



Long-term biomass dynamics of temperate forests in Europe after cessation of management

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ABSTRACT

Forests can contribute to climate change mitigation by sequestering carbon when management intensity is reduced. However, there is high uncertainty regarding biomass dynamics in temperate forests after the cessation of management. We used forest inventory data from an extensive network of 224 plots in 37 natural forest reserves (NFR) covering a wide environmental gradient with mean annual temperatures ranging from 1 to 10.4 °C and mean annual precipitation ranging from 901 to 2317 mm. Inventories had been conducted approximately every 10 years during the last 60 years. We used mixed effect models to (i) analyse biomass development, (ii) assess the role of time since the cessation of management (TSCM) and (iii) disentangle the environmental and forest structural drivers of biomass change. After the cessation of management and in the absence of high-severity natural disturbances, biomass accumulated gradually along a saturation curve. There were large differences in biomass among reserves and plots, with values ranging from 101 Mg ha⁻¹ to 851.2 Mg ha⁻¹, with a median of 362.1 Mg ha⁻¹ (SD = 122.5 Mg ha⁻¹). The biomass curve did not yet tend towards an equilibrium, most likely because the majority of the NFRs do not exceed 100 years of TSCM. Compared to higher elevations, forests at lower, warmer sites showed a larger total biomass and higher rates of biomass accumulation. We found a reduction by 148 Mg ha⁻¹ of biomass per 1000 m of elevation gain. The strongest positive rate of change (>8 Mg ha⁻¹ year⁻¹) was found in forests with high basal area (>60 m² ha⁻¹) and medium to high levels of tree density (1500 to 2000 stems ha⁻¹). Overall, most reserves have not reached a biomass equilibrium yet and continue to act as carbon sinks in tree biomass. This highlights the carbon sequestration capacity of forest reserves and their role as carbon pools.

1. Introduction

Biomass dynamics in terrestrial ecosystems are of increasing scientific and practical interest, particularly in forests due to their important role as global carbon pools, containing 77 % of the global terrestrial aboveground carbon (IPCC, 2000). Unmanaged forests provide an excellent and unique opportunity for studying forest biomass dynamics as they can serve as a baseline for the potential of both carbon sequestration and storage (EUROPARC-España, 2017; IPCC, 2006). However, such forests are rare, especially in the temperate zone, due to the long history of human settlement, intensive forest management and land transformation. For example, only 0.7 % of European forests are considered to be in a primary state (Sabatini et al., 2018), and the majority of forest reserves in Europe have formerly been managed. Many of

them were established multiple decades ago to study the structure and dynamics of natural forest development, and to gain reference values for close-to-nature forestry (Korpel, 1995; Leibundgut, 1993). Despite not being considered primary, they can serve as case studies for long-term biomass dynamics after the cessation of management.

Bormann and Likens (1979) proposed a hypothesis to explain natural biomass development in forests over time. Accordingly, forest stands exhibit high productivity after disturbance, and biomass gradually accumulates until they reach a maturity phase with a maximum amount of biomass. Thereafter, a transitional phase follows during which biomass is decreasing due to the mortality of the initial cohort. This decrease, induced by the death of large trees, typically outweighs biomass gain from the younger cohorts (Sillett et al., 2020), in spite of their potential growth release (Halpin and Lorimer, 2016; Luyssaert et al., 2008).

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Understorey trees will then fill in the available space, and the stand enters a steady state characterised by a constantly changing mosaic of patches of different ages, with an average biomass that is lower than the maximum. In this steady state and under a low-intensity disturbance regime, biomass fluctuates around a carrying capacity determined by the abiotic and biotic site conditions (Muller-Landau et al., 2014).

Permanent plots are the main tool to monitor long-term processes in forest ecosystems (Muller-Landau et al., 2014; Seedre et al., 2020). The importance of continuous monitoring to provide long-term data is widely acknowledged (Anonymous, 2022; Gessler et al., 2022). However, such data are scarce as systematic forest inventories are time-consuming and expensive. Multiple studies have addressed forest biomass dynamics over long time periods and large environmental gradients, but most have focused on tropical ecosystems (Baker et al., 2004; Chave et al., 2008; Muller-Landau et al., 2014; Phillips et al., 1998) or on temperate and boreal forests in North America (Halpin and Lorimer, 2016; Jenkins et al., 2001; Keeton et al., 2011; McMahon et al., 2010; Sillett et al., 2020; Zhang and Chen, 2015; Zhu et al., 2018).

