

Long-term tree species population dynamics in Swiss forest reserves influenced by forest structure and climate

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ARTICLE INFO

Keywords:

Forest dynamics
Forest reserves
Species dynamics
Ingrowth
Tree mortality
Climate change

ABSTRACT

Changes in tree species composition can have strong effects on ecosystem functioning and the services provided by forests. Empirical observations can provide an improved understanding of the drivers of species population dynamics, yet long-term datasets are scarce in natural forests. This study used inventory data of the Swiss forest reserve network to assess tree population dynamics over the past 60 years. Tree status, species and dbh were repeatedly measured between 1956 and 2018 in 211 permanent plots of 34 forest reserves that covered a wide environmental gradient. Differences in species richness and tree density were compared between the first and last inventory. Furthermore, we used generalized linear mixed effect models to estimate the processes of ingrowth and tree mortality of seven abundant species (*Abies alba*, *Acer pseudoplatanus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Picea abies*, *Pinus sylvestris* and *Quercus* spp.) separately as a function of stand structural attributes and climate. We found a general decline in the density of the dominant species, with a low recruitment of light-demanding species and an increase in species richness, particularly in the colline vegetation zone. Both species-specific ingrowth and tree mortality were influenced by stand density and climate variables. Tree mortality increased with live tree density and increasing temperature. Ingrowth increased with tree density and decreased with higher temperature. Therefore, forest structural properties and climate have a strong influence on species population dynamics, and both are essential for predicting ingrowth and tree mortality in forest ecosystems.

1. Introduction

Forest succession and the associated changes in tree species composition can lead to changes of important ecosystem services such as carbon cycling, habitat availability and the potential for timber and fuel production (Balmford and Bond, 2005; Millennium Ecosystem Assessment, 2005). However, quantifying the processes that influence tree population dynamics is challenging, particularly in natural forests. Long-term inventory datasets in forest reserves are crucial to improve our knowledge on changes in forest structure and demographic rates. Utilizing such datasets allows to examine historical trends in tree population dynamics and to identify the underlying drivers. This information can improve our understanding of species dynamics and the natural processes that are driving tree regeneration and mortality (Leibundgut, 1959; Brang, 2005). In the absence of management, the local abundance of a tree species can only increase with natural regeneration and decrease with natural tree mortality. Monitoring natural forest dynamics in forest reserves allows us to therefore understand the effects of forest

succession without human intervention.

Only limited forest inventory data exist from natural forests, often covering short time periods or focusing on specific forest types (Franklin, 1989; Pretzsch et al., 2010). The vast majority of permanent plots are located in managed forests (Forrester, 2019; Cioldi et al., 2010; Torresan et al., 2020), thus limiting the ability to monitor long-term natural forest dynamics. In Europe, this can be in part explained by the vast majority of forests being managed for > 500 years, with only few primary forests remaining, especially in western Europe (Sabatini et al., 2018; Kaplan et al., 2009; Leibundgut, 1959). Extensive forest clearing for agriculture and timber since the beginning of the Holocene has diminished the area of primary forest, with approximately 4% of unmanaged forest remaining (FOREST EUROPE, 2015). Consequently, only few long-term monitoring networks in forest reserves have been established in Europe that offer opportunities for case studies on processes occurring in specific forest types (Nagel et al., 2019; Vašíčková et al., 2019; Brzeziecki et al., 2020). Although an increasing number of forest reserves have been established and protected in recent years, the

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<https://doi.org/10.1016/j.foreco.2020.118666>

Received 2 August 2020; Received in revised form 2 October 2020; Accepted 2 October 2020

Available online 28 October 2020

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structure and species composition of these forests are still affected by past management, even after many decades (Heiri et al., 2009; Bradshaw et al., 2005).

In this study, we used forest inventory data from the Swiss Forest Reserve Network to determine long-term changes in tree populations and the associated drivers. The network is unique because it contains a large number of permanent plots, with monitoring efforts existing for over half a century. The network is composed of numerous reserves distributed across Switzerland and provides a comprehensive coverage of forest types found in different biogeographic regions and at widely different elevations. It provides important information on forest structure, species composition and habitat quality and how these are changing over time. Using this long-term network allowed us to examine natural tree population dynamics after the cessation of human interventions.

Another factor that has been increasingly influencing forest ecosystems is climate change, which affects species distribution patterns and composition worldwide (Barros et al., 2017; Bugmann et al., 2015; Mathys et al., 2018). In recent years, summer drought has had a major impact on forests in Central Europe, leading to increased stress and tree die-off as well as changes in species composition (Rigling et al., 2013; Allen et al., 2015). Such extreme events are leading to shifts in species distributions and migration to higher elevations and latitudes (Harsch et al., 2009; Mathys et al., 2018; Hernández et al., 2014; Lenoir et al., 2009).

Since multiple structural and environmental drivers act on natural forest succession, the question arises on which factors have the strongest influence on tree population dynamics? To address this, it is important to differentiate the natural processes of ingrowth and mortality. Most studies focus on one of the two processes or combine them into one to determine the net change in species abundance (Etzold et al., 2019; Zell et al., 2019; Bose et al., 2017; Canham and Murphy, 2017). In this study, we examined ingrowth and tree mortality as separate processes and identify the unique drivers that affect each of them over time. To this end, we first determined long-term changes in tree populations in the permanent plots of the Swiss forest reserve network over the past half-century. We then analysed the factors influencing the observed changes in both ingrowth and mortality of major tree species, thus determining the drivers of natural forest development within and across the reserves. With this in mind, we aimed to address the following research questions:

1) What long-term changes in species richness and tree density have occurred between the first and the most recent inventory across the environmental gradient of forest reserves?

2) What biotic and abiotic factors contributed the most to the processes of ingrowth and tree mortality for the major tree species?

2. Materials and methods

2.1. Forest inventory dataset

We used inventory data from the Swiss Forest Reserve Network that Professor Leibundgut at ETH Zurich initiated in the 1940s (Hobi et al., 2020; Leibundgut, 1957). Since then, the network has increased in size by adding 16 new reserves to 33 of the original dataset. It currently contains up to 60 years of information on natural forest succession. Forest inventory campaigns were undertaken at approximately 10-year intervals within permanent plots with a size between 0.1 and 3.47 ha. Within the permanent plots, individuals of all woody species (mostly trees and large shrubs) were individually tagged and repeated measurements were made to record information on tree status (dead or alive), diameter at breast height (dbh) and species. The minimum dbh threshold for a tree to be included was 4.0 cm. Further details on the inventory campaigns are provided in Brang et al. (2011) and Wunder et al. (2007).

