supported us in:
(a) identifying climate parameters that are locally and regionally decisive for modelling AVBs, range shifts of AVBs, and changes of distributional area of selected tree species; (b) mapping sample data for calibrating the models; (c) formulating a rule base for projecting ST changes induced by climatic changes; (d) assessing the quality of the modelling results; and (e) selecting representative climate scenarios from an ensemble of climate simulations. Figure 1 shows the structure of the participatory modelling approach.

The development of vegetation models for Switzerland must consider the complex topographical settings of the Alps and the related high variability of local and regional climate conditions. Local experts supported us in identifying specific local and regional constraints, e.g., the influence of the foehn winds on regional vegetation characteristics, and to select the most relevant climate variables for consideration in the model development from a list of potential climate variables (Huber et al., 2015), ranging from temperature characteristics (mean, minimum, maximum, and variation of monthly, seasonal or annual temperatures), wind, solar radiation, relative air humidity, precipitation, freezing days, foehn wind conditions, actual and potential evapotranspiration, and soil characteristics. We asked ecologists and forest engineers from different regions to assess the regionally most influencing environmental parameters for modelling the AVBs and their upward shifts, thus complementing information from published research. In an iterative process, we showed the AVB modelling results to the individual experts, and in the case of model results differing remarkably from reality, we discussed the reasons for these local and regional differences and developed proposals for model improvement. Moreover, the regional experts provided data from their maps of current AVBs. These data enlarged the sample data for developing and calibrating regression models for modelling the upper limits of AVBs. The simulation results were only finalized after the plausibility check by the expert group. After the development of the models for the AVBs, representative climate projections were selected from the ensemble of climate simulations of CH2018 Project Team (2018) to be used in the simulation of the range shifts of AVBs for different emission pathways. One climate projection, which seemed to fit well in all regions of Switzerland, was selected for modelling the climate change impacts for each of three representative concentration pathways (RCP2.6, RCP4.5, RCP8.5, Remund et al., 2020). To assess the ST transformation, we used the rule base for ST projection pathways of Frehner and Zürcher-Gasser (2019). These rules of ST transformation pathways are linked to the AVBs describing the climatic conditions and to specific edaphic conditions (soil reaction and moisture). Finally, we discussed the results of the simulated changes in AVBs and their impacts on ST changes with the experts.

2.2 | Swiss classification scheme of forest site types

The Swiss forest ST classification scheme NaIS (Frehner et al., 2005/2009) builds upon previous classification concepts (Ellenberg & Klötzli, 1972; Wasser & Frehner, 1996; Ott et al., 1997) and on existing cantonal classification systems. It currently encompasses 266 STs. For each ST, the presence and abundance of indicator plants, forest floor vegetation, species-specific tree growth, variation in stand structure, basic soil properties, terrain information and tree species recommendations are available. To show the relative position of each ST in the environmental space, ecograms with the two

![Diagram](image-url)
axes of soil reaction and moisture are used. Ecograms are valid each in one of the ecoregions (Figure 2) and in one of the AVBs (Table 1). For each ST, the composition of tree species is described systematically. To classify a ST, the AVB of the site must be known.

2.3 Modelling altitudinal vegetation belts and zonal distribution of key tree species

Modelling the range shifts of AVBs and projecting them to maps requires modelling the current and future location of the borders between the vegetation belts. In a country with complex topography and variable climate such as Switzerland, the location of the AVBs depends on factors like bedrock, macro-climate (e.g., continental or oceanic), and meso-climate like the influence of foehn winds. Thus, modelling of climate change impacts on the AVBs should address at least a spatial resolution of a few decametres. We therefore invited forestry experts from different Swiss regions to give advice for regional particularities. We developed a set of regression models for modelling the upper limits of the AVBs (colline, hyperinsubric, mediterrane, submontane, lower montane, upper montane, combined lower and upper montane [in southern Switzerland], high-montane, and subalpine vegetation belt, Table 1). The upper tree line was modelled with a temperature threshold. Moreover, we developed models to describe the potential distribution area (range) of the two main tree species European beech (Fagus sylvatica, henceforth beech) and silver fir (Abies alba, henceforth fir), which are needed to classify the AVBs. While the first approach aims at modelling the vertical gradients, the second approach aims at modelling the horizontal distribution of the beech and the fir area. In a subsequent step, the outcomes of both models were combined in a map showing the AVBs in Switzerland.

2.3.1 Modelling the upper limits of altitudinal vegetation belts

We conducted a literature review on the climate variables that are relevant for determining the AVBs in the European Alps (Huber et al., 2015) and asked our expert panel to complement our literature review with local knowledge (own observations, grey literature and government reports) and to support us in identifying the most relevant climate variables for each region of Switzerland. The experts thus helped us to identify the main climatological parameters that should be considered in the regression models that describe the relationships between the altitudinal limits of the AVBs and climate data. Specifically, they identified and selected locally relevant climate parameters. In addition, the selected parameters were checked for relevance by comparing the scores of the various possible parameter values. For example, if the literature review and the expert assessments identified the July temperature for modelling an AVB, we checked if either the daily minima, the mean, or maxima of the temperature in July was the most relevant parameter in terms of optimizing the model score (root-mean-squared error, RMSE).