Yet, there is a long monitoring history of forest reserves in Europe going back to the first half of the 20th century. The resulting data have been used for various purposes, such as the analysis of successional changes after stand-replacing disturbance (Jaloviari et al., 2017), multi-decadal mortality rates (Woods et al., 2021) or biomass dynamics in beech-dominated forests (Meyer et al., 2021). Specifically, Meyer et al. (2021) found that aboveground biomass in European broadleaved forests tends to increase in the first decades after the cessation of management. Thereafter, different pathways emerge, some of them potentially approaching the theoretically expected steady state (Bormann and Likens, 1979). Another study focusing on a semi-natural broadleaf forest in Denmark showed that a steady state appears to be attained at a TSCM (time since the cessation of management) of ~200 years (Nord-Larsen et al., 2019).

The studies on biomass dynamics in European unmanaged forests were based on data of limited temporal and geographical coverage, or they focused on specific forest types (e.g., Glatthorn et al., 2018; Matović et al., 2018; Matuszkiewicz et al., 2021; Merino et al., 2007; Molina-Valero et al., 2021; Piovesan et al., 2005). At a larger spatial scale, Szwagrzyk and Gazda (2007) provided biomass values for 36 forest stands in 24 forest reserves and eight National Parks in the Czech Republic, Poland and Slovakia. Still, there is a lack of studies on biomass dynamics in European forests with long temporal coverage over large gradients of temperature and precipitation.

The rate at which biomass is changing in a forest stand over time is influenced by multiple drivers. For instance, in managed European temperate forests, growth rates are positively correlated with temperature (Hilmers et al., 2019; Janda et al., 2019), forest structural diversity (Glatthorn et al., 2018), site fertility and water holding capacity (Holeksa et al., 2009). However, little is known on the effects of climate, site quality and competition on biomass change in unmanaged forests. Furthermore, most studies have examined changes in basal area (BA), which can be considered a rough proxy for biomass change, whereas studies are rare that focus on change rates using tree-level live biomass calculated with species-specific equations.

Our study is based on data from a large network of natural forest reserves (NFR) located along an elevation gradient of almost 2000 m in Switzerland (Hobi et al., 2020). The data are thus distributed across a large climatic and environmental gradient with mean annual temperatures ranging from 1 to 10.4 °C and mean annual precipitation from 901 to 2317 mm (Federal Office of Meteorology and Climatology, MeteoSwiss, reference period 1991–2020) and cover the major forest types of temperate Europe (Mathys et al., 2021). Permanent plots have been established in these reserves since 1955, thus providing a unique dataset to comprehensively analyse biomass development since the cessation of management. To our knowledge, this is the first study that explores biomass dynamics in unmanaged forests in Europe over such a wide environmental gradient and long time frame. Based on these data, we

developed statistical models to study long-term biomass dynamics and aimed to answer the following research questions:

- i) How has biomass developed over time in the different NFR and forest types? We expect that it has generally increased towards a site-specific carrying capacity (Bormann and Likens, 1979).
- ii) What is the relationship between biomass development and TSCM? We expect reserves with a long TSCM to have reached a steady state, following an asymptotic saturation curve (Meyer et al., 2021). In most cases, the reserves were already well-stocked when monitoring began. Thus, we anticipate that the curve depicting the relationship between biomass and TSCM will reach an equilibrium. In addition, we expect the amount of biomass sustained to vary along an elevation gradient, with lower aboveground biomass found at higher and cooler locations.
- iii) What are the effects of environmental and forest structural variables on biomass change? We expect the rate at which carbon is sequestered (i.e., biomass change) to depend on specific biotic and abiotic drivers that capture stand-level resource competition as well as climate. We expect to find positive biomass changes when forest stands have low to medium levels of BA and tree density (low competition), in warm-wet climates, and on fertile soils.

2. Methods

2.1. Forest reserves and selection of permanent plots

The Swiss NFR network was established in the 1940s. The first permanent plot was set up in 1948, laying the foundation for a long-term monitoring with inventories in regular intervals of typically 5–10 years. Currently, 49 reserves are monitored throughout Switzerland (Hobi et al., 2020).