We used data from 211 permanent plots within 34 reserves of the

Reserve Network in the analysis, covering a time span from 1956 to 2018 (Fig. 1, Table A1). Long-term annual temperature means during the inventory period (1950–2018) ranged from a minimum of 3.07 °C in Scatlè to a maximum of 9.75 °C in Umikerschachen. Total annual precipitation averaged over the long-term was between 678 mm in Pfynwald and 2247 mm in Böldmerenwald. The lowest elevation plot was at 334 m in Umikerschachen and the highest elevation at 1750 m in Scatlè.

Deciduous tree species such as beech (*Fagus sylvatica*), oak (*Quercus petraea*, *Q. robur* and *Q. pubescens*) and ash (*Fraxinus excelsior*) dominate low-elevation forests within the forest reserves. At higher elevations within the high montane and subalpine zones, conifer forests are widespread, dominated by Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and silver fir (*Abies alba*). In general, species diversity is higher at lower elevations, i.e. in the colline, submontane and lower montane vegetation zones, compared to higher elevations.

2.2. Data analysis

The data analysis consists of two components to address the research questions of this study. First, we examined changes in species richness and tree density that occurred over the long-term from the first to the most recent inventory of the forest reserves. Second, we determined the drivers of the observed changes by modeling ingrowth and mortality using all measured inventories in the dataset. To determine long-term changes in tree density and species richness for the first part of the analysis, we selected permanent plots of the Forest Reserve Network with the following criteria: (1) at least two consecutive inventories, (2) a minimum size of 0.1 ha and (3) at least 20 years between the first and last inventory campaign. This amounted to a total of 177 plots. We assessed gamma-diversity as a measure of species richness by counting the number of woody species in the first and last inventory, for all trees with a minimum dbh of 8 cm (i.e., pole stage and larger). This threshold was used in order to exclude small recruits appearing only in the understorey. Tree density of all woody species was compared based on their mean live stem density (stems ha⁻¹) in the first and last inventory. We determined elevational patterns of species richness and tree density by categorizing the plots according to the vegetation zones: colline, submontane, lower montane, upper montane, high montane, and subalpine (Frehner et al., 2005, Fig. 1). The number of permanent plots differed in each vegetation zone, since the size of forested area covered by each zone varies in Switzerland. We accounted for this by dividing the total species richness and tree numbers by the total area of permanent plots in each zone. We acknowledge the asymptotic relationship that exists between species richness and sample area. Because the plot areas of our dataset are rather small (0.1–3.47 ha) we were not able to accurately determine this relationship and assumed that the plot sizes were in the lower part of the species accumulation curve where the relationship is linear. Given that the focus of this study was on temporal changes in species richness, an accurate assessment of the plot area was not crucial as it remained constant over time.

For the second part of the analysis, the drivers of the observed changes in tree density were determined by modeling ingrowth and tree mortality as response variables in two separate models. This was undertaken for seven abundant tree species that are well represented within the forest reserves: beech, Norway spruce, silver fir, ash, oak, Scots pine and sycamore maple (*Acer pseudoplatanus*). Species-specific ingrowth (subsequently referred to as “ingrowth”) occurred when a new tree in the recruitment layer reached the caliper threshold of 4 cm for each of the seven species. In contrast, species-specific mortality (denoted “mortality”) resulted from tree mortality in any diameter between two consecutive inventories of a permanent plot. The absolute values (N) of ingrowth and mortality were used in the models and differences in plot size and time intervals were accounted for in the model specifications detailed in Section 2.4. This dynamic analysis of changes in tree populations was undertaken for all inventories of permanent plots with the same criteria mentioned above but by including all

Legend

- colline
- submontane
- lower montane
- upper montane
- lower and upper montane
- high montane
- subalpine
- forest reserves

