

# Soil and climate-dependent ingrowth inference: broadleaves on their slow way to conquer Swiss forests

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October 18, 2023

## Abstract

Forests provide essential ecosystem services that range from the production of timber to the mitigation of natural hazards. Rapid environmental changes, such as climate warming or the intensification of disturbance regimes, threaten forests and endanger forest ecosystem services. In light of these challenges, it is essential to understand forests' demographic processes of regeneration, growth, and mortality and their relationship with environmental conditions. Specifically, understanding the regeneration process in present-day forests is crucial since it lays the foundation for the structure of future forests and their tree species composition. We used Swiss National Forest Inventory (NFI) data covering vast bio-geographic gradients over four decades to achieve this understanding. Trees that reached a diameter at breast height of *12 cm* between two consecutive NFI campaigns were used to determine regeneration and were referred to as ingrowth. Employing three independent statistical models, we investigated the number, species, and diameter of these ingrowth trees. The models were subsequently implemented into a forest simulator to project the development of Swiss forests until the mid-21<sup>st</sup> century. The simulation results showed a decrease and a shift in the species composition of ingrowth, marked by a significant decrease in Norway spruce (*Picea abies*) and concurrent increases in broadleaves. Nevertheless, the pace of this change towards a more natural species composition is relatively slow and is likely to slow down even further as ingrowth declines in the future, in contrast to the fast-changing climatic conditions. Hence, support through adaptive planting strategies should be tested in case ingrowth does not ensure the resilience of forests in the future. We conclude that since the regeneration of forests is becoming increasingly challenging, the current level at which ecosystem services are provided might not be ensured in the coming decades.

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22 **Keywords** National forest inventory, climate change, natural regeneration, ecosystem sustainability,  
23 forest development, forest simulations.

# 1 Introduction

Forests provide essential ecosystem services, including timber resources, biodiversity, or natural hazard mitigation (Winkel et al., 2022). However, rapid and substantial environmental changes, such as climate warming or the intensification of disturbance regimes, threaten forests and endanger these ecosystem services (Fischer and Knutti, 2015). Consequently, forests need to adapt quickly to changing conditions to maintain the current level of provision of these essential services. Adaptation might be particularly challenging for forests in Switzerland and central Europe, where forest management has significantly shaped forest development over centuries. Notably, practices from the 19<sup>th</sup> century continue to influence the composition and structure of Swiss forests today (Seim et al., 2022; Scherrer et al., 2023a; Temperli et al., 2023). A deep understanding of the processes governing forest development is thus crucial, considering the situation from today and the climate from tomorrow.

Besides human activities, forest developments are driven and shaped by the demographic processes regeneration, growth, and mortality (Bormann and Likens, 1979). While modeling growth and harvesting dynamics has a long tradition in forest science (Pretzsch, 2009; Weiskittel et al., 2011; Rohner et al., 2018), and mortality has recently gained increased attention (Nothdurft, 2013; Senf et al., 2020; Frei et al., 2022), the emphasis on regeneration has been comparatively limited. Regeneration studies often focused on specific tree species or regions (Klopčič et al., 2012; Axer et al., 2021; Trifković et al., 2023). This situation has led to a research gap in the comprehensive assessment of the tree species composition in the regeneration across diverse environmental contexts, hindering projections into the future and to broader areas. While Li et al. (2011), Zell et al. (2019), and Mathys et al. (2021) attempted such a holistic perspective on temperate forest regeneration, their scope was mainly confined to explaining past and current patterns. Hence, understanding how regeneration – together with growth, and mortality and given the climate pressure – will shape future forest dynamics remains a crucial challenge that needs to be tackled.

National Forest Inventory (NFI) data are a fundamental cornerstone to investigate forest states and changes from regional to national scales. They provide comprehensive and representative national-level insights into the complex realm of forest development (Tomppo et al., 2010; Vidal et al., 2016; Fischer and Traub, 2019). The Swiss NFI, in particular, embodies a unique wealth of information that captures the range of forest dynamics across Switzerland’s large environmental gradients, from lowlands to alpine regions and from northern, cold slopes to warmer southern climates. This vast bio-geographical gradient over forty years makes it an invaluable repository for studying forest developments. It allows extrapolating into the future and drawing transferable conclusions to other temperate forests. In NFIs, regeneration can be measured with newly observed trees reaching a given caliper threshold between two consecutive sampling campaigns. These newly observed trees are referred to as ingrowth trees that, in the context of the Swiss NFI, reached a 12 *cm* diameter at breast height (*dbh*).

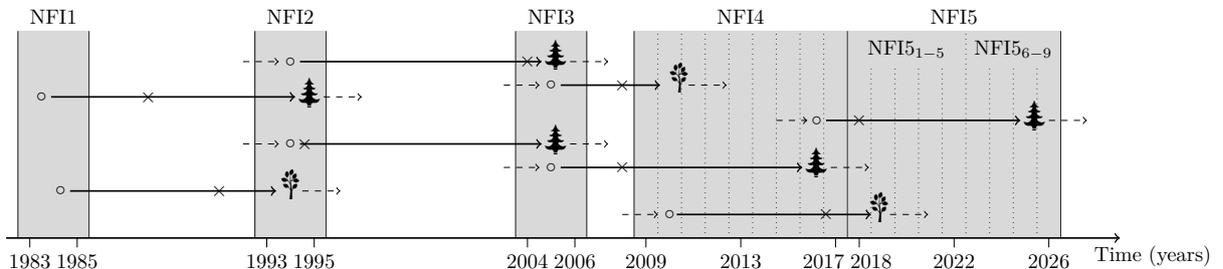
Simulations have proven valuable tools for predicting future trajectories of forest development (König et al., 2022). Forest simulation frameworks, particularly those tailored to NFIs, have gained importance due to their capacity to use actual observations as input, enabling the dynamic modeling of plausible

62 forest development trajectories (Barreiro et al., 2017). In the context of the Swiss NFI, the forest growth  
 63 simulator MASSIMO (Stadelmann et al., 2019) is an established tool used to predict future scenarios  
 64 for governmental and international protocols (Stadelmann et al., 2021). MASSIMO allows predictions of  
 65 forest developments across Swiss regions, leading to a deeper understanding of the forest dynamics under  
 66 varying environmental conditions. Until now, the focus of MASSIMO has been on predicting growth and  
 67 biomass estimates under different management scenarios.