The NFR network covers the major forest types of Switzerland, i.e., forests dominated by the deciduous species beech (*Fagus sylvatica* L.), oak (*Quercus petraea* Matt., *Q. robur* L. and *Q. pubescens* Ehrh.) and ash (*Fraxinus excelsior* L.) as well as forests dominated by the coniferous species Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.) and silver fir (*Abies alba* Mill.). Compared to other networks in Europe, the availability of permanent plots at higher elevations in the Alps, and thus under cooler conditions, is outstanding. The network covers a large climatic and environmental gradient (see Table 1) encompassing elevations between 350 to 2200 m a.s.l. (Fig. 1), which corresponds to a gradient of ca. 1800 km in latitude (Halbritter et al., 2013). The minimum and maximum mean annual temperature and precipitation sum recorded were −0.2 to 11.7 °C, and 620 to 2970 mm respectively, between the years 1990 to 2020 (Federal Office of Meteorology and Climatology, MeteoSwiss).

The NFR network comprises reserves with widely different management histories, ranging from a few reserves with virtually no management to forests that have been managed until a few years prior to their designation as a reserve. The two reserves with the longest TSCM are Scatlè and Derborence. Scatlè is located on a remote, very steep and rocky slope that has averted management for centuries. Pollen analysis suggests that there was no human impact on the forest, neither through charcoal burning nor logging, at least as far back as the 13th century (Brang et al., 2011; Kral and Mayer, 1969). Derborence has remained virtually untouched since 1714, when an earthquake and a subsequent landslide made the valley nearly inaccessible.

Each reserve is monitored by several permanent plots, ranging in size from 0.03 to 3.47 ha, with a median of 0.42 ha. On average, inventories have been carried out every 10 years, resulting in one to seven inventories per permanent plot, depending on the date of the establishment of the reserve (cf. Table 1 for a detailed description of plot and reserve characteristics).

Within the permanent plots, all trees above the caliper threshold

Table 1

Main characteristics of the 37 Swiss forest reserves used in this study. The reserves are ordered from low to high elevation. Not all the plots within a reserve were established or measured at the same time, and in some reserves the monitoring was discontinued. The column ‘time since cessation of management’ (TSCM) shows the values for the reference year 2021. Values preceded by the approximation sign (~) are used for reserves in which there was greater uncertainty in assigning a specific date to the last management. Mean annual precipitation sum and mean annual temperature (MeteoSwiss) were averaged for the reference period 1991–2020.

Forest reserve	Number of plots	Inventories			Elevation (m a.s.l.)	TSCM (year)	Area (ha)			Mean annual precipitation sum (mm)	Mean annual temperature (°C)
		Number	First	Last			Minimum	Mean	Maximum		
Umikerschachen	4	6	1977	2019	336	59	0.26	0.44	0.54	992	10.4
Thurspitz	3	4	1992	2019	347	44	0.78	1.01	1.24	901	10.3
Hüntwangenhalde	2	4	1971	2017	367	71	0.45	0.66	0.87	947	10.2
Langgraben	5	5	1973	2014	421	76	0.13	0.24	0.50	1014	9.9
Bannhalde	1	1	2000	2000	425	76	2.76	2.76	2.76	1017	9.9
Bonfol	2	5	1961	2001	440	60	0.46	0.52	0.58	989	10.1
Unterwilerberg	1	6	1962	2017	452	59	0.25	0.25	0.25	1086	9.8
Fürstenhalde	2	4	1971	2012	464	78	0.52	0.55	0.57	1075	9.7
Seldenhalde	9	5	1977	2019	473	76	0.14	0.34	0.87	947	9.3
Strassberg	4	4	1976	2014	476	76	0.26	0.53	0.82	1090	9.6
Rinsberg	1	5	1973	2016	490	76	0.68	0.68	0.68	1084	9.6
Mettlenrain	1	1	2016	2016	501	27	0.69	0.69	0.69	1136	9.6
Adenberg	5	5	1970	2012	511	76	0.44	0.45	0.46	1046	9.5
Vorm Stein	11	4	1972	2012	522	51	0.21	0.31	0.57	1144	9.4
Bois de Chênes	11	5	1970	2017	525	60	0.21	0.63	1.38	1119	10.3
Krummenlinden	4	6	1956	2011	551	66	0.23	0.31	0.49	1177	9.3
Tariche Bois Banal	9	4	1974	2014	558	71	0.26	0.39	0.60	1097	9.5
Steibruchhau	6	3	1985	2016	580	36	0.26	0.33	0.49	1077	9.1
Tutschgenhalden	5	3	1984	2013	591	51	0.26	0.36	0.58	1223	9.2
Weidwald	5	4	1976	2011	634	121	0.27	0.55	0.79	1170	9.1
Josenwald	12	4	1980	2019	677	63	0.18	0.33	0.60	1556	9.0
Girstel	15	6	1964	2017	704	64	0.10	0.22	0.36	1311	8.6
Tariche Haute Côte	7	4	1973	2012	738	81	0.42	0.60	0.91	1217	8.5
Follatères	11	4	1974	2015	764	111	0.10	0.25	0.60	954	9.5
Weidel	1	3	1976	2014	770	46	0.42	0.42	0.42	1307	8.2
Leihubelwald	12	4	1973	2011	1147	101	0.19	0.36	0.55	1721	6.5
Combe Biosse	21	2	1986	2011	1173	51	0.19	0.49	0.90	1325	6.2
St. Jean	6	6	1961	2017	1347	121	0.18	0.36	0.62	1404	5.2
Seeliwald	5	4	1973	2016	1448	54	0.47	0.79	1.10	1871	5.0
Bödmerenwald	3	4	1973	2018	1521	~71	0.84	1.21	1.65	2307	4.4
Derborence	4	3	1981	2010	1561	~307	0.26	0.38	0.69	1483	5.0
Scatlè	2	5	1965	2018	1694	~321	2.89	3.18	3.47	1566	3.0
Murgtal	4	1	2016	2016	1870	100	0.13	0.32	0.48	2317	2.6
Swiss National Park	23	3	1977	2013	1929	~174	0.24	0.64	1.47	957	2.3
Aletschwald	2	1	2013	2013	2003	98	0.50	0.50	0.50	1323	2.5
La Niva	2	1	2015	2015	2011	28	0.51	0.53	0.55	1198	2.0
Tamangur	3	1	2015	2015	2185	57	0.55	0.62	0.65	999	1.0