The upper limit of the tree line was modelled by the temperature threshold of 11°C for the daily maxima in July (Huber et al., 2015). In contrast, the threshold temperature at each upper limit of the AVBs is expected to vary from region to region, depending on macroclimatic influences like continentality, the mountain mass effect, and foehn winds. After the identification of relevant climate parameters, high-resolution maps (25 m × 25 m spatial resolution) of the selected climate parameters were developed (Zischg et al., 2019). In a subsequent step, the experts identified the border lines between AVBs from existing ST maps. Where cantonal maps are missing, the local experts partly mapped and determined the border lines (cantons of Geneva, Valais, Jura, Uri, Ticino) in order to obtain a representative distribution of sample points over Switzerland. These sample data (120,479 locations) were used to develop and calibrate regression models for determining the threshold temperature of the upper limit of each AVB based on site characteristics. For each point (grid cell) of the respective sample (upper altitudinal limit of each AVB), the values of all site parameters were extracted from the climate maps and used to calibrate the regression models. Since no soil maps are available at the required spatial scale for the whole of Switzerland, we used geological maps to estimate the pH range and the clay content of the soil to roughly characterize the soil-forming substrate. These maps were derived from the harmonized geology maps of Switzerland (Meyer, 2017; Swisstopo, 2021). The procedure for the preparation of these maps is described in Zischg et al. (2021). We used four methods for modelling the upper limits of the AVBs: a linear regression model, a random forest regression model, a decision tree regression model, and an extra tree regression model, applying the scikit-learn Python module (Pedregosa et al., 2011).

For each grid cell, the average of the ensemble of the resulting regression equations provides a temperature threshold (dependent variable) value that describes the upper limit of the respective vegetation belt at that location based on the selected maps of prediction variables. This threshold value is compared with the real temperature value from the (current) temperature map. As long as the real temperature of a certain grid cell is higher than its calculated temperature threshold, the corresponding grid cell belongs to the AVB below the respective upper limit. If the temperature of a certain grid cell is lower than the calculated threshold temperature, the grid cell is above the corresponding AVB. In this way, the AVB was modelled spatially. The lower limit of an AVB is defined by the upper limit of the adjacent lower AVB. The model quality was iteratively assessed by the expert panel as described above.

2.3.2 Modelling tree species’ zonal boundaries

In addition to the vertical extension of the AVBs, the Swiss ST classification scheme requires also to map the horizontal extension of the key tree species beech and fir. Thus, we developed zonal tree species distribution models for the ranges of beech and fir. In addition, we developed a zonal distribution model for the colline vegetation belt in the Valais because this belt has no lower altitudinal
We combined this zonal model for the colline AVB in Valais with the AVB models for northern and southern Switzerland. In the high-montane vegetation belt, the fir area is subdivided into three distinct areas (Frey, 2003; Frey et al., 2021) which are relevant for silvicultural practice. In the main fir area, fir is strongly represented in the natural forest and is very shade-tolerant. This area is dominated by oceanic or insubric climate. The secondary fir area is located in the transition zone from the oceanic or insubric climate to the inner Alpine continental climate, and fir here often occupies only sites with ample water supply which occur mostly on northern slopes. The relic fir area is located in the inner Alps with a continental climate, a relatively high foehn wind frequency, and a high diurnal temperature variation (Huber et al., 2015). Here, fir occurs merely in isolated stands which are considered as relics of a formerly much larger fir area during the postglacial (Frey, 2003). The zonal distribution of fir was modelled with a decision tree classifier of the scikit-learn Python module (Pedregosa et al., 2011).

The zonal distribution of the beech was modelled with a fuzzy logic rule base (Zadeh, 1965). The rule base and the inference algorithm were developed on the basis of expert knowledge on how local and regional characteristics of climate and geology affect beech distribution (Huber et al., 2019). This consists in as a first step deriving fuzzy membership functions for the selected climate parameter describing the membership of a value of the climate parameter to the zone favourable for the tree species. The membership value is 1 for the average of all values of the climate parameters within the zone and 0 for the minimum or maximum value at the zonal boundary of the sample data. All values between the average and the minimum/

maximum have a linearly interpolated membership value. This enables modelling the zonal boundaries on the basis of climatological gradients. A membership function was derived for each of the considered climate parameters. The fuzzy logic rule base infers all membership functions. The combination of the membership functions with a fuzzy overlay function (“gamma” function or “and” function, Gubelmann et al., 2019) gives a membership of the grid cell (forest site) to the distribution areas of the selected tree species or zone. Finally, a threshold was determined to de-fuzzify the membership values and to map the distribution areas with sharp boundaries (Gubelmann et al., 2019).

For developing the distribution models of the European beech and fir area, the boundaries from the Swiss forest ecoregions map (Frehner et al., 2005/2009) were refined and used as a reference for model development (Figure 2). The zonal boundaries of the current spatial distribution of beech and fir were used as the basis for calibration in order to determine the horizontal climate gradients (separation of the factors resulting from altitudinal gradients and factors representing regional, horizontal differentiation). Therefore, the modelling of zonal boundaries only includes the horizontal gradients of climate parameters at selected altitude levels (the average altitude of the species distribution range). In contrast to the regression models for the altitudinal limits of the AVBs in northern and southern Switzerland, the colline vegetation belt in the central Alpine valley Valais was modelled with a distribution model, because this belt is related to the zonal distribution of pubescent oak (Quercus pubescens) and vine-growing areas. Representative samples from the Valais were defined by experts and used as reference areas for
TABLE 1 Description of the altitudinal vegetation belts