68 In this study, we employed statistical modeling to gain insight into the future evolution of ingrowth and  
 69 its effects on forest development in Switzerland. Therefore, we improved existing models from Zell et al.  
 70 (2019) by revisiting their formulations and including the latest forest data as well as climate and state-  
 71 of-the-art information on soil properties. Our primary objective was to enhance the predictive accuracy  
 72 of these models and give insight into the influence of diverse predictor variables on the three aspects of  
 73 ingrowth, i.e., number, species composition, and diameter of ingrowth trees. To project ingrowth into  
 74 the future, we updated the existing MASSIMO ingrowth module with the newly developed statistical  
 75 ingrowth models and improved the linkage between these models by modeling the *dbh* of the ingrowth  
 76 trees species-specific. We then used MASSIMO to simulate forest development until the mid-21<sup>st</sup> century  
 77 to understand better how ingrowth might develop into the future and how this could affect the species  
 78 composition of Swiss forests.

## 79 2 Material and Methods

### 80 2.1 Data



**Figure 1:** NFI sampling campaigns: the grey area represents the period during which an NFI sampling campaign is conducted, 'o' indicates the timepoint of one plot's previous measurement, the tree symbols show when that plot was remeasured (and therefore when ingrowth was observed), 'x' is the actual but unknown time point when an ingrowth tree passed the caliper threshold of 12 cm, and the dashed arrows symbolize the continuous measurements of plots (i.e., permanent plots).

81 Since the 1980s, forests in Switzerland have been monitored by NFI campaigns. The Swiss NFI  
 82 currently comprises five campaigns with roughly 6'000 permanent sample plots on a regular 1.4 km grid.  
 83 Each plot consists of two concentric circles around the plot center with an area of 200 m<sup>2</sup> and 500 m<sup>2</sup>,  
 84 with diameter thresholds of 12 cm and 36 cm, respectively. NFI1-3 were carried out as three-year sampling  
 85 campaigns, with each plot being revisited after eight to twelve years. From NFI4 onward, a transition  
 86 from serial to nine-year continuous sampling campaigns was implemented, with one-ninth of the plots

87 being revisited annually (Lanz et al., 2019); cf. Figure 1. In this study, we also included the first five  
88 years of the NFI5 campaign (NFI5<sub>1-5</sub>), including 2'267 plots.

89 In the context of the Swiss NFI, ingrowth refers to living and standing trees within the inner plot  
90 circle that reach the threshold of 12 cm diameter at breast height (*dbh*; [cm] rounded to the next smaller  
91 integer) between two consecutive inventory campaigns. The number of new ingrowth trees per plot  
92 is referred to as the number of ingrowth ( $n_{in}$ ; [#]). The species of ingrowth trees are classified into  
93 twelve so-called main-species groups (*species*; {*spruce* (*Picea abies*), *fir* (*Abies alba*), *pine* (*Pinus spp.*),  
94 *larch* (*Larix spp.*), *stone pine* (*Pinus cembra*), *other conifers*, *beech* (*Fagus sylvatica*), *maple* (*Acer spp.*),  
95 *ash* (*Fraxinus spp.*), *oak* (*Quercus spp.*), *chestnut* (*Castanea sativa*), *other broadleaves*}); cf. Supporting  
96 information for detailed description and summary statistics of the main species groups.

97 In the Swiss NFI, many plot- and tree-level characteristics are assessed and measured, some of which  
98 were used as predictor variables in the statistical models and are described below. Forest stand char-  
99 acteristics were represented by basal area per hectare (*ba*; [ $m^2/ha$ ]), the share of basal area harvested  
100 since the previous sampling campaign (*bah*; [%]), number of stems per hectare (*nph*; [#/*ha*]), and mean  
101 tree diameter ( $\overline{dim}$ ; [cm]). Furthermore, we used categorical data describing the leading species, i.e., the  
102 species with the highest basal area per plot (*lead<sub>species</sub>*), using the same groups as *species*. The mixture  
103 variable (*mixture*; {*conifers*, *mixed*, *broadleaves*}) contained the categories *conifers* if at least 90% of the  
104 basal area was conifer trees, *broadleaves* if less than 10% of the basal area was conifer trees and *mixed*  
105 otherwise. Additionally, the Swiss NFI records many site-level characteristics, from which we used slope  
106 (*slope*; [%]) and – as categorical predictor variables – forest type (*ft*; {*unstocked*, *regeneration*, *coppice*,  
107 *selection*, *pole*, *timber*}) and ownership (*os*; {*private*, *public*}). Whether a plot has a protective function  
108 against rockfall and avalanches is contained in the variable *protection* {*no*, *yes*}. Furthermore, forests in  
109 Switzerland are divided into five production regions, which share similar geologic, topographic, climatic,  
110 environmental, and economic characteristics (*pr*; {*Jura mountains*, *Plateau*, *Pre-Alps*, *Alps*, *Southern*  
111 *Alps*}).

112 We used climate variables: temperature, precipitation, and solar radiation (Brunner et al., 2019). A  
113 recent study by Etzold et al. (2021) found that spring conditions mainly drive temperate trees' growth.  
114 Accordingly, we considered as predictor variables the average temperature (*temp*; [ $^{\circ}C$ ]), precipitation  
115 (*precip*; [mm]), and solar radiation (*ra*; [ $W/m^2$ ]) values of March, April, and May over the ten vegetation  
116 periods leading up to the sampling date. Hence, if a sampling date occurred before the end of May, the  
117 ten vegetation periods ending the year before were considered. Vegetation periods are defined in the Swiss  
118 NFI as May to September and aim at representing the period when tree growth occurs. We calculated a  
119 drought index (*di*; [-]) based on the precipitation and potential evapotranspiration ratio for the summer  
120 months of June, July, and August over the previous ten vegetation periods. In addition, we used modeled  
121 yearly data about Nitrogen-depositions (*ndep*; [ $kgN/ha$ ]) interpolated for each plot location (Rihm and  
122 Künzle (2019, 2023)) that we averaged over the ten vegetation periods before the sampling date.

123 We included a set of predictor variables reflecting soil properties. These predictors were extracted  
124 for each plot location from modeled soil maps, which provide information on clay content (*clay*; [wt%]),  
125 acidity (*pH*; [-]), and humus carbon content (*humus (C)*; [wt%]) from Baltensweiler et al. (2021), as

126 well as available water capacity (*awc*; [ $km^3$ ]) from Meusburger et al. (2022). We considered soil variables  
 127 within a layer between ground level and one-meter depth, as suggested by Walthert et al. (2013) to reflect  
 128 optimal nutrient availability. In cases where multiple layers between ground level and one-meter depth  
 129 were available, we computed the mean of these layers for our analysis.