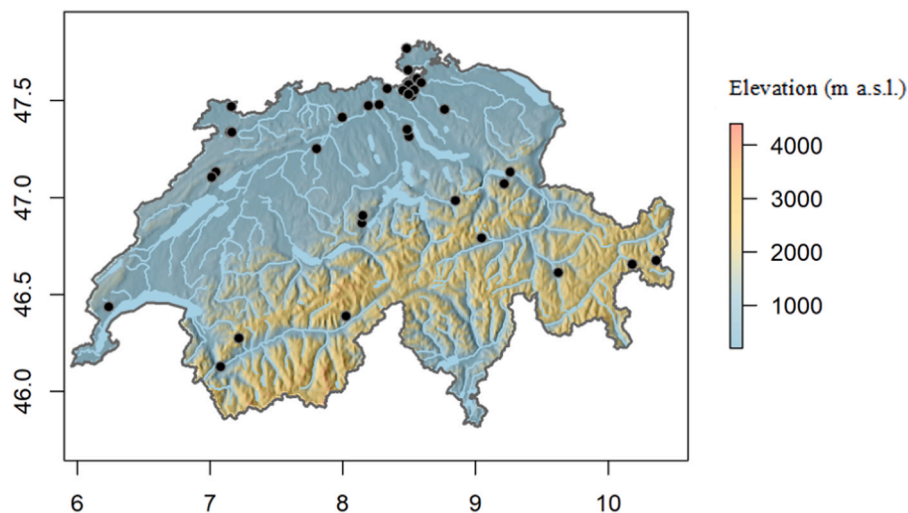


Fig. 1. Map of Switzerland showing the location of the 37 reserves included in this analysis. Longitude (x-axis) and latitude (y-axis) are given in degrees. Elevation data are from the NASA Shuttle Radar Topographic Mission 90 m digital elevation model (Jarvis et al., 2008).

(in most cases 4.0 cm diameter at breast height, DBH) were stem-tagged, the DBH was measured, and their status (dead/ alive), species identity, and other tree characteristics were assessed. More information on the monitoring and sampling design of the NFR can be found in [Stillhard et al. \(2021\)](#), [Hobi et al. \(2020\)](#) and [Brang et al. \(2011\)](#).

2.2. Data processing

2.2.1. Biomass calculations

We estimated tree-level live biomass at each inventory using the species-specific allometric equations from [Forrester et al. \(2017\)](#). They take into account the level of competition in the stand (in terms of total BA), its location (latitude) and climate (mean annual temperature and precipitation sum). Tree-level biomass was calculated as aboveground (stem, branches and leaves) and belowground (roots), and the sum of both was considered as total live biomass ([Molina-Valero et al., 2021](#)), hereafter referred to as “biomass”. Tree-level biomass was converted to Mg ha^{-1} when summing up within plots. The change in biomass between inventories was averaged over the inventory interval to obtain annual means ($\text{Mg ha}^{-1} \text{ year}^{-1}$).