| Altitudinal vegetation belt | Description |
|-----------------------------|-------------|
| Mediterrane                 | Heat- and drought-tolerant broad-leaved forests with Quercus ilex and Quercus suber as well as Ficus carica. This altitudinal belt is not yet present in Switzerland. With climate change, it is expected in the areas with mild winter temperatures outside the beech area |
| Hyperinsubric               | Evergreen broad-leaved forest in the southern Alps. Mild winter temperatures and sufficient moisture for beech favour evergreen deciduous tree species such as Ilex aquifolium, Taxus baccata, and Laurus nobilis, but also non-native evergreen tree species such as Cinnamomum sp., Ligustrum lucidum, Prunus laurocerasus, and Trachycarpus sp., which can compete with deciduous broad-leaved tree species due to the mild winter temperatures |
| Colline                     | Deciduous broad-leaved forest. Thermophilic tree species such as Quercus petraea, Quercus robur, Tilia sp., Prunus avium, Acer platanoides and in the southern Alps Castanea sativa dominate |
| Colline with beech          | Deciduous broad-leaved forest in the southern Alps. Thermophilic tree species such as Quercus petraea, Tilia spec., and Castanea sativa are represented; Fagus sylvatica can still dominate on fine-grained soils. The secondary stand contains evergreen tree species such as Ilex aquifolium and Taxus baccata |
| Submontane                  | Mixed beech forest in the Northern Alps. Fagus sylvatica dominates, but there are also thermophilic tree species such as Quercus petraea, Quercus robur, Tilia sp., Prunus avium, Acer platanoides in the stand |
| Lower montane               | Beech forest. Fagus sylvatica dominates strongly, Abies alba, Acer pseudoplatanus, Fraxinus excelsior, etc. are admixed. The difference in top height between beech and silver fir is small |
| Upper montane               | Fir–beech forest. Abies alba and Fagus sylvatica dominate; Picea abies, Acer pseudoplatanus, etc. are admixed. Silver fir and Norway spruce reach significantly higher top heights than beech |
| High montane                | Fir–Norway spruce or pure spruce forest. Abies alba and Picea abies or in the inner Alps Picea abies, and as pioneers Larix decidua and Pinus sylvestris dominate. Closed stands with trees with relatively low taper and strong competition between the trees |
| Subalpine                   | Norway spruce forest, in the inner Alps with Larix decidua as pioneer, in the southern Alps also mixed Larix decidua and Abies alba forest. Stands contain edaphic gaps, Picea abies forests show cluster structure. The trees have high taper and narrow, long crowns |
| Upper subalpine             | Larch–stone pine (Pinus cembra) forest. Stands contain many gaps and have low cover. The trees have high taper and long crowns. It is too cold for the Norway spruce, which is why it survives only south of the Alps on warm, rocky sites |

calibrating the decision tree classifier model for the boundaries of the colline vegetation belt. For this model, we also used the decision tree classifier of the scikit-learn module of Python. The modelling results were assessed by the involved experts and the models were iteratively optimized.

2.3.3 Combining altitudinal vegetation belts and tree species’ zonal boundaries

By combining the models for the upper limits of the AVBs and the zonal tree species distribution models, a combined map of AVBs was created. The submontane vegetation belt outside the beech area was classified as colline belt (Jura, Swiss Plateau, northern Pre-Alps) following the Swiss ST classification scheme. In southern Switzerland, a distinction was made between a colline vegetation belt and a colline vegetation belt with beech on the basis of the beech distribution area. The hyperinsubric vegetation belt can only occur within the beech area. The hyperinsubric belt outside of the beech area was classified as mediterranean belt. The resulting map of combined vertical and horizontal classifications was validated, in addition to the expert assessment described above, by means of an overlay with data of the national forest inventory (Fischer et al., 2014), which classifies the AVBs of each inventory plot (Frehner et al., 2021). An exact match between the modelling result and the observation data was counted as a hit. For assessing the model performance of the regression models for the upper limits of the AVBs, we calculated the RMSE by using 20% of the sample data as validation data.

2.4 Modelling range shifts of altitudinal vegetation belts and changes of forest site types due to climate change

2.4.1 Range shifts of altitudinal vegetation belts

The regression models and zonal distribution models were applied to model boundary locations using future climate scenarios. We used the outcomes of the newest climate model simulations for Switzerland, the CH2018 scenarios (CH2018 Project Team, 2018), provided by the National Centre of Climate Services and the Federal Office for Meteorology MeteoSwiss. These include grid data with a spatial resolution of about 2 km as well as point data for MeteoSwiss measurement sites (daily values) for various scenarios. A group of experts from climatology, forestry, ecology, geography, and modelling disciplines (Meteotest, MeteoSwiss, Federal Office for the Environment, cantonal governments, WSL, and the authors) selected three climate models for the representative concentration
pathways RCP2.6, 4.5 and 8.5. For the RCP2.6 scenario, the model DMI_HIRHAM_ECEARTH_EUR11 (roughly corresponding to meeting the 2°C target of the Paris Agreement) was selected. For the RCP4.5 scenario, the model SMHI-RCA_MPIESM_EUR44 was closest to the "target values" in terms of a regional distribution of precipitation corresponding nearly to the ensemble mean (Remund et al., 2020). For the RCP8.5 scenario, the model CLMCOM-CCLM5_HADGEM_EUR44 was selected. The model results were then down-scaled to 250 m resolution (Remund et al., 2020). For the simulation of the AVBs, the climate variables were further resampled to a 25-m resolution to bring all datasets to the same resolution and extent as the digital elevation model. From the climate simulations, we selected the period 2070–2099 as the target climatology period. In Table 4, the anomalies of the summer values (April–August) of the climate models are presented.