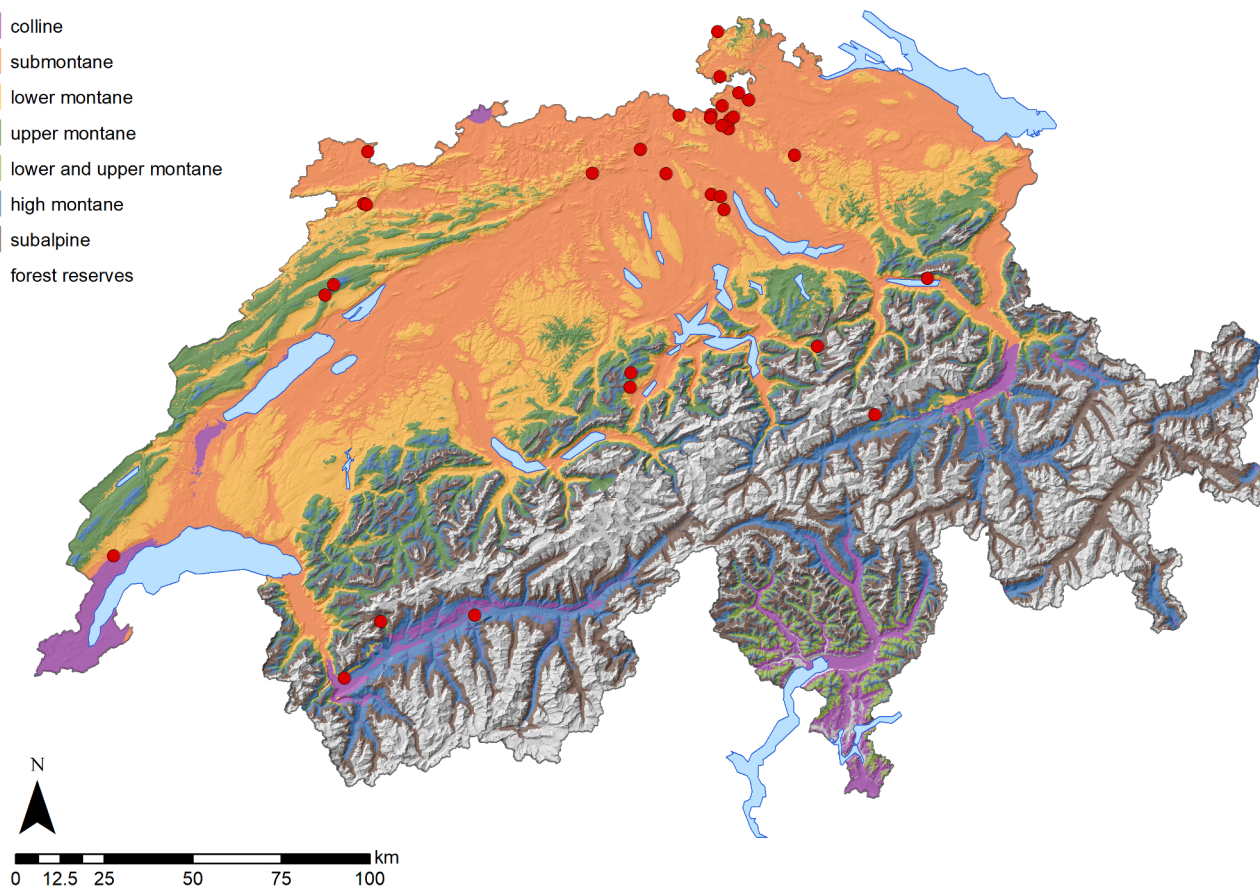


Fig. 1. Location of the 34 Swiss forest reserves containing 211 permanent plots used in this study. Digital elevation model dh25 © 2019 obtained from swisstopo (5704 000 000). The vegetation zone map is based on [Frehner and Huber \(2019\)](#).

observation periods, amounting to a total of 211 plots. The number of inventories in each permanent plot ranged from 2 to 7 campaigns.

2.3. Model input variables

The explanatory variables used to model ingrowth and mortality included both stand characteristics and climate conditions. Stand characteristics included live tree stem number and basal area in each inventory, calculated as sums per plot and for individual tree species. Basal area was calculated from dbh, which is rounded to the nearest millimeter using a caliper threshold of 4 cm. Relative basal area increment (relBAI) were used in this study as a proxy for both site growth potential and species-specific growth rates ([Bigler and Bugmann, 2004](#); [Hülsmann et al., 2016](#)). relBAI was calculated for each tree using the basal area of the current inventory campaign (BA_t) and the previous one (BA_{t-1}) and the time interval between the two inventories (Δt):

$$\text{relBAI} = \left(\frac{BA_t}{BA_{t-1}} \right)^{\frac{1}{\Delta t}} - 1$$

relBAI between each pair of consecutive inventories was then averaged by plot and by species. Climate variables included annual means of monthly temperature and precipitation averaged over each inventory period. The climate data for each permanent plot were obtained at 100 m resolution from a spatial interpolation of MeteoSwiss weather station data using the DAYMET model ([Thornton et al., 1997](#)). Stand density and climate data were centered and scaled for the analysis using the means and standard deviations shown in [Table 1](#) to allow for the comparison of the effect size of the model coefficients. Elevation data were obtained from a digital elevation model (dh25) of Swisstopo, the Swiss

Table 1

Mean and standard deviation (SD) of the explanatory variables used to center and scale the model input data. The sample size ($N = 1918$) represents each inventory measurement per plot for each of the selected species.

Predictor	Acronym	Mean	SD
Live tree density (stems ha^{-1})	N	1227.2	681.3
Live stand basal area ($\text{m}^2 \text{ha}^{-1}$)	BA	39.0	11.7
Relative basal area increment	relBAI	0.02	0.01
Live species-specific density (stems ha^{-1})	N.sp	206.3	316.3
Live species-specific basal area ($\text{m}^2 \text{ha}^{-1}$)	BA.sp	8.2	11.1
Relative basal area increment by species	relBAI.sp	0.02	0.02
Mean annual temperature ($^{\circ}\text{C}$)	Temp	8.3	1.6
Annual precipitation sum (mm)	Precip	1347.0	295.0

Federal Topographical Agency.

2.4. Modeling tree mortality and ingrowth

To determine the drivers of species dynamics, we built two separate models, one for ingrowth and one for mortality ([Table 2](#)). The predictor variables used in both models included stand density based on stem number per ha (N), basal area (BA) and relBAI for each inventory at the plot and species level, as well as precipitation and temperature. Elevation was also considered as an explanatory variable, but omitted because of its strong correlation with temperature. The ingrowth model was fitted with a generalized linear mixed model with a negative binomial error distribution using the package glmmTMB ([Brooks et al., 2017](#)) in R 3.6.1 ([R Core Team, 2019](#)). For the mortality model we used a generalized linear mixed effect model with a Poisson error distribution ([Zuur](#)

Table 2

Overview of the models used to predict species-specific ingrowth and tree mortality. The variables in the two models included the structure and climate characteristics described in Table 1, species (sp) and the two random effects year of measurement (year) and plot id (plot). The sample size of the two models was 1918.

Model	Equation	Model type	Link function
Ingrowth	Ingrowth $\sim \log(N) + BA + \log(\text{relBAI}) + \text{precip} + \text{temp} + \text{temp}^2 + \log(N.\text{sp}) + BA.\text{sp} + \log(\text{relBAI}.\text{sp}) + \text{sp} + \log(N) * \text{sp} + BA * \text{sp} + \text{precip} * \text{sp} + \text{temp} * \text{sp} + \log(\text{relBAI}) * \text{sp} + (1 \text{year}) + (1 \text{plot})$	Negative binomial	Log
Mortality	Mortality $\sim \log(N) + \log(BA) + \text{relBAI} + \text{precip} + \text{precip}^2 + \text{temp} + \log(N.\text{sp}) + \log(BA.\text{sp}) + \text{relBAI}.\text{sp} + \text{sp} + \log(N) * \text{sp} + \log(BA) * \text{sp} + \text{precip} * \text{sp} + \text{temp} * \text{sp} + \text{relBAI} * \text{sp} + (1 \text{year}) + (1 \text{plot})$	Poisson	Log

BA*sp is an example of an interaction term; (1|x) represents the random effect (variable x).

et al., 2009; Bolker et al., 2009) using the *glmer* function of the package lme4 (Pinheiro et al., 2014). We included plot id and year as random effects in both models, to account for repeated sampling over time and space, whereby year represented the calendar years of measurement. A species interaction term with both stand characteristics and climate variables was also included. Beech was selected as a reference species, as it is a widely distributed, shade-tolerant species in the study region. The logarithm of plot size and time interval were included as offsets in the models to correct for varying plot size and time intervals between successive inventories. This allowed us to calculate standardized mortality and ingrowth rates ($\text{N ha}^{-1} \text{ yr}^{-1}$). Model performance was evaluated based on the Akaike Information Criterion (AIC) and by assessing the residuals of both models for zero inflation and overdispersion using the package DHARMA (Hartig, 2020, Figs. A1 and A2). No model selection was performed, since the purpose of this study was to test prior hypothesis on the importance of structural and climatic variables that drive ingrowth and mortality patterns.