## 130 2.2 Statistical ingrowth models

131 We analyzed three aspects of ingrowth – the number, *species*, and *dbh* of ingrowth trees – using three  
 132 independent statistical models (Zell et al., 2019). To fit these models, we used data from NFI1-4 and  
 133 NFI5<sub>1–5</sub> data for validation. Standardizing predictor variables enabled the comparison of estimated  
 134 effects. We evaluated the fitted models rigorously using various metrics such as residual analysis, root  
 135 mean squared error, and  $R^2$ . Variable selection was performed independently for the three models  
 136 through a comprehensive approach leveraging ecological knowledge, literature, and statistical criteria.  
 137 Ecological knowledge served as the primary basis for selecting variables for each model, while an additional  
 138 selection of predictor variables based on the Bayesian information criterion (BIC) helped identify the most  
 139 parsimonious models (Stoica and Selen, 2004). We performed these analyses using the statistical software  
 140 R (R Development Core Team, 2022).

### 141 2.2.1 Number of ingrowth trees

142 The number of ingrowth trees exhibited a high frequency of zero occurrences and was therefore mod-  
 143 eled according to a zero-inflated count distribution. This zero-inflated model has two components: the  
 144 probability of observing ingrowth and the count of ingrowth. Both components were estimated simulta-  
 145 neously. Thereby, the counts were modeled with a Poisson distribution. The probability mass function  
 146 of a zero-inflated Poisson (ZIP) random variable  $Y_i$  for  $i \in 1, \dots, n$  (where  $n$  is the total number of plots  
 147 visited from NFI1-4; each plot can be revisited up to three times) is defined as follows. Let  $\lambda > 0$  be the  
 148 rate parameter,  $p \in (0, 1)$  the probability of no ingrowth, respectively  $p - 1$  the probability of ingrowth  
 149 characterized with the probability mass function of a Poisson random variable. Thereby, the probability  
 150 of observing no ingrowth is corrected to account for the possibility of a zero realization from the Poisson  
 151 distribution (Lambert, 1992), such that its probability mass function corresponds to:

$$f_{ZIP}(n_{in}; p, \lambda) = \Pr(Y_i = n_{in}) = \begin{cases} 0 & \text{with } p + (1 - p) \exp(-\lambda) \\ n_{in} & \text{with } (1 - p) \frac{\lambda^{n_{in}} \exp(-\lambda)}{n_{in}!} \end{cases} \quad \text{for } n_{in} \in \mathbb{N}^+.$$

152 Based on existing literature (Zhang et al., 2012; Walthert et al., 2013; Zell et al., 2019), several  
 153 predictor variables were *a priori* identified as crucial for modeling  $n_{in}$ . These variables include *ft*, *ba*, *nph*,  
 154 *bah*, *temp*, *precip*, *di*, *ndep*, *awc*, *clay*, and an interaction term between *ba* and *nph*. Through stepwise  
 155 BIC optimization, the additional variables *slope*,  $\overline{dim}$ , *ra*, and *ph* were selected to define the best-fitting  
 156 model.

### 157 2.2.2 Species of ingrowth trees

158 We used the twelve *species* groups as a nominal response variable in a multinomial logistic regression  
 159 model (Agresti, 2002). The model is constructed by choosing the most dominant *species* (*spruce*) as

160 the baseline category and then regressing the remaining eleven species groups against this baseline with  
 161 binary logistic models. To model the *species* as a set of eleven binary choices, we must assume that  
 162 the probability of selecting a particular *species* over *spruce* is independent of the presence or absence of  
 163 other alternatives in the choice set. The odds that an ingrowth tree  $y_\ell$  belongs to a specific species group  
 164 instead of *spruce* are modeled using  $m$  predictor variables  $\mathbf{x}_1$  to  $\mathbf{x}_m \in \mathbb{R}^{n_{\text{tree}}}$  with species-specific effects  
 165  $\beta_{\text{species},0}, \dots, \beta_{\text{species},m}$  (i.e., dependent on the species-specific effects the odds are higher or lower for  
 166 another *species* than *spruce*). Thereby,  $\ell = 1, \dots, n_{\text{tree}}$ , and  $n_{\text{tree}}$  denotes the total number of ingrowth  
 167 trees in the data.

$$\frac{\Pr(Y = \textit{fir})}{\Pr(Y = \textit{spruce})} = \exp(\beta_{\textit{fir},0} + \beta_{\textit{fir},1}\mathbf{x}_1 + \dots + \beta_{\textit{fir},m}\mathbf{x}_m),$$

$$\frac{\Pr(Y = \textit{pine})}{\Pr(Y = \textit{spruce})} = \exp(\beta_{\textit{pine},0} + \beta_{\textit{pine},1}\mathbf{x}_1 + \dots + \beta_{\textit{pine},m}\mathbf{x}_m),$$

...

168 For the predictor variable selection, i.e., the final  $\mathbf{x}_1$  to  $\mathbf{x}_m$ , the null-model included the  $\textit{lead}_{\textit{species}}$   
 169 representing potential seed trees, site conditions ( $\textit{nph}$ ,  $\textit{ba}$ ,  $\textit{bah}$ ), climatic factors ( $\textit{temp}$ ,  $\textit{precip}$ ,  $\textit{di}$ ), and  
 170 soil predictors ( $\textit{awc}$ ,  $\textit{clay}$ ) (Li et al., 2011; Walthert et al., 2013; Zell et al., 2019). The final selection was  
 171 performed using a BIC optimization; cf. Supporting information for the final model, which includes 17  
 172 predictor variables and three interactions.

### 173 2.2.3 Diameter of ingrowth trees

174 We independently modeled the  $\textit{dbh}$  divided by the number of vegetation periods (henceforth:  $\textit{dbh}$  rate) of  
 175 ingrowth trees for each *species*. It is determined by the measured  $\textit{dbh}$  divided  $\textit{vegper}$  between consecutive  
 176 NFI campaigns. The  $\textit{dbh}$  rate is modeled using a Weibull distribution function (Weibull, 1951), which is  
 177 suitable for such rates:

$$f_W(x; \lambda, k) = \begin{cases} \frac{k}{\lambda} \left(\frac{x}{\lambda}\right)^{(k-1)} \exp\left(-\left(\frac{x}{\lambda}\right)^k\right), & x \geq 0 \\ 0 & x < 0. \end{cases}$$

178 The parameters  $\lambda > 0$  and  $k > 0$  in the Weibull distribution represent the scale and shape, both positive  
 179 real numbers. The expected value and the mode of a Weibull distribution are defined as:

$$\mathbb{E}[X] = \lambda * \Gamma(1 + 1/k)$$

180 Assuming that the shape parameter  $k$  is fixed, the scale parameter scales the expected value. Hence,  
 181 re-parameterizing  $\lambda$  with a linear model offers the same scale interpretation of its effects. Therefore, we  
 182 used the predictor variables  $\textit{nph}$ ,  $\textit{slope}$ ,  $\textit{awc}$ ,  $\textit{clay}$ ,  $\textit{temp}$ ,  $\textit{precip}$ , and  $\textit{ndep}$  such that:

$$\lambda = \exp(\beta_0 + \beta_1 * \textit{nph} + \beta_2 * \textit{slope} + \beta_3 * \textit{awc} + \beta_4 * \textit{clay} + \beta_5 * \textit{temp} + \beta_6 * \textit{precip} + \beta_7 * \textit{ndep}).$$