Constancy was assumed for the climate parameters relative air humidity, global radiation, and foehn wind frequency. These parameters either depend mostly on the topography, or it is unknown whether they will change and if so, to what extent. The range shifts of AVBs were modelled for each region separately, covering the whole of Switzerland.

2.4.2 Changes in forest site types

Our approach is based on the assumption that any shift of the AVB induced by climate change does not affect the position of a ST in its ecogram (Frehner et al., 2017). This implies that the relative position of a ST in an ecogram remains unchanged if the AVB, and thus the associated ecogram, changes. To check this assumption, Braun et al. (subm.) analyzed all available ST data in Switzerland, for which also soil data were available. The aim was first to explain and quantify the moisture axis of the ecograms, and second to calculate the effect of changing climate on the position of a ST in the ecogram. The moisture axis can be mostly explained by topographic factors, soil characteristics (water holding capacity, wetness indicators) and the vapour pressure deficit of the air. The projection of the ST used for the study revealed in most cases only minor shifts towards drier conditions. It was concluded that only in cases of doubt the next "drier" ST should be taken into account for tree species choice.

We combined all STs in a database and derived transformation pathways from one ST to another as a consequence of a range shift in the AVB. These transformation pathways were summarized in a rule base, described in detail by Frehner and Zürcher-Gasser (2019). The rule base describes the ST transformation pathway, i.e., to which future ST a current ST will be transformed in the long run if the AVB changes. If the AVB at a specific location changes by more than one belt, the ST projection pathways are concatenated. From this ST transformation pathway, tree species recommendations can be derived (tree species in current ST in current AVB compared to the tree species in future ST in future AVB, given climate change). To this end, the expert system compares the tree species recommendation of the current and future ST. It then lists the overlap in tree species (today and in future), the tree species recommended today but not in future, and those recommended not yet but in future as well as tree species recommended today and in future. This module of the expert system is schematized in Figure 3. The application of the procedure has been implemented in a web-based application for computers and mobile devices (www.tree-app.ch, Brang et al., 2020).

2.5 Data

For the analyses we used high-resolution maps of climate parameters of Switzerland developed by Zischg et al. (2019). These data are available at the data repository ZENODO (Zischg, 2019). The precipitation data of the current climate (periods 1961–1990 and 1981–2010) are from the norm value charts of the Federal Office for Meteorology (MeteoSwiss, 2021). Topographical and geological data were delivered by the Federal Office for Topography Swisstopo (Swisstopo, 2019). The downscaled climate change simulation results and the map of the ratio between actual and potential
The data for the first and last freezing day in the year and the duration of the frost-free period come from Wild (2020). The rule base for ST transformation under climate change was taken from Frehner and Zürcher-Gasser (2019). The table for relating STs with AVBs and tree species is available in Arge Frehner et al. (2020).

3 | RESULTS

3.1 | Range shifts of altitudinal vegetation belts and zonal boundaries of key tree species

The majority of the altitudinal limits are thermal boundaries and vary regionally with daily temperature variation and radiation (regression models, Tables 2 and 3). When addressing the limits for specific AVBs in the following section, we always refer to the upper limits. The altitudinal limits of the colline vegetation belts were determined by the maximum temperature in January and the minimum temperature in April. The limit of the hyperinsubric belt depended on the absolute minimum temperature. For the altitudinal limits of the submontane and lower montane belts, the mean annual temperature, the diurnal temperature variation, the annual global radiation and radiation in April, respectively, the ratio between actual and potential evapotranspiration (ETa/ETp), and the summer precipitation were important. The upper limit of the subalpine and high-montane vegetation belt correlated best with mean temperature maximum in July, and the upper limits of the upper montane vegetation belt with the mean and maximum annual temperature.

The zonal distribution of today’s beech range was modelled by considering annual foehn frequency, relative air humidity at noon, summer precipitation (June–August), mean annual diurnal temperature variation standardized to an altitude of 1000 m a.s.l., ETa/ETp, and mean last freezing day. However, in some regions, threshold values of additional climate variables coincided well with the boundary

| TABLE 2 | Overview of the regression models for modelling the upper altitudinal limits of the vegetation belts |