3. Results

3.1. Long-term changes in tree populations

When comparing the absolute number of species between the first and last inventory of all plots in one vegetation zone, we found that species richness was generally higher at lower elevations compared to high elevations (Fig. 2). The greatest change occurred in the colline zone where species richness increased over time from 5.3 to 7.2 N ha^{-1} ($0.54 \text{ N ha}^{-1} \text{ decade}^{-1}$). In the other zones, the number of species remained very similar over time, with the exception of the high montane zone, where a small increase was notable.

Mean live tree density decreased between the first and last inventory in all vegetation zones except for the colline zone, where it increased slightly by $10.9 (\pm 24.8) \text{ N ha}^{-1} \text{ decade}^{-1}$ (Fig. 3). Tree density for common species such as Scots pine and oak decreased in the colline zone, whereas for sycamore maple it increased slightly. In the submontane zone, the mean density of many species decreased over time, including beech, oak, spruce and ash, by $-158.0 (\pm 7.9) \text{ N ha}^{-1} \text{ decade}^{-1}$. At higher elevations, i.e. in the lower, upper and high montane and subalpine zones, most of the species densities decreased, including fir, spruce, oak and sycamore maple. Here the decadal changes in tree densities decreased with elevation from $-88.0 (\pm 8.5) \text{ N ha}^{-1} \text{ decade}^{-1}$ in the upper montane to $-7.1 (\pm 2.9) \text{ N ha}^{-1} \text{ decade}^{-1}$ in the subalpine zone. Among the non-dominant species, the density of Cornelian cherry (*Cornus mas*) and hazel (*Corylus avellana*) increased over time at lower elevations, with most density increases occurring

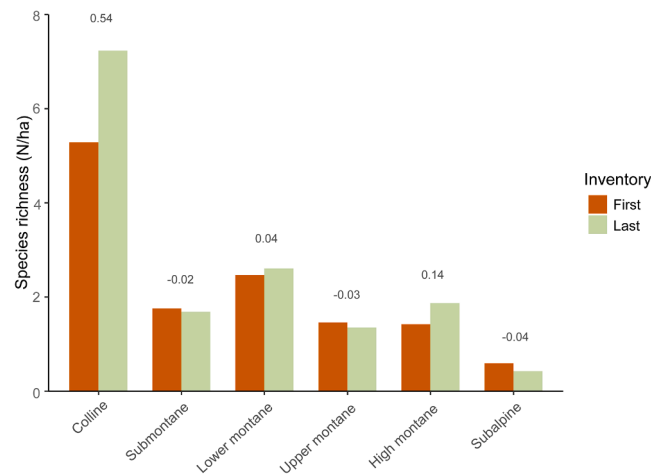


Fig. 2. Species richness (N ha^{-1}) expressed as gamma-diversity, during the first and last inventory within the permanent plots located in six vegetation zones in Switzerland: colline ($n = 17$), submontane ($n = 68$), lower montane ($n = 42$), upper montane ($n = 22$), high montane ($n = 21$) and subalpine ($n = 7$). All permanent plots cover a measurement period of 20–62 years between the first and last inventory. Rate of change in richness per decade are also indicated for each zone above the bars.

within the colline zone.

The change in the shape of the diameter distribution for seven dominant species across all plots showed that the number of trees up to a dbh of about 25 cm decreased over time. Tree density in the smallest dbh sizes remained high for beech, silver fir and spruce in the last inventory. Tree numbers of the middle to large-sized trees increased slightly for all seven species (Fig. 4). Thus, the general decline in stem density shown in Fig. 3 was driven by a lower number of recruits across the permanent plots. The development of the diameter structure varied by species, reflecting their distinct life history strategies.

3.2. Drivers of changes in mortality and ingrowth

Both stand density and climate variables significantly influenced tree mortality (Table 3). Live tree density of the individual species and precipitation had the strongest effect on predicted mortality. Mortality rates increased with increasing species-specific tree density and stand basal area for all seven species (Fig. 5a and 5b). Predicted mortality increased with increasing temperature for all species at varying rates, with the strongest effect on beech and the lowest on sycamore maple (Fig. 5c). High precipitation values also increased the predicted mortality of all species (Fig. 5d). relBAI at the stand level had a weak negative effect on all species (Table 3).

Species-specific live tree density and temperature had the greatest effect on predicted ingrowth (Fig. 6, Table 3). The explanatory variables of the ingrowth model also reflected species-specific responses with a decrease in predicted ingrowth for all species at higher temperatures and an increase at higher tree density to varying extents (Fig. 6). Silver fir responded the most to an increase in density and oak the least. relBAI had a positive effect on the predicted ingrowth of most species. Tree species generally had a reduced number of recruits when their basal area increased except for silver fir that showed an opposite trend.