183 An exponential transformation is applied to the linear effects to ensure that the linear scale parameter  
 184 remains well-defined, i.e.,  $\lambda > 0$  holds. We jointly estimated the linear effects  $\beta_0, \dots, \beta_7 \in \mathbb{R}$  of the

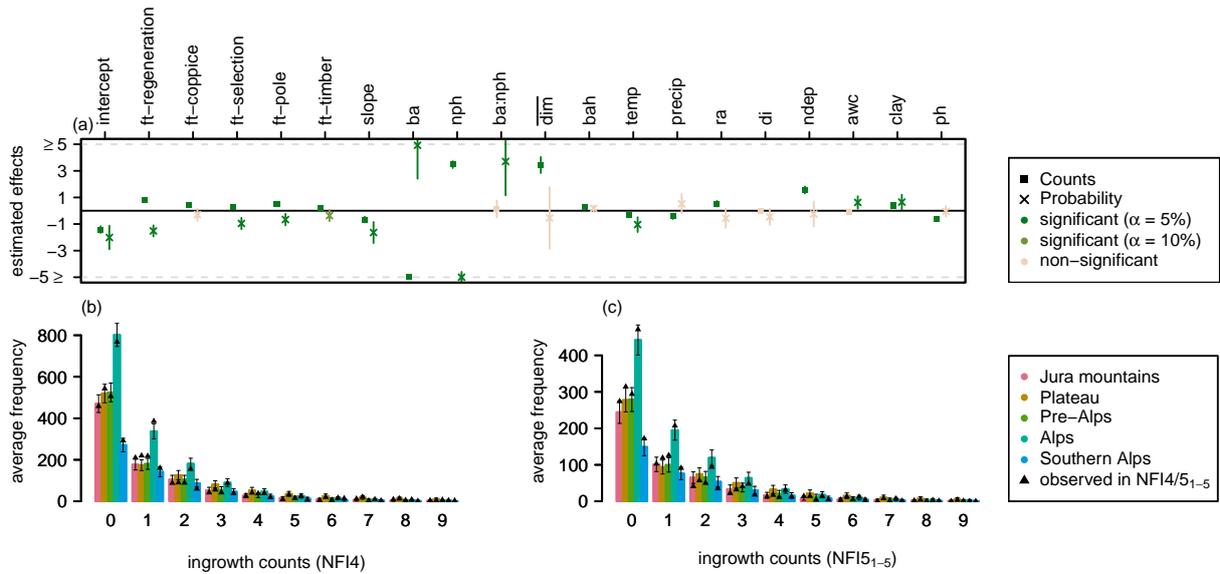
185 predictor variables and the shape parameter  $k$  via the likelihood function of the Weibull distribution (Held  
186 and Sabanés Bové, 2014). The predictor variables were selected based on the literature (Walthert et al.,  
187 2013; Rohner et al., 2018; Zell et al., 2019), and the optimal model was chosen based on the BIC, but  
188 considering numerical stability while optimizing the likelihood function.

## 189 2.3 MASSIMO simulations

190 MASSIMO is a climate-sensitive individual-tree growth simulator that operates on the Swiss NFI grid to  
191 produce outputs representative of Swiss forests (Stadelmann et al., 2019). The processes implemented in  
192 MASSIMO were empirically derived from NFI observations. In addition to ingrowth, this includes the  
193 other demographic processes growth (Rohner et al., 2018), mortality (Stadelmann et al., 2021), as well  
194 as management and disturbances.

195 We added the new ingrowth module to MASSIMO based on the statistical ingrowth models previously  
196 described, replacing the former module by Zell et al. (2019). This module predicts for each plot the number  
197 of ingrowth trees. Then, their *species* is predicted, and subsequently, the *dbh* for each ingrowth tree.  
198 Changing the order of the *species* and *dbh* models compared to the previous approach, thus allowing *dbh* to  
199 be modeled species-specific, was expected to improve the predicted species composition in the simulations.  
200 To assess the impact of the newly developed ingrowth module and its effect on the species composition  
201 in Swiss forests, we ran simulations using the *Recent Management Practices* (RMP) scenario described in  
202 (Stadelmann et al., 2021). This scenario assumes increasing growing stock in Swiss forests until mid-21<sup>st</sup>  
203 century, i.e., the year 2056. We applied a moderate RCP 4.5 climate warming scenario from Brunner et al.  
204 (2019) based on the CH2018 (2018) climate scenario that results in a global warming of approximately  
205 2.5°C (IPCC, 2013). Regional climate models were downscaled to MeteoSwiss stations (Feigenwinter  
206 et al., 2018). To derive elevation-dependent point estimates on the NFI plots, data at Swiss weather  
207 stations were further downscaled (Brunner et al., 2019). The MASSIMO simulations were run for fifty  
208 years, corresponding to five time steps. To account for stochasticity in the plot and tree selection for  
209 harvesting, storm damage, and other processes, we ran hundred replicates of the simulation. Simulation  
210 results were upscaled to the forest area per production region as well as for the entire country (Kaufmann,  
211 2001).

212 To analyze the predicted changes in the *species* composition of Swiss forests until 2056, as projected  
213 by the MASSIMO simulations, we calculated the proportion of ingrowing trees belonging to each species  
214 group (i.e., the per *ha* species-specific number of ingrowth trees divided by the total per *ha* number of  
215 ingrowth trees) in 2056 as well as in 2016. The proportion in 2056 minus the proportion in 2016 was then  
216 referred to as the change of proportion of a *species*. This comparison was also made for survivor trees  
217 (i.e., living trees excluding ingrowth trees) and total trees (ingrowth plus survivor trees).



**Figure 2:** Results from the ZIP model of the number of ingrowth trees: (a) regression effects explaining the ingrowth counts and the probability of ingrowth; (b) barplots demonstrating the goodness of fit of the model based on only NFI4 data by displaying the distribution of modeled ingrowth counts and observed  $n_{in}$  for each production region; (c) barplots validating the predictive accuracy of the model by displaying the predicted  $n_{in}$  based on NFI5<sub>1-5</sub> data and observed  $n_{in}$  for each production region.