| Forest ecoregion | AVB | Regression model | Model |
|------------------|-----|------------------|-------|
| Southern Switzerland | Hyperinsubric | TABSMIN = f(ETAPYY, GLOBRADJAN, PH, TG) | Ensemble of regression models |
| Northern Switzerland | Colline | TJANMAX/TAPRMIN = f(pJJA, CONTYY10000, ETAPYY, GLOBRADJAN, ET0JUL, PH, TG) | Ensemble of regression models |
| Southern Switzerland | Colline | TJANMAX = f(pJJA, ETAPYY, GLOBRADJAN, PH, TG) | Linear regression model |
| Northern Switzerland | Submontane | TYYMAX = f(pJJA, CONTYY10000, ETAPYY, GLOBRADYY, PH, TG) | Ensemble of regression models |
| Jura | Submontane | TYYMAX=f(pJJA, CONTYY10000, ETAPYY, GLOBRADYY, PH, TG) | Ensemble of regression models |
| Northern Switzerland | Lower montane | TYYMEAN=f(pAMJJA, CONTAPR1400, ETAPYY, FOEHNYY, GLOBRADAPR, PH, TG) | Ensemble of regression models |
| Jura | Lower montane | TYYMAX = f(pAMJJA, CONTYY1000, ETAPYY, GLOBRADYY, PH, TG) | Ensemble of regression models |
| Northern Switzerland | Upper montane | TYYMEAN = f(pAMJJA, CONTAPR1400, ETAPYY, FOEHNYY, GLOBRADAPR, PH, TG) | Ensemble of regression models |
| Jura | Upper montane | TYYMAX=f(ETAPYY, GLOBRADYY, PH, TG) | Ensemble of regression models |
| Southern Switzerland | Montane (upper and lower) | TYYMEAN = f(CONTAPR1400, GLOBRADAPR, PH, TG) | Ensemble of regression models |
| Northern Switzerland | High montane | TJULMAX = f(pAMJJA, CONTAPR1400, FOEHNYY, GLOBRADAPR, PH, TG) | Ensemble of regression models |
| Southern Switzerland | High montane | TJULMAX = f(CONTAPR1400+GLOBRADAPR, PH, TG) | Ensemble of regression models |
| Northern Switzerland | Subalpine | TJULMAX = f(pAMJJA, CONTYY2000, FOEHNYY, GLOBRADAPR, PH, TG) | Linear regression model |
| Southern Switzerland | Subalpine | TJULMAX = f(CONTYY2000+GLOBRADAPR, PH, TG) | Ensemble of regression models |
| Switzerland | Upper subalpine | TJUML < 11°C | Threshold |

Note: The parameters are named according to the data sets of Zischg et al. (2019): CONTAPR1000, mean diurnal temperature variation in April at 1000 m a.s.l.; CONTAPR1400, mean diurnal temperature variation in April at 1400 m a.s.l.; CONTYY1000, mean daily temperature variation in the year at 1000 m a.s.l.; CONTYY2000, mean daily temperature variation in the year at 2000 m a.s.l.; ET0JUL, potential evapotranspiration in July; ETAPYY, ratio between actual and potential annual evapotranspiration; FOEHNYY, mean frequency of foehn conditions in the year; GLOBRADAPR, average global radiation in April; GLOBRADJAN, average global radiation in January; GLOBRADYY, average annual global radiation; pAMJJA, precipitation April–August; PH, pH value of the geologic substrate; pJJA, precipitation sum of June–July, August; TABSMIN, mean temperature minimum in the year; TG, clay content of the geologic substrate; TJANMAX, mean temperature high in January; TJULMAX, mean temperature high in July; TYYMAX, mean temperature high in the year; TYYMEAN, mean temperature in the year. AVB, altitudinal vegetation belt.
between beech occurrence and absence. Thus, the distribution of beech (especially in the inner and in the southern Alps) seems to be strongly limited by low relative air humidity, which is promoted mainly by foehn winds. An annual frequency of days with foehn exceeding 13% excluded beech in general, even if other factors are favourable for beech. Summer precipitation was also important, especially in
Valais. If summer precipitation falls below 250–300 mm, beech was limited independently of other factors. To a lesser extent, the risk of late frost (especially in cold air pockets) and \( \text{ET}_a/\text{ET}_p \) were further contributing factors.

The modelling of the zonal distribution of fir also produced reliable results. For modelling the boundaries between the main, secondary, and relic fir area, the diurnal temperature variation, the precipitation sum June–August, the foehn frequency, the last freezing day, the duration of the vegetation period, and the mean annual relative air humidity were decisive. In the inner and southern Alps, the daily temperature range, the relative air humidity, and the frequency of foehn in the year were decisive for the boundary between main and secondary fir area. The transition from the main to the secondary fir area was determined by a diurnal temperature variation of 3.5–4°C at 1000 m a.s.l., even if other factors are still favourable. If the diurnal temperature variation exceeds 5°C at 1000 m a.s.l., independent of other factors, fir occurs only in relic stands. The foehn wind (and thus the relative air humidity) also played an important role in certain regions. In the upper valleys of the southern side of the Alps, an annual foehn frequency of 12%–15% disadvantages fir to such an extent that it retreats to northern slopes and deep soils. As high foehn frequencies and a relatively high daily temperature variation co-occurred in this region, we cannot decide which of the two factors is more important. The summer precipitation, and the relative air humidity were determining factors for the boundary between the secondary and the relic fir area.

In northern Switzerland, the colline vegetation belt was best modelled by taking into account mean daily temperature maximum in January, mean daily temperature low in April, summer precipitation, annual mean diurnal temperature variation, \( \text{ET}_a/\text{ET}_p \), mean global radiation in January, and mean potential evapotranspiration in July. In southern Switzerland, the main determining factors for the extension of the colline vegetation belt were \( \text{ET}_a/\text{ET}_p \), mean daily temperature maximum in January, and mean global radiation in January. The colline belt in Valais was mainly determined by the mean daily temperature maximum in July and temperature minimum in April, \( \text{ET}_a/\text{ET}_p \), and mean global radiation in July. Particularities were found in several regions. With a high frequency of frost, oak leaves room to Scots pine (Pinus sylvestris) or sometimes aspen (Populus tremula). These tree species are part of the high-montane vegetation belt, which is why this belt occurs at lower altitude in the regions without than in those with beech. Along the southwestern, northwestern and northern country borders, summer precipitation and average potential evapotranspiration in July is decisive.