4. Discussion

In this study we assessed regional-scale changes in species occurrence and tree density within the Forest Reserve Network of Switzerland. By utilizing the rich dataset on long-term forest dynamics in 34 reserves we were able to determine natural tree population dynamics that have occurred over the 60 years since the first reserves were

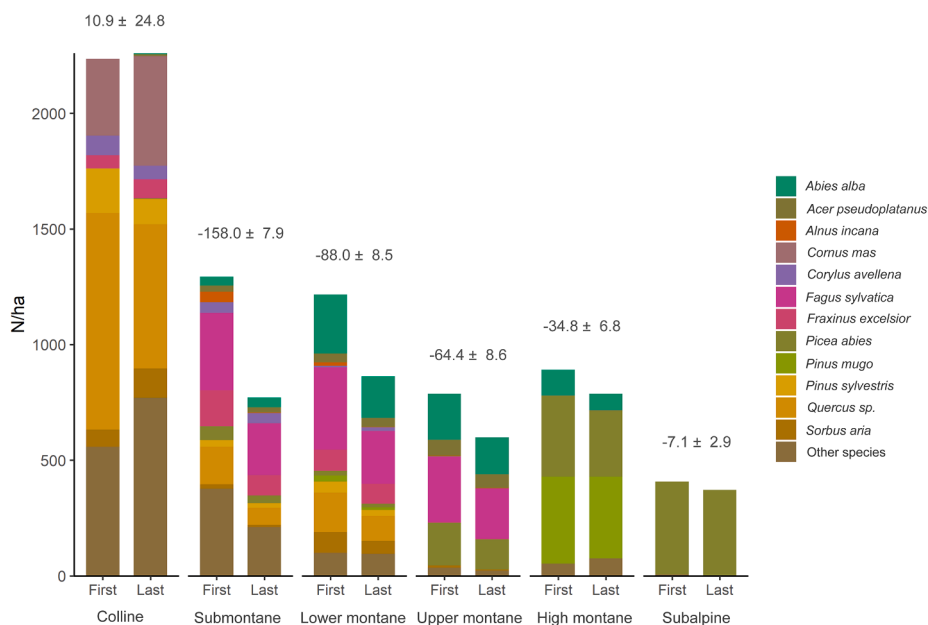


Fig. 3. Tree density ($N\ ha^{-1}$) by vegetation zone and species in the 177 permanent plots during the first and last inventory. Rate of change per decade in tree density between the two inventories (mean $\pm$ standard deviation) of each zone are shown above each pair of bars. For the number of plots per zone, cf. caption of Fig. 2.

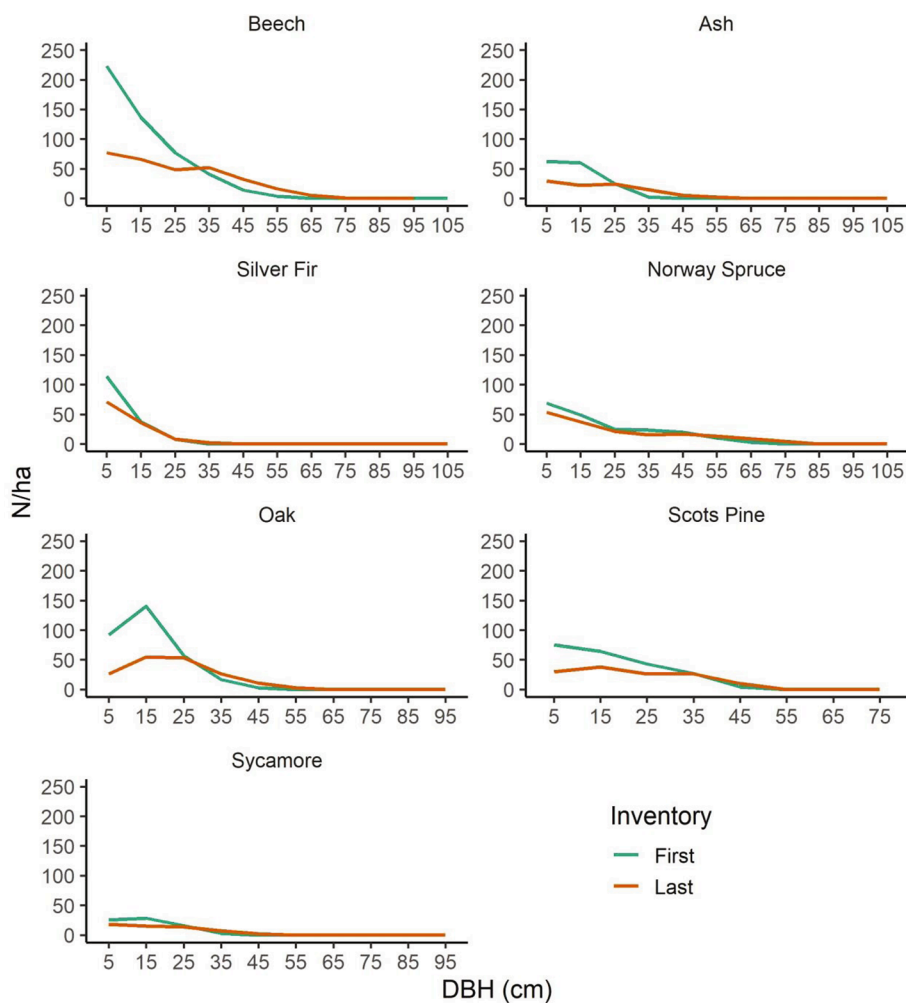


Fig. 4. Diameter distribution of seven tree species during the first (1960–1979) and last (2000–2018) inventory period averaged across all permanent plots.

Table 3

Parameters of the generalized linear mixed effect model for ingrowth and tree mortality with beech as a reference (SE = Standard error). The coefficients were scaled based on the means and standard deviations shown in Table 1. For a complete list of model parameters including interaction terms, cf. Tables A2 and A3.

Variable	Mortality model		Ingrowth model	
	Coefficient $\pm$ SE	p-value	Coefficient $\pm$ SE	p-value
Intercept	-0.598 ± 0.092	0.00	-1.018 ± 0.155	0.00
N.sp	2.008 ± 0.085	0.00	1.042 ± 0.172	0.00
N	-0.056 ± 0.038	0.14	0.074 ± 0.115	0.52
BA.sp	-0.211 ± 0.084	0.01	-0.277 ± 0.121	0.02
BA	0.352 ± 0.051	0.00	0.137 ± 0.116	0.24
relBAI.sp	-0.036 ± 0.076	0.64	0.363 ± 0.203	0.07
relBAI	-0.044 ± 0.056	0.43	0.631 ± 0.152	0.00
Temp	0.492 ± 0.057	0.00	-0.838 ± 0.645	0.19
Temp ²	–	–	1.164 ± 0.600	0.05
Precip	1.502 ± 0.171	0.00	0.310 ± 0.173	0.07
Precip ²	-1.427 ± 0.160	0.00	–	–
Ash	0.432 ± 0.071	0.00	-1.713 ± 0.226	0.00
Fir	0.762 ± 0.075	0.00	0.564 ± 0.221	0.01
Spruce	0.190 ± 0.074	0.00	-0.646 ± 0.168	0.00
Oak	0.556 ± 0.078	0.00	-3.234 ± 0.382	0.00
Pine	0.372 ± 0.135	0.00	-3.114 ± 0.576	0.00
Sycamore	0.110 ± 0.071	0.12	-0.941 ± 0.324	0.00

established. We found that the density of major tree species decreased over time and that species fluctuations were most pronounced at lower elevations. A combination of both structural and climatic attributes contributed to these population responses.