### 3 Results

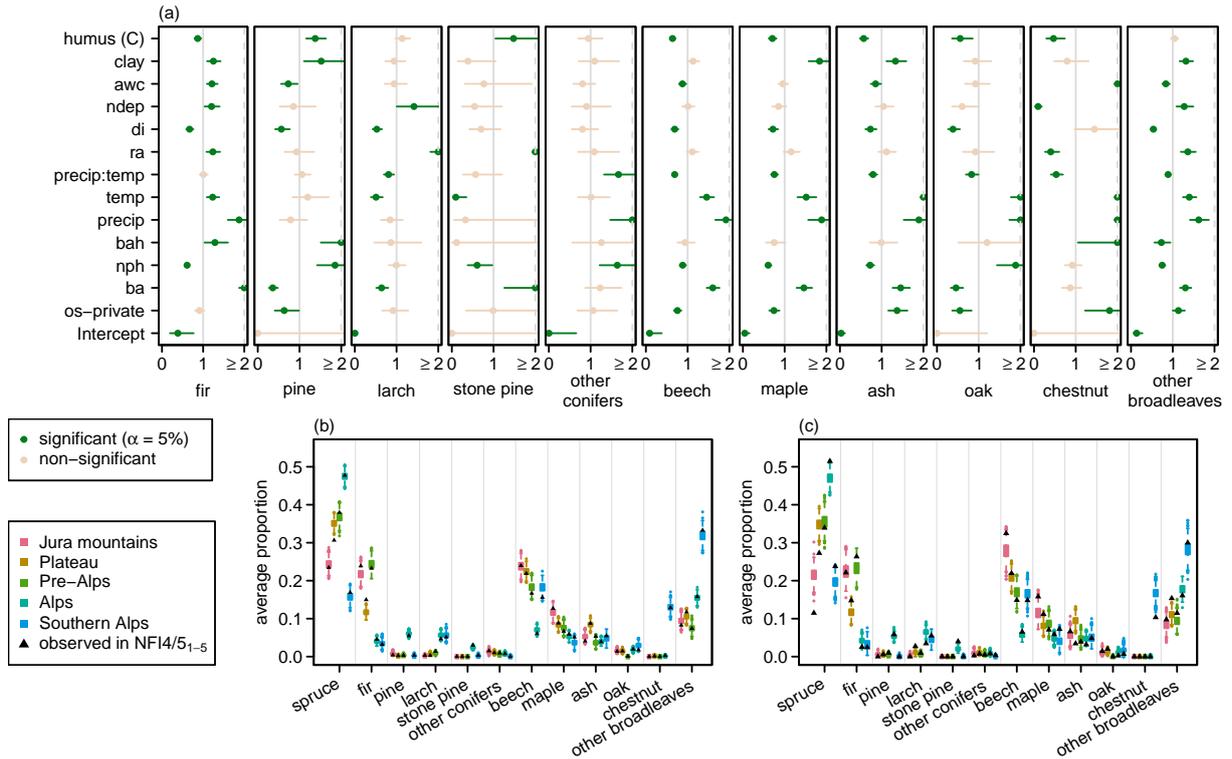
#### 3.1 Number of ingrowth trees

The zero-inflation model for the number of ingrowth trees per sampling plot provided estimates of the effects of predictor variables on the probability of ingrowth occurrence and the count of ingrowth trees per plot; cf. Figure 2. The model achieved a root-mean-squared error of 3.20, signifying a good fit to the data. Furthermore, this value closely aligns with the square root of the variance of the observed  $n_{in}$  (2.90), indicating unbiased estimates. The model's  $R^2$  value is 0.37, showcasing a substantial level of explained variance. Panels (b) and (c) of Figure 2 compare the observed  $n_{in}$  of NFI4 and NFI5<sub>1-5</sub> with the corresponding fitted predicted ingrowth counts for each production region. In both cases, the proportion of plots containing one ingrowth tree was slightly underestimated, but this effect was balanced out by the plots with two or three ingrowth trees.

Several significant factors influenced the number of ingrowth trees. Notably, climate variables like spring temperatures and precipitation negatively affected ingrowth counts, while radiation had a positive influence. Soil properties played a role, with increased *awc* and *clay* positively correlating with ingrowth probability and counts, and soil *pH* negatively affecting ingrowth.

#### 3.2 Species of ingrowth trees

When the selected model was applied to NFI1-4 data, *species* were, on average, 54.09% fitted correctly, and when applied to NFI5<sub>1-5</sub> data, on average, 48.46% were predicted correctly. A comparison of the boxplots with the corresponding observed proportions suggests an overall highly accurate fit. The



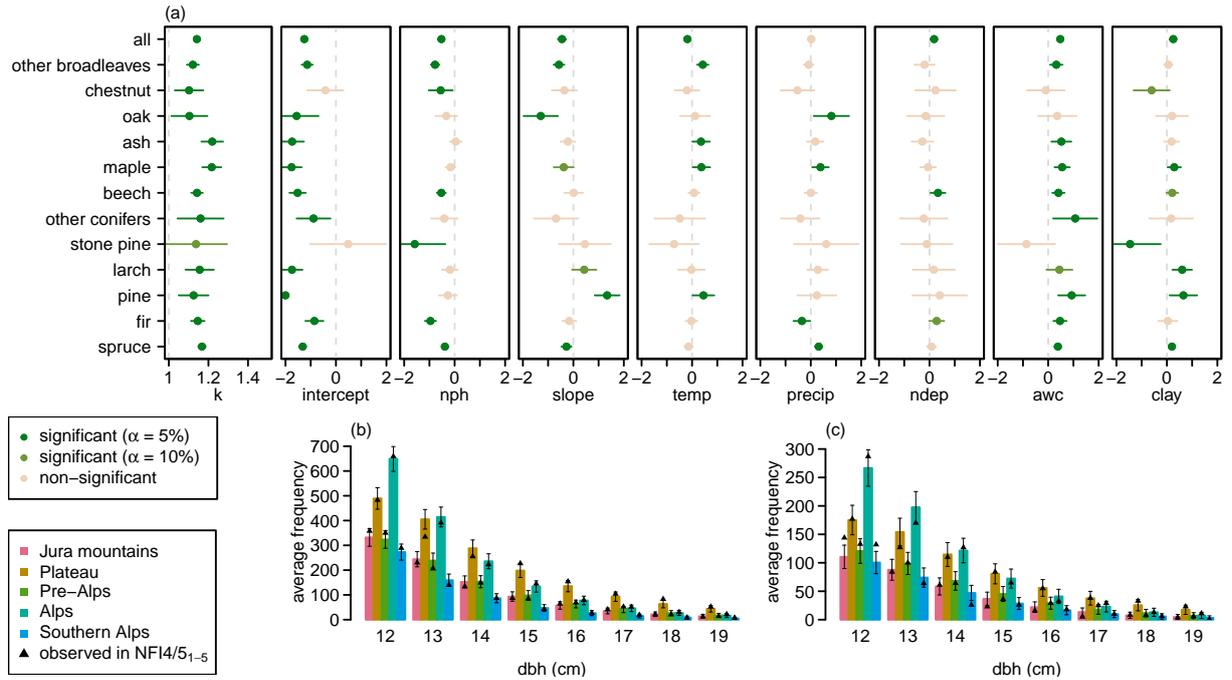
**Figure 3:** Results from the multinomial logistic regression model of the *species* of ingrowth trees: (a) selection of noteworthy odds ratios between the baseline species *spruce* compared to each other *species*; (b) boxplots demonstrating the goodness of fit of the model based on only NFI4 data by displaying the proportions of modeled and observed *species* for each production region; (c) boxplots validating the predictive accuracy of the model by displaying the predicted and observed *species* based on NFI5<sub>1-5</sub> data for each production region.