Until the period 2070–2099, upward shifts of the altitudinal belts compared to present-day conditions (1961–1990) are projected in all regions (Figure 4 versus Figures 5–7), especially for the RCP8.5 climate simulation run (Table 4). In most cases, the magnitude of the shift amounted to 1–2 altitudinal belts. In the period 2070–2099, the RCP8.5 scenario showed no habitat suitability for beech in large parts of the western and northern Swiss Plateau (area “M” in Figure 2). Conversely, beech has an expansion potential towards higher altitudes, which markedly increases its potential distribution range in the Pre-Alps, the Jura mountain range, the northern Grisons and Ticino. The RCP8.5 for the period 2070–2099 shifted the montane vegetation belts markedly upwards (Figure 7 vs. Figure 4). The future colline belt as projected in this scenario showed large area expansions (horizontally and vertically) in the western and eastern Swiss Plateau, in the Valais, and in the Central Alps (Figure 7). Even the high inner Alpine valleys in southwestern Switzerland showed a certain proportion of the colline belt in future. The colline vegetation belt in RCP8.5 on the northern side of the Alps as well as in the cantons Valais and Grisons showed that fir retracts in future to north-exposed slopes and topographically wet sites. The future colline belt in the Lower Engadine is characterized by a high maximum temperature in July and high global radiation, which favour oak species (Quercus pubescens, Quercus petraea) and the colline vegetation belt to rise. As a consequence of the extension of the colline belt, new STs, i.e., site types currently not found in Switzerland, will appear (Allgaier et al., 2017).

The range shifts were sensitive to the climate scenario. The RCP8.5 which entails warmer temperatures and less precipitation than the RCP2.6 (Figure 5) and RCP4.5 scenarios (Figure 6), and thus, e.g., in a larger expansion of the colline vegetation belt. Table 5 summarizes the areal changes of the AVBs. In the RCP8.5 scenario, the colline belt increases by a factor of 9, and the colline belt with beech decreases to 60% of the area in the period 1990–1961. The submontane belt increases by 68%, while the lower and upper montane belts shrink to 20% and 12% of its original area in the northern part of Switzerland, and to 61% in the southern part of Switzerland. The extent of the high-montane belt remains relatively constant. The subalpine and upper subalpine belts shrink remarkably. However, this is because we did not consider the upward shift of the tree line.

### 3.1.1 | Model evaluation

Comparison of the modelled current AVBs with those derived from the ST which were assessed on the sample plots of the national forest inventory (Arge Fehrenbacher et al. (2020) showed consistently reliable predictions. In 5,287 out of 6,348 plots, the model predicted the exact AVB. This corresponds to a hit rate of 83%. At the remaining points, the wrong AVB predictions are located within a maximum distance of 50 m to the correct observation. The regression models for the upper limits of the AVBs had RMSE values of 0.13–0.78°C, i.e., 0.55–0.77°C for the hyperinsubric belt, 0.05–0.64°C for the colline belt, 0.13–0.42°C for the submontane and lower montane belt, 0.15–0.68°C for the upper montane belt (including the combined lower and upper montane belt in southern Switzerland), 0.12–0.53°C for the high-montane belt, and 0.13–0.78°C for the subalpine belt. In terms of altitude levels, these RMSE values mean that the worst-performing models in the ensemble deviate maximally by 100 m from the validation data. Overall, the extra tree regression approach showed the best performance.
3.2 | Changes in forest STs and tree species recommendations for future climates

The procedure for modelling changes in forest STs on the basis of modelled upward shifts of AVBs was implemented by the Federal Office for the Environment FOEN and the Swiss Federal Institute for Forest, Snow and Landscape Research WSL in the web-based application tree-app.ch (Brang et al., 2020). For each forest location in Switzerland, the current ST and future ST under a selected climate scenario can be queried. The user must enter the coordinates of the site. In the mobile version of the application, the coordinates can be read from the GPS of the mobile device or the user can click on a map to select the location of interest. Based on the coordinates, the app checks for the current AVB and according to this, a pre-selection of possible STs is given to the user. With the help of this pre-selection of STs and ST descriptions, the user must assess the current ST and enter it into the app. The results of this query in the web-based application are the future AVBs of the forest site (i.e., among the tree species recommendations for the current ST) and will find favourable climate conditions in future (tree species to promote or sustain) or are currently possible but will not find favourable climate conditions in future (tree species at risk). Moreover, it lists tree species that are not present at the site under current climate conditions but will find favourable climate conditions in future. Finally, *Ailanthus altissima*, an invasive neophytic species, is separately listed. Figure 8 exemplifies the querying of the information related to a selected location for the RCP8.5 climate scenario.

4 | DISCUSSION AND CONCLUSIONS

4.1 | Changes in altitudinal vegetation belts and tree species distributions due to climate change

With the presented approach the effects of climate change on Swiss forests can be quantified in terms of the potential shifts in AVBs and in terms of the potential changes in the zonal distribution of beech and fir. The AVBs are geographical regions where a group of forest STs (plant communities) are subject to similar climatic factors. The upper boundaries of the AVBs are influenced by several factors...
which represent their "climate character," given topographical and geomorphologic conditions. The quantitative description of the AVBs and the zonal distribution of beech and fir with predominantly climatic parameters, which had been delineated by expert opinions so far, provides now a reliable knowledge base basis for forest management. A key factor of the presented modelling framework was the set of maps of climate parameters (Zischg et al., 2019) in a high spatial resolution (25 m × 25 m). The range shifts of the upper boundaries of the AVBs in the complex topography of Switzerland could only be modelled at such a high spatial resolution (Fischer et al., 2019). The modelled AVBs were also repeatedly checked by the participating experts.