4.1. Shifts in species richness and tree density

The observed trend in the forest reserves was towards a decrease in tree density of the major species and an increase in species richness over the past half-century. The greatest changes occurred in low-elevation forests, with larger fluctuations in both species richness and population density compared to high elevations.

Species richness was generally higher at low elevations and increased over time, whereas a slight decline in the number of species occurred at high elevations, except for the high montane zone where it increased. A temporal decline in species richness of other European forest reserves has been reported (Heiri et al., 2009; Nagel et al., 2019; Brzeziecki et al., 2020), mostly focusing on beech-dominated stands. In old-growth forests of Slovenia, a decline in species richness was associated with a decline of silver fir and an increase of beech in the recruitment layer that suppressed other understory species (Nagel et al., 2019). When examining the multiple forest types occurring in the forest reserves, we found a different picture, with a general increase in species richness, a trend that was also recently reported in a study using national forest inventory data in Switzerland (Nikolova et al., 2019). This phenomena could be explained by the occurrence of natural disturbances in the forest reserves that open canopy gaps and can lead to the emergence of new species.

Total tree density declined across all vegetation zones except for the colline zone, where it increased slightly, together with species richness. Disturbance events (including a forest fire) that occurred during the measurement period within some permanent plots of this zone led to a more open canopy that allowed new individuals to emerge and explains the observed increase in tree density and richness. The abundance of the seven major tree species declined over time especially in the smaller

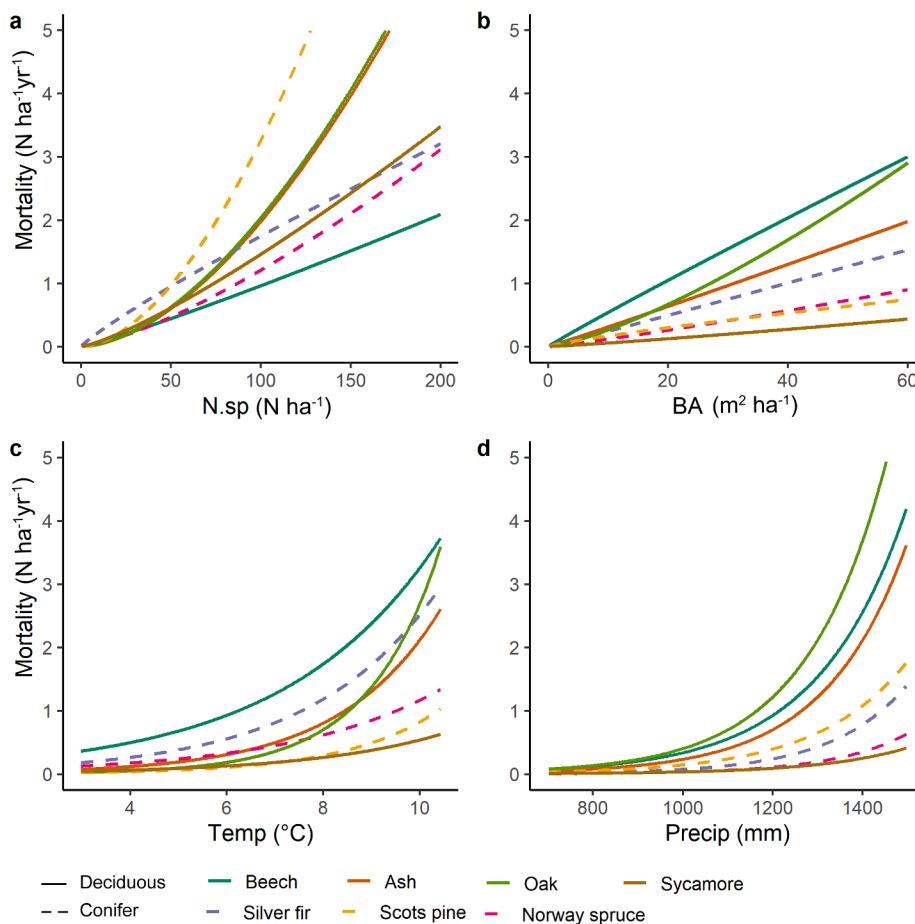


Fig 5. Predicted tree mortality for seven abundant species against the explanatory variables (a) species-specific tree density (N.sp) and (b) stand basal area (BA), (c) air temperature (Temp), and (d) precipitation (Precip). Mortality predictions were obtained by varying predictor variables while holding the other variables constant based on their mean and by setting offsets to zero. Relationships between response and predictor variables were displayed within the range where model predictions were realistic compared to the observed values. Deciduous species are shown with solid lines, conifers with dashed lines. A list of the model parameters are shown in Table A2.