237 performance of the model was also relatively high within each production region (Figure 3 (b) and (c)),  
 238 except for *spruce* for which predictions appeared to be overestimated in NFI5<sub>1-5</sub>.

239 Figure 3 (a) presents the most noteworthy estimated odds ratios (likelihood of observing a *species*  
 240 other than the baseline *species* (*spruce*)) of the *species* model. Cf. the Supporting information for the  
 241 coefficients of the final model. Climatic predictor variables played a crucial role, with spring temperature  
 242 and precipitation significantly affecting most *species*. Higher *temp* increased the odds of *fir* and *other*  
 243 *broadleaves*, while the interaction between *temp* and *precip* generally favored the odds of *spruce* ingrowth.  
 244 Moreover, increased solar radiation promoted *fir*, *larch*, *stone pine*, and *other broadleaves*. Soils with high  
 245 *awc* positively influenced the odds of *fir* and *chestnut* but negatively affected the odds of *pine*, *beech*, *ash*,  
 246 and *other broadleaves* compared to *spruce*. *clay* had a positive effect on several *species*, including *fir* and  
 247 *pine*, *maple*, *ash*, and *other broadleaves*. An increase in *humus (C)* amplified the odds of *pine* and *stone*  
 248 *pine* but reduced the odds of *fir*, *beech*, *maple*, *ash*, *oak*, and *chestnut* compared to *spruce*.

### 249 3.3 Diameter of ingrowth trees

250 Across all production regions and *dbh* values, the observed *dbh* is within the confidence intervals based  
 251 on the predictions, indicating high predictive accuracy of our model; cf. Figure 4. The *dbh* ingrowth  
 252 rates of *pine*, *maple*, *ash*, and *other broadleaves* were significantly positively affected by higher spring



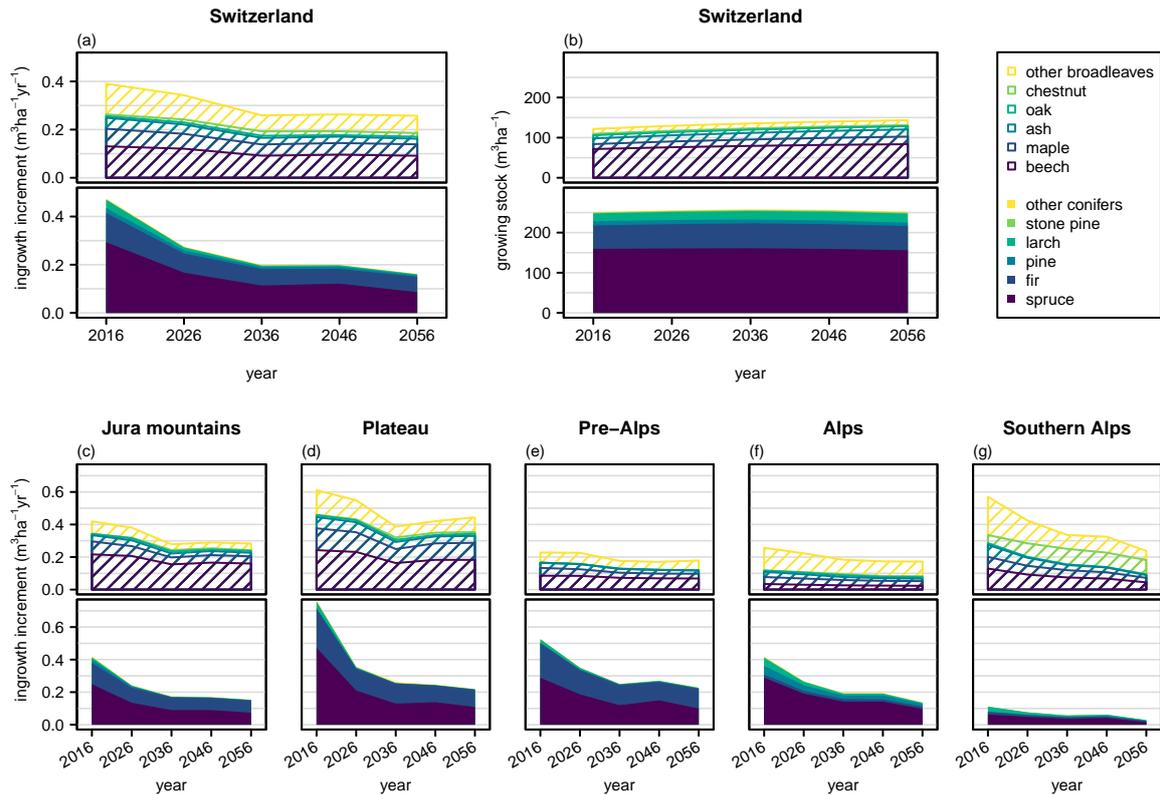
**Figure 4:** Results from the Weibull model of *dbh* of ingrowth trees: (a) effects of different predictor variables on the scale parameter  $\lambda$  of the Weibull distribution and the shape parameter  $k$ ; (b) barplots demonstrating the goodness of fit with random draws from the Weibull distribution based on the estimated maximum likelihood estimates for NFI4 for each production region; (c) barplots validating the predictive accuracy of the model by displaying the predicted and observed *dbh* based on NFI5<sub>1-5</sub> data for each production region.

253 temperatures. Spring precipitation exhibited a positive association with *dbh* ingrowth rates for *spruce*,  
 254 *maple*, and *oak*, but a significant negative association was observed for *fir*. Regarding the influence of  
 255 *ndep*, significant positive effects were observed for *fir* and *beech*. Regarding soil, a positive association  
 256 was found between *awc* and *dbh* ingrowth rates for most species, except for *stone pine*, which showed  
 257 a non-significant negative effect. A similar trend was observed for *clay*, although a negative association  
 258 was observed for *stone pine* and *chestnut*.