The climatic characterization of the AVBs and zonal distribution of tree species made it possible to project them into the future (2070–2099 with three representative concentration pathways, greenhouse gas concentrations, and climate scenarios). The results of the RCP8.5 scenario show that the climatic conditions for the tree species change in many areas so strongly that it is questionable whether these changes can be termed as a "shift" or must be considered as a "regime change." A shift implies a more or less slight change of the climatic conditions, and that the forest STs remain similar to those known today. In contrast, a regime change implies larger deviations from the present state. In terms of the hierarchical theory of ecosystems (O’Neill et al., 1986), a hierarchy break takes place if the system is no longer able to buffer external signals (here: climate change) and to maintain its identity. The result is a new ecosystem, which is adapted to the new environment. It depends on the ST classification whether the ST transformation can be considered as a shift or as a gradual transition. Any classification system does not perfectly capture gradients since it is based on partly arbitrary boundaries between types. Moreover, it might make it harder to distinguish between abrupt and gradual changes. However, a classification using distinct types has advantages for decision-making since it simplifies the complexity of environmental gradients by reducing it to a limited number of STs.

Uncertainties exist in the forest composition of the future colline and hyperinsubric vegetation belts. The future colline vegetation belt is expected to contain additional climatically distinguishable biogeographic (sub-)units. This cannot be clearly predicted from today’s perspective. In Switzerland, no reference forests for future tree species composition in the colline and hyperinsubric altitudinal belts exist (Huber et al., 2017), with the exception of the current colline vegetation belt in Ticino (Allgaier et al., 2017). A comparative analysis of the future climate in regions of Switzerland with current climate in Europe showed that the future climate (RCP8.5) of the Geneva region is similar to current climate.
in southern and southwestern France (Zischg et al., 2021). Lugano in southern Switzerland will in future (RCP8.5) have a climate similar to that in Genova today, the climate of Basel will be similar to that of the Cevennes and southern France today. Scuol in the Engadine will be similar to the region between Serbia and Hungary. Frehner et al. (2018) have listed potential tree species for the future colline vegetation belt in the Swiss Plateau, in the Jura and in the northern Pre-Alps. In these regions as well as in the colline and hyperinsubric vegetation belt in the southern Pre-Alps, tree species not currently occurring in Switzerland will find favourable conditions in future (Frehner & Zürcher-Gasser, 2019).

The chosen approach for mapping the AVBs proved to be reliable, as the comparison of the results with the samples from the national forest inventory (Frehner et al., 2021) showed. The limitation of the beech area mainly by foehn frequency and relative air humidity is in accordance with the ecophysiological properties of beech, e.g., Lendzion and Leuschner (2008). However, our approach did not allow disentangling the single factors that are influencing the tree species distribution. In the future, a decrease in relative air humidity can be expected (Ficklin & Novick, 2017), which could make it an important factor for tree species distribution in large parts of Switzerland. With increasing continentality in the inner Alps, the

**TABLE 4** Changes in temperature and precipitation for northern and southern Switzerland, modelled with the selected climate model runs, based on RCPs 2.6, 4.5, and 8.5 anomalies during the growing season (April–August) of the period 2070–2099 compared to 1981–2010

| RCP 2.6 | | | RCP 4.5 | | | RCP 8.5 | | |
|--------| -------- | -------- |--------| -------- | -------- |--------| -------- | -------- |
|        | Northern Switzerland | Southern Switzerland | Temperature [°C] | +1.0 | +0.8 | +1.8 | +2.3 | +4.4 | +4.4 |
|        | Northern Switzerland | Southern Switzerland | Precipitation | -2.1% | -1.7% | -4.0% | -0.5% | -17.0% | -24.9% |

Note: The values for temperature, precipitation and dry days were calculated for the north and south sides of the Alps for the following representative locations: Region “northern Switzerland”: Aarau (47.38° N/8.08° E/394 m); region “southern Switzerland”: Locarno (46.17° N/8.80° E/223 m). Source: (Remund, 2020). RCP, representative concentration pathway.
vegetation belts increase in altitude from the northern and southern Pre-Alps towards the Central Alps (Frehner et al., 2005/2009; Leuschner, 1996). For this reason, the belt boundaries determined in the cantons of St. Gallen and Appenzell Ausserrhoden cannot be directly transferred to the canton of Grisons located mainly in the inner Alps. Here, the continental climate, the strong frost and foehn conditions as well as the high global radiation are determining factors for the location of the AVBs. By considering them in the regression equations, these regional differences could be included in the model for northern Switzerland.