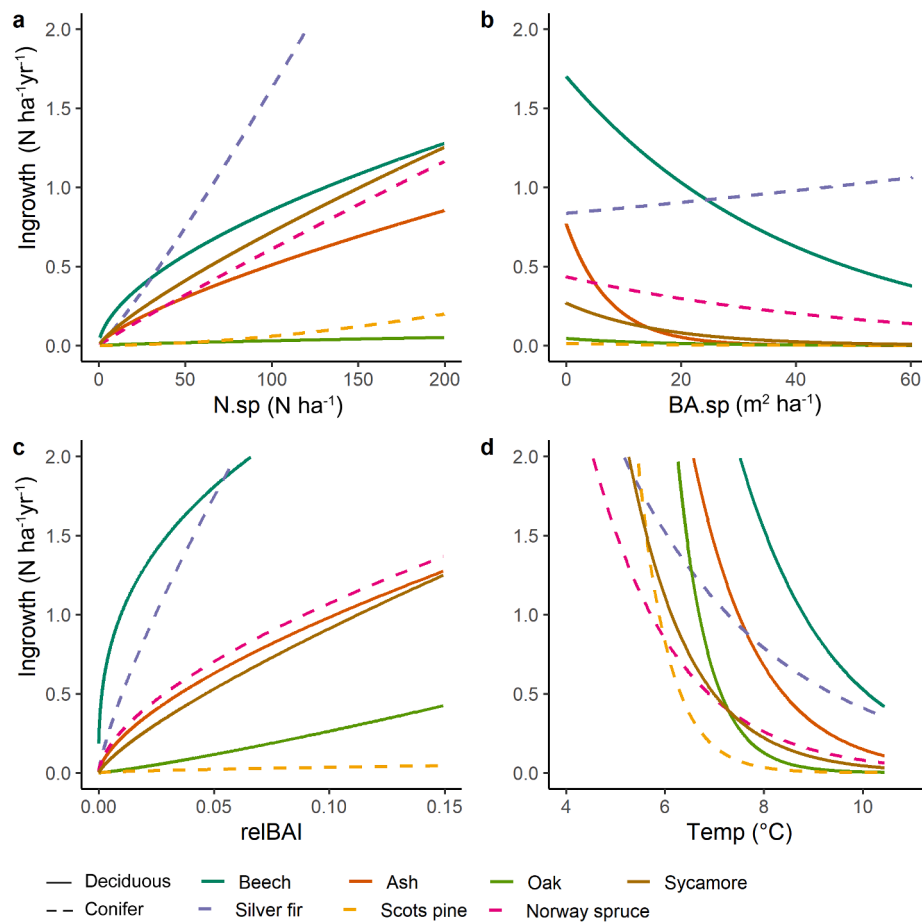


Fig 6. Modelled ingrowth for seven abundant species against (a) species-specific tree density (N.sp), (b) species-specific basal area (BA.sp), (c) relative basal area increment (relBAI) and (d) temperature (Temp). For the procedure of calculating and displaying model predictions, cf. caption Fig. 5. Dashed lines represent deciduous species and solid lines conifers. The model parameters are provided in Table A3.

diameter sizes. These species had a high number of recruits in earlier inventories, which decreased over time. The trend towards a decline in small trees and a broadening of the dominant diameter range as existing trees increased in size is characteristic of classical even-aged forests as they grow old and recover from past management practices, which is a characteristic pattern in our reserve network. An increase in stand basal area in different forest types of the Swiss forest reserves has been reported after management was abandoned, with values reaching levels similar to old-growth forests (Heiri et al., 2009, Rohner et al., 2012). This development towards later successional stages could explain the decline in species-specific tree density in our study. With increasing stand density, less space is available for new trees to emerge, and competition for resources such as light, water and nutrients increases. A similar trend was observed in the Swiss national forest inventory, with a decline of the overall stem density of living trees over time (Cioldi et al., 2010). Lastly, it is notable that the decline in tree density was most pronounced at low elevations and decreased strongly with elevation, reflecting the general slow-down of forest dynamics with decreasing temperatures (cf. Ott et al., 1997), which is the major environmental gradient along elevation in our study.

4.2. Driving factors of mortality and ingrowth

The driving factors for species-specific tree mortality were stand density and climate. The predicted mortality of a given species increased with stem density of the individual species and stand basal area. This density effect had the greatest impact on survival reflecting tree competition and self-thinning within the stands. Previous studies have

also found competition to be the main driver of tree mortality in both the Swiss forest reserves and other natural forests (Hülsmann et al., 2016, Rohner et al., 2012, Wunder et al., 2007, Gillner et al., 2013). Canham and Murphy (2017) found that the survival of small trees in the US was influenced by structural attributes such as tree size and competition. This could be attributed to their lower competitive ability for resources such as light compared to large trees (Coomes and Allen, 2007).

In our study, climate variables also had a significant impact on predicted tree mortality. Wetter conditions led to high species-specific losses. Generally, the opposite trend would be expected as drought is increasingly reported to impact tree survival on a global scale (Rigling et al., 2013, Allen et al., 2015). However, a previous study in beech-dominated stands of the Swiss forest reserves attributed this trend to an increase in the leaf area of large trees under wet conditions leading to a reduction in available light reaching the understory and thus an indirect decline of smaller, less vigorous trees (Rohner et al., 2012, Dobbertin et al., 2010). Additionally, soil water availability is a better proxy of drought than precipitation alone, and is therefore an important factor to include in future models (Piedallu et al., 2013, Mathys et al., 2014). Increasing temperature led to a higher predicted mortality in our study, indicating a sensitivity of tree mortality to warmer conditions, which may be driving tree growth and competition at higher temperatures. Furthermore, it indicates that higher rates of tree mortality occurred at lower elevations where temperatures are generally higher than at high elevations. Changes in species responses by elevation have been reported in other studies (Vašíčková et al., 2019, Di Filippo et al., 2007). Di Filippo et al. (2007) sampled beech forests along an elevational gradient in the Eastern Alps and found that growth rates declined at

higher elevations. In our study, increased growth, as shown with *relBAI*, led to lower mortality for all species. Existing ecological knowledge has long described this relationship between higher stress and mortality risk with lower growth rates (Monserud, 1976; Wyckoff and Clark, 2002; Waring, 1987). However, in our study the responses of mortality to growth were weaker and non-significant compared to the effects of species-specific density and precipitation.

The driving factors for ingrowth were a combination of structural and climatic attributes. Temperature had a strong effect on the model predictions, with warmer conditions leading to a lower number of ingrowth for all species. Other studies have found a similar relationship between temperature and tree recruitment (e.g., Zell et al., 2019). The temperature effect on ingrowth reflects the influence that climate change can have on demographic processes. This highlights the importance of including both forest structure and climate variables when predicting recruitment of juvenile trees (Dobrowski et al., 2015; Canham and Murphy, 2017). Predicted ingrowth of most species increased with higher growth values, as indicated by *relBAI*. Thus, conditions suitable for growth of a given species also had a positive effect on the number of recruits. A similar pattern was found on a global scale, where species turnover rates were related to net primary production (Stephenson et al., 2011). Ingrowth declined for most species with increasing species-specific basal area. Thus, there was a lower number of recruits with increasing stand density, in agreement with other studies (Zell et al., 2019; Li et al., 2011). An increase in basal area following forest recovery from former management normally leads to greater crown closure and a lower availability of light and water for juvenile trees. Shade-tolerant species such as beech and fir generally benefit from higher basal area, sustaining a higher number of recruits compared to light demanding species (Ellenberg, 2009).