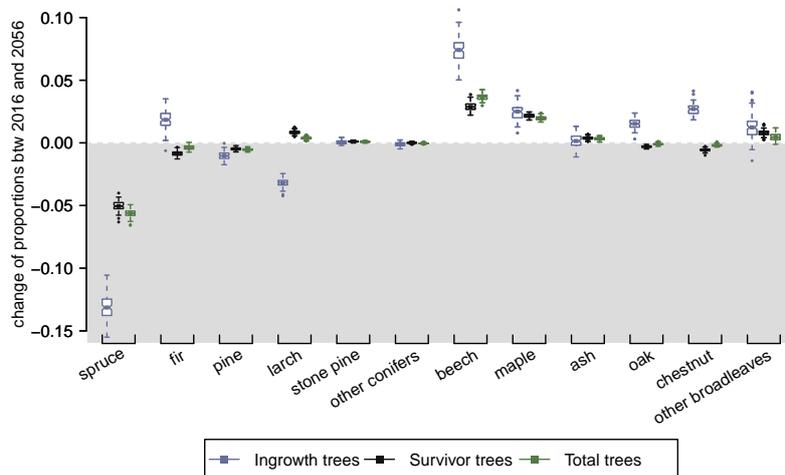
### 259 3.4 MASSIMO simulations

260 At the national scale, simulations revealed a substantial drop in ingrowth until 2056: the cumulative (all  
 261 species) ingrowth declined from  $0.86 \text{ m}^3/\text{ha}$  per year in 2016 to  $0.42 \text{ m}^3/\text{ha}$  per year in 2056; cf. Figure 5.  
 262 The total growing stock increased for all *species* slightly except for *spruce*, *pine*, and *chestnut*, with  
 263 an overall increase from  $373 \text{ m}^3/\text{ha}$  in 2016 to  $395 \text{ m}^3/\text{ha}$  in 2056. Note that the total growing stock  
 264 development is driven by the scenario RMP (Stadelmann et al., 2021).

265 At the national scale, we found more pronounced *species* changes in ingrowth than survivor trees  
 266 (Figure 6). For detailed results per production region, cf. Supporting information. Results notably  
 267 showed a strong decrease in *spruce* and *larch* ingrowth, while *fir* and broadleaves generally increased.  
 268 These trends were also visible for survivor trees but to a lesser extent.



**Figure 5:** Results from the MASSIMO simulations based on the RCP 4.5 climate and RMP management scenarios: (a) ingrowth increment (annual volume increase per *ha*) and (b) total growing stock development of each *species* from 2016 until 2056 for Switzerland; (c)-(g) ingrowth increment of each *species* from 2016 until 2056 per production region.



**Figure 6:** Projected changes in *species* compositions for Switzerland based on MASSIMO simulations: the proportion of ingrowth trees per *species* (number of ingrowth trees per *ha* of a given *species* divided by the total number of ingrowth trees per *ha*) in 2056 minus the proportion of ingrowth trees of the same *species* in 2016. Changes are also shown for the number of survivors (i.e., living trees without ingrowth) and total living trees (survivors plus ingrowth). A positive value indicates an increase in the proportion of trees of a given *species* between 2016 and 2056, while a negative value indicates a decrease.

## 4 Discussion

While NFIs traditionally focused on monitoring and reporting topics related to timber production and forest management (Vidal et al., 2016), recent studies demonstrated its applicability to ecological questions (Portier et al., 2022; Scherrer et al., 2022). The Swiss NFI data holds outstanding relevance in comprehending forest development processes across large environmental gradients, underscoring its relevance in understanding European temperate forests. The temporal dimension of this dataset, spanning over four decades, offers a unique lens into recorded management practices and evolving forest dynamics in a warming climate. These wide temporal and spatial dimensions make the Swiss NFI an ideal resource for analyzing and projecting forest development processes, such as regeneration.

### 4.1 Ingrowth models

Building on the research by Zell et al. (2019), we analyzed ingrowth dynamics in Swiss forests employing a trilogy of statistical models targeting at the prediction of number, *species*, and *dbh* of ingrowth. All three models exhibited robust predictive accuracy and adaptability to data temporally independent from the data used in the model fitting, as shown by the model validation process. A novel aspect introduced here is the species-dependent *dbh* model, capturing the growth responses of different tree *species*, each with their specific set of predictor variables and corresponding effects (Rohner et al., 2018). Another original aspect of this study is the integration of state-of-the-art model-derived soil data, in addition to the commonly used predictors (Baltensweiler et al., 2021; Meusburger et al., 2022), which are known to affect tree growth and health. This enabled a more comprehensive depiction of ingrowth dynamics, elevating the credibility of estimated effects by better depicting the complex and interacting relationships between environmental conditions (González de Andrés, 2019). Our models effectively captured this previously unexplored interplay of climate and site characteristics. For instance, soil variables allowed the effect of temperature on ingrowth to be modulated by soil characteristics. Four soil variables principally affected ingrowth: *awc*, *clay* content, *pH*, and *humus (C)* content. Soils with higher *awc* are better able to retain water, subsequently positively influencing ingrowth *dbh* rates and number. By mitigating water stress resulting from high temperature and/or low precipitation, a higher soil *awc* enhances tree resilience to drought and fosters favorable conditions for tree development. Our analysis reveals that higher clay content positively influences ingrowth numbers and *dbh* of *spruce*, *pine*, *larch*, *beech*, and *maple*. Indeed, soils rich in *clay* retain water and nutrients, fostering tree development and growth (Walthert et al., 2013).

Our findings confirmed previous findings depicting the effects of environmental factors on ingrowth (Klopčič et al., 2012; Li et al., 2011; Zell et al., 2019). For instance, increasing temperatures led to lower numbers of ingrowth trees due to temperature-induced stress, to a higher share of broadleaves, potentially even in alpine regions (Condés et al., 2022), and finally to higher *dbh* rates in *maple*, *ash*, and *other broadleaves*. Solar radiation emerges as a statistically significant positive driver of the number of ingrowth trees, likely because it leads to more light and energy resources. Areas with higher elevations and steeper slopes exhibit higher radiation levels, particularly in alpine regions. The adverse effects of higher

306 temperatures on tree growth may be linked to drought stress at lower elevations, while radiation helps to  
307 counterbalance the harsh cold climate typical to higher elevations. Moreover, more precipitation promotes  
308 the ingrowth of broadleaves *species* over *spruce* and leads to an increased *dbh* rate for oak. Higher *ndep*  
309 generally fosters the number of ingrowth trees, likely due to its fertilization effect on trees (Braun et al.,  
310 1999).

311 Traditional stand and site predictor variables complete the set of effects on ingrowth (Zell et al.,  
312 2019). High *ba* and *nph* hinder the number of ingrowth trees as they reduce light and space availability,  
313 leading to the competitive exclusion of juvenile trees (Kimmins, 2004). However, young, even-aged forests  
314 can exhibit high *nph* alongside relatively low *ba*, while old forests can comprise few large trees with high  
315 *ba* and relatively low *nph*. This explains the contrasting effects of these variables on the ingrowth tree  
316 counts and probabilities. This is also supported by the effect of  $\overline{dim}$ , where a higher value leads to more  
317 ingrowth trees. Due to intensified competition, high *nph* also leads to lower *dbh* ingrowth rates across  
318 *species* (Monserud and Sterba, 1996; Castagneri et al., 2021). Harvesting activities tend to create open  
319 space and light, which is reflected by the positive effect of *bah* on the count of ingrowth trees.