4.2 | Participatory modelling approach

The study could not have been conducted without the knowledge of the regional particularities of AVBs and STs provided by

| AVB                                           | 1961-1990 (km²) | 1981-2010 (km²) | RCP2.6 (km²) | RCP4.5 (km²) | RCP8.5 (km²) |
|-----------------------------------------------|-----------------|-----------------|--------------|--------------|--------------|
| Hyperinsubric                                 | 155             | 148             | 223          | 223          | 86           |
| Mediterrane                                    |                 |                 | 41           | 190          | 701          |
| Colline                                       | 1,101           | 1,574           | 1,466        | 4,353        | 9,992        |
| Colline with beech                            | 379             | 532             | 614          | 484          | 229          |
| Submontane                                    | 9,759           | 13,291          | 16,023       | 16,716       | 16,437       |
| Lower montane                                 | 6,074           | 4,573           | 2,842        | 1,727        | 1,185        |
| Upper montane                                 | 4,459           | 3,326           | 2,756        | 1,937        | 524          |
| Lower and upper montane (southern Switzerland)| 579             | 562             | 569          | 730          | 355          |
| High montane in main fir areal                | 1,420           | 1,434           | 1,748        | 2,003        | 949          |
| High montane in secondary fir areal           | 1,149           | 1,049           | 1,173        | 1,140        | 1,129        |
| High montane in relic fir areal               | 1,149           | 1,854           | 1,987        | 2,352        | 1,695        |
| Subalpine                                     | 3,515           | 2,857           | 2,197        | 1,300        | 16           |
| Upper subalpine                               | 3,559           | 2,096           | 1,661        | 142          | 0            |

FIGURE 8 Example of the information content of a highlighted forest site. Transition from site type (ST) “12a” (Cardamino-Fagetum typicum) to “9a” (Pulmonario-Fagetum typicum), climate scenario RCP8.5 and model run CLMCOM-CCLM5_HADGEM_EUR44. AVBs, altitudinal vegetation belts
the experts. In contrast to data-driven or machine-learning approaches, the iteration of formulating and testing hypotheses as well as the extensive discussions of regional particularities with experts and practitioners enabled the consideration of various sources of knowledge. The involvement of local and regional experts enhances the information content of a modelling framework, leads to more reliable results, and increases the acceptance of models by forest managers (Polk, 2015; Nelson et al., 2016). Moreover, the participatory modelling approach contributed to attenuating the science-practice gap in forest management (Fabian et al., 2019). The presented approach can be used as an example for a participatory modelling in climate impact and adaptation assessments. By complementing other methods (Zimmermann et al., 2016), the presented approach furthermore supports the assessment of the uncertainties in modelling climate change impacts to forests (Lindner et al., 2014).

4.3 Limitations

In the presented modelling framework, the soil characteristics could only be considered indirectly with the estimated pH values and the clay content of the soil-forming substrates. More soil information would also be desirable in the future, since the climatic dryness limit of tree species also depends on the soil nutrient status (Mellert et al., 2018). Scherrer and Guisan (2019) also emphasize that information on soil water and nutrient decisively improves plant distribution models and that the predominant temperature effects which are often found may sometimes result from the non-consideration of these edaphic factors.

Our results indicate the potential future forest community, but no information on the rate of vegetation change is possible. The approach presented is reductionist in that only the final climax under a new climate is modelled. The adaptation capacities of the tree species are neglected. Although the upward shifts of the AVBs consider topographical and edaphic characteristics beside the climate variables, possible feedback mechanisms arising from parameter combinations that differ from those of today may influence the ST transformation. Also, the method shows only the upper boundaries of future ST transformation due to climate change. However, the rate of change of the environmental conditions will probably be smaller than in lower altitudes, as demonstrated for the last decades (Rumpf et al., 2018). Without human intervention, forests will probably not be able to track rapid climatic developments (Bertrand et al., 2011). In particular, the risk of late frost in some regions can limit the spread of broad-leaved trees (Kollas et al., 2014; Vitasse et al., 2018). To a certain extent, however, trees can adapt slowly at the expense of potential growth (Lenz et al., 2013). Finally, the impacts of forest disturbance have been neglected here but must be considered in forest management (Bebi et al., 2017; Reyer et al., 2017).

4.4 Management implications

The climate impact study shows that forestry in Switzerland faces huge challenges in adapting forests to a warmer and drier climate, since at the end of the century a considerable upward shift in the vegetation belts is expected. However, the results are sensitive to the climate scenario. The RCP8.5 scenario has markedly higher impacts to Swiss forests in terms of upward shifts of AVBs than the RCP4.5 scenario. Therefore, the implementation of the presented approach into the web-based application for tree species selection tree-app.ch considers two climate scenarios. This gives the user the ability to assess the sensitivity of the forest of interest to the climate scenario. The change in tree species composition as a result of climate change requires adaptive management practices (Schelhaas et al., 2015; Yousefpour et al., 2017). The future biogeographic arrangement presented here allows a quantitative assessment of how the changing climate alters the environment for forest communities until the end of the century. This allows to list tree species suitable and unsuitable in future conditions. Moreover, this gives forest managers an important decision basis for selecting tree species to be promoted today or not. A broad tree species portfolio including drought- and heat-tolerant tree species is a further precautionary measure to safeguard ecosystem services. The significance of the results was highlighted in silvicultural guidance for adapting forests to climate change (Allgaier Leuch et al., 2017).

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AUTHOR CONTRIBUTIONS

M.F., B.H., and A.Z developed the presented methods. A.Z. performed statistical analyses and developed the simulation models. P.G. prepared data and contributed to the validation. M.F. classified the geological maps. A.Z. conducted the simulations and wrote the paper. S.A. and P.B. coordinated the work on this paper with other projects of the research initiative. All authors were involved in the participatory modelling, discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The maps of the modelled AVBs have been implemented in the official web mapping information system of the federal government of Switzerland (https://map.geo.admin.ch). The rule base for the transformation pathways of forest site types in a changing climate is available at https://doi.org/10.3929/ethz-b-000341108. The web application for supporting tree species selection is available at www.tree-app.ch.
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