4.3. Species-specific responses

The species-specific variations in the responses of ingrowth and tree mortality can be partly explained by traits that reflect specific life history strategies (Griffith et al., 2016; Grime, 1977). Here we examine responses in terms of the two traits shade and drought tolerance, which can serve as indicators of a species' sensitivity to forest development and climate change (Syphard and Franklin, 2009; Dobrowski et al., 2015).

Shade-tolerant species such as beech and fir sustained the highest number of ingrowth over time as seen in their diameter distributions, which displayed a wider diameter range in the last inventory as stem density decreased and dbh increased. Thus, they have a competitive advantage within their realized niche of the forest reserves as they develop towards late successional phases (Heiri et al., 2009). Their predicted ingrowth responses also featured the highest number of recruits at higher basal area compared to other species. In the recruitment layer of an old-growth forest in Slovenia, shade-tolerant beech showed a competitive advantage compared to light-demanding species. Light was even considered to be the main driver of a decline in rare species within these stands (Nagel et al., 2019).

Beech is considered to be less drought tolerant than species such as oak and fir (Ellenberg, 2009) and showed higher mortality rates under warm and dry conditions in our dataset. Increased drought events from climate change have been associated with a decline in growth rates in beech forests across Europe (Aertson et al., 2014; Charru et al., 2010). Our predictions featured high mortality of fir under warm conditions and an intermediate response to low precipitation. Other studies have also reported an intermediate sensitivity of fir to dry conditions, with responses varying by elevation (van der Maaten-Theunissen et al., 2013; Vanoni et al., 2016).

Light-demanding species such as Scots pine and oak displayed a decline in stem numbers over time as well. However, unlike the shade-tolerant species there was very limited ingrowth in the later inventories, instead a shift in their diameter distributions occurred towards larger diameters leading to a broadening of the dominant diameter range. The

number of recruits of both species declined with higher temperatures, which may reflect their response to changes in microclimate with canopy closure in later seral stages (Dobrowski et al., 2015; Ellenberg, 2009). Oak, a species that is generally considered to be drought-resistant (Ellenberg, 2009), displayed a sensitivity to warm conditions that led to an increase in mortality rates. Indirect effects of drought on oak have been reported in other studies, leading to a lagged growth decline a few years after drought events (Vanoni et al., 2016; Di Filippo et al., 2010).

Ash, spruce and sycamore maple are considered to have an intermediate shade tolerance (Ellenberg, 2009). They showed a decline in the number of recruits and an increase in the number of large trees, although they had lower recruit numbers to begin with in the early inventory compared to the more shade-tolerant species. Spruce, a species considered to have a low drought tolerance, displayed a high number of recruits with low temperatures and increased mortality under high temperatures, reflecting its competitive advantage at cold sites, where it currently occurs at higher elevations. Sycamore maple is considered to be in the medium spectrum of drought tolerance and showed a weak response to dry conditions, a finding supported by Vanoni et al. (2016) in a selected number of the forest reserves.

4.4. Limitations and future research directions

The forest reserve dataset covers a 60-year timespan and a large variety of forest types along a wide environmental gradient. Nonetheless, the long time period does not yet cover the entire life span of a tree, and therefore continued monitoring efforts are essential to identify pathways in forest succession (Franklin, 1989). Obtaining tree records at shorter time intervals would be beneficial for monitoring tree mortality, but would require significantly more financial resources (Lutz, 2015). Information on disturbance events at the tree-level is currently lacking in the majority of the forest reserves, which is why we were unable to include such information in the models of our study. It is well known that disturbances can have a profound impact on tree population dynamics, and future research could benefit from incorporating this information, e.g. by taking advantage of remote sensing technologies (Hobi et al., 2015; Vašíčková et al., 2019). The inclusion of soil parameters such as soil water availability would likely improve the outcomes of future statistical models (Piedallu et al., 2013; Mathys et al., 2014) by capturing the impact of drought periods on population dynamics. Furthermore, employing process-based rather than empirical models, would allow to extrapolate the predictions beyond the spatial and temporal range of measurement (Bugmann et al., 2015; Mathys et al., 2018). Lastly, including international datasets from other forest reserves would allow to determine species responses throughout their distributional range. To meet this need, a network of forest reserve datasets across Europe is currently being established to combine monitoring efforts at an international scale.

5. Conclusion

The Swiss Forest Reserve Network is a valuable dataset to assess the long-term drivers of tree population dynamics in natural forests. Over the past half century, changes in both species richness and tree density have occurred, with responses varying by elevation. Species richness generally increased over time in lower elevation forests. Tree density of the dominant species decreased over time, especially at lower elevations, alluding to the development towards later successional stages in the forest reserves. Furthermore, our results showed that both forest structural properties and climatic variables influenced demographic processes in the forest reserves, and that both need to be considered when predicting ingrowth and tree mortality of different species. By modelling ingrowth and mortality separately, we were able to identify the unique drivers of each process. Competition was the main driver of tree mortality for all species, followed by precipitation. Ingrowth declined with higher temperatures and lower species-specific tree

density. Species-specific variations in demographic rates could be explained by their individual traits of shade and drought tolerance, giving them a competitive advantage as the reserves develop towards later successional stages. Continuing the monitoring efforts in the Swiss Forest Reserve Network in the future is crucial for an improved understanding of tree population dynamics. This will allow for the observation of long-term changes in species richness and tree densities under forest development and climate change.

CRedit authorship contribution statement

A.S. Mathys: Conceptualization, Methodology, Software, Writing - original draft. **P. Brang:** Conceptualization, Supervision, Funding acquisition, Writing - review & editing. **J. Stillhard:** Software, Validation, Data curation. **H. Bugmann:** Supervision, Writing - review & editing. **M.L. Hobi:** Conceptualization, Project administration, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This study was made possible by the monitoring efforts of the countless scientific and technical staff that have contributed to the Swiss Forest Reserve Network over the past 60 years. We appreciate the support provided by the Swiss Federal Office for the Environment (FOEN). We also thank Lisa Hülsmann and Jeanne Portier for their valuable input to the statistical analysis and two anonymous reviewers for their editorial comments.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118666>.

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