320 Except for *stone pine*, conifers are highly abundant in all production regions of Switzerland, ensur-  
321 ing robust modeling. Similarly, the localized ecological niche of *stone pine* in alpine regions facilitated  
322 comprehensible modeling in these areas. The timber industry has strongly promoted *spruce* in recent  
323 centuries and is, therefore, strongly over-represented in the *Plateau* region (Seim et al., 2022; Scherrer  
324 et al., 2023a). Its dynamics may, however, differ at higher elevations where it naturally occurs. Due to  
325 its current high abundance, *spruce* still has the highest likelihood of ingrowth, even in regions where it  
326 does not naturally prevail. Broadleaved *species* have also been successfully modeled, with *beech* being  
327 particularly well-represented in Swiss forests. Less abundant broadleaves such as *maple*, *ash*, and *oak*  
328 share similar ecological niches, leading to comparable effects, particularly in the *species* model. Con-  
329 versely, interpreting results for the *species* groups *other conifers* and *other broadleaves* poses challenges.  
330 These categories encompass different species with varying properties, complicating their representation  
331 and predictions. Further studies could consider defining new and possibly more species groups according  
332 to their ecological niches or functional traits.

## 333 4.2 MASSIMO simulations

334 Based on the RCP 4.5 climate and RMP management scenarios, MASSIMO simulations point to declining  
335 ingrowth by the mid-21<sup>st</sup> century for all Swiss production regions. This is due to a lower number of  
336 ingrowth trees rather than reduced *dbh* rates, which results in halving ingrowth volume. Besides a lower  
337 number of ingrowth and a decreasing share of conifers (which typically have higher growth rates), we  
338 hypothesize that the decreasing ingrowth volume could be related to poorer growing conditions and  
339 higher mortality rates, both resulting from climate warming and decreasing water availability (Trotsiuk  
340 et al., 2020, 2021; Senf et al., 2020). This simulated decrease in ingrowth volume aligns with the newest  
341 results of the Swiss NFI<sub>1-5</sub> (Abegg et al., 2023). Further, we observed a shift in species composition,  
342 with ingrowth trees shifting much faster than survivor trees. In all regions of Switzerland, the projected  
343 decline in *spruce* is expected to occur not only in ingrowth but also in survivor trees. In addition to

344 the increase in ingrowth of *beech*, *fir*, *maple*, and *other broadleaves*, this indicates a shift towards more  
345 natural tree species compositions (Scherrer et al., 2022). However, this shift may be slower than necessary  
346 and potentially results in more forests becoming prone to disturbances, endangering the provision of  
347 important ecosystem services (Scherrer et al., 2023b). The drought-resistant *oak* holds promise as a  
348 significant *species* for future lower elevation forests in Switzerland (Zimmermann et al., 2014; Scherrer  
349 et al., 2023b). Nevertheless, their establishment is hindered in dense and closed *beech* forests due to their  
350 high light requirements during the juvenile stage. Our projections indicate that forests are expected to  
351 become denser (higher *ba*) and darker (increasing *beech* ingrowth) in the future. Consequently, *oak* is  
352 unlikely to gain prominence without implementing targeted management interventions.

353 The potential increase in forest vulnerability and the intensification of disturbance regimes (Seidl et al.,  
354 2017) could lead to more significant large-scale damages than MASSIMO projected, which in turn, may  
355 quicken the transition towards a more natural forest composition. Currently, the disturbance module of  
356 MASSIMO is limited to storm damage. Nevertheless, interactions between bark beetle outbreaks, storm  
357 damage, and droughts are increasingly affecting forests, especially those dominated by *spruce* (Stadelmann  
358 et al., 2013; Netherer et al., 2021). Drought, particularly on soils prone to water limitations (Klesse  
359 et al., 2022; Meusburger et al., 2022), also strongly weakens *beech* (Rohner et al., 2021; Frei et al., 2022).  
360 Recent extreme drought events after the NFI4 field campaign have not been included in the model fitting  
361 of the demographic processes in MASSIMO, which may result in underestimating their effects. Similarly,  
362 MASSIMO modules do not account for the influence of future, currently unknown, or only recently  
363 observed pathogens. For example, ash dieback has significantly affected ash mortality since the middle  
364 of the NFI4 period, with a pronounced amplification in recent years (Klesse et al., 2021), although its  
365 impact on ingrowth has not yet manifested. *chestnut* is currently threatened by drought, gall wasps, and  
366 ink disease (Prospero et al., 2023), which according to Conedera et al. (2021) could lead to a decrease  
367 in survivor trees by mid-21<sup>st</sup> century in the *Southern Alps*. While MASSIMO predicted no change in  
368 the ingrowth of *chestnut* in the *Southern Alps*, an increase was predicted for all of Switzerland, likely  
369 due to larger areas where favorable climate conditions will prevail. Nevertheless, the predictions of the  
370 number and diameter distribution of ingrowth species in MASSIMO remained accurate, as independently  
371 validated with NFI5<sub>1-5</sub> data. Thus, MASSIMO can reasonably predict ingrowth and its future species  
372 composition, while amplifying disturbance regimes could have further adverse effects.

### 373 4.3 Conclusions

374 The trilogy of statistical models, which incorporate soil and climate information, exhibits strong predic-  
375 tive performance, especially at the scale of production regions that are the intended application scale.  
376 We project shifts in ingrowth species composition towards more broadleaves under a moderate RCP 4.5  
377 climate warming scenario. Testing other climate warming scenarios could offer an interesting avenue  
378 for future investigations, shedding more light on how altered climatic conditions might influence species  
379 composition changes. While these changes suggest a transition towards more natural forest compositions,  
380 it remains unclear whether the pace of these changes will be fast enough for forests to sustain ecosystem  
381 services under future climate conditions. Other factors add to these uncertainties: the expected intensi-

382 fying of disturbance regimes, as well as the low availability of seed trees where they should but do not  
383 naturally occur might further hinder the adaptation of forests to future conditions.

384 Assisted migration strategies (i.e., planting) could be assessed as a mitigation option to foster higher  
385 levels of naturalness in forests. To this end, tree species well-suited to anticipated future site conditions  
386 should be selected for planting. Given the predicted decrease in ingrowth and expected changing environ-  
387 mental conditions, we conclude that the natural regeneration of forests might become more challenging  
388 in the future.

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