As forest inventories were not carried out annually, it is not possible to determine the exact year in which individual trees died. For the trees that disappeared or died between inventories, we assumed zero growth after the last inventory in which they had been recorded as being alive ([Halpin and Lorimer, 2016](#)). Although in most inventories a caliper threshold of 4 cm was used, the highest caliper threshold employed since monitoring has begun was 8 cm. Therefore, with the aim of obtaining a homogeneous biomass dataset, trees with a DBH smaller than 8 cm were excluded from the analysis. A study in primeval forests in the Slovakian Carpathians found that live aboveground biomass of trees <7 cm was merely 0.77 % in comparison with trees >7 cm ([Glatthorn et al., 2018](#)), showing that small trees contribute little to biomass dynamics overall.

2.2.2. Plot selection

We defined a set of criteria for selecting the permanent plots to be included in our analysis (see [Fig. A1](#)). First, we set a minimum plot size of 0.1 ha, as very small plots are not suitable for characterising stand biomass. Furthermore, plot size affects the comparison of multiple attributes such as forest structure or species richness ([De Cáceres et al., 2015](#); [Portier et al., 2022](#)). In this step, homogeneous neighbouring plots <0.1 ha were merged, and heterogeneous plots <0.1 ha were removed from the data set. Second, we excluded plots that had >1000 or <100 Mg ha^{-1} of biomass to avoid extreme estimates not supported by the literature, thus (1) reducing the “majestic forest” bias that is due to the selection of small mature forest plots without gaps ([Phillips et al., 2004](#)) and (2) excluding plots that had been affected by high-severity natural disturbances (e.g., large-scale windthrow events or forest fires), as this study does not focus on recovery after disturbance. To exclude these latter plots, we furthermore used the criterion of >20 % loss of biomass or >3 % loss of annual biomass between two inventories, respectively, relative to the initial value. These thresholds were selected based on a compromise between fulfilling the objective of the filter without losing large amounts of data. Affected plots were excluded for the entire analysis and not just for the respective inventory period. In total, we excluded 70 plots and used the remaining 224 plots (distributed across 37 reserves). Most plots were re-measured several times, up to a maximum of six times, which yielded a total of 695 plot-level observations.

Within our dataset, 130 permanent plots (66.1 % of the observations) in 25 forest reserves are located between 334 and 800 m a.s.l. (subsequently referred to as “low elevation”). Fifty-seven plots (22.3 %) in 8 reserves are located between 801 and 1600 m a.s.l. (“medium elevation”). The remaining 37 plots (11.7 %) in 7 reserves are located between 1600 and 2227 m a.s.l. (“high elevation”). The reserves at low elevation are predominantly mixed broadleaved forests, followed by a

gradual dominance of beech and then mixed spruce-fir-beech forests at medium to high elevations. At high elevation, conifer forests dominate.

2.2.3. Metrics of forest structure and time since cessation of management (TSCM)

Forest structure at the plot level was characterized by the density of live stems (stems ha^{-1}), the density of large trees using three DBH thresholds (>40, >60 and >80 cm), BA ($\text{m}^2 \text{ ha}^{-1}$), the richness of those species that had at least 10 occurrences per ha, the share of conifers in total biomass (%), the stand density index (SDI) and the Gini coefficient of BA. SDI is often used as a measure of stocking because it contains information on both BA and tree density and is based on allometric theory ([Reineke, 1933](#); [Pretzsch and Biber, 2016](#)). It was calculated for each plot as:

$$SDI = N \times (25/D_q)^{-1.605} \quad (1)$$

where N is the density of live stems per hectare and D_q is the quadratic mean diameter of all trees in the plot (in cm).

The Gini coefficient is a measure of structural heterogeneity because it assesses the inequality of tree sizes based on BA ([Zeller and Pretzsch, 2019](#)). Theoretical values range from 0 (complete equality) to 1 (highest dispersion); yet it has been questioned whether these extremes are ecologically plausible ([Valbuena et al., 2013](#)). The Gini coefficient was calculated as follows ([Gini, 1921](#)):

$$GC_{BA} = \frac{\sum_{j=1}^N BA_j(2j - N - 1)}{\sum_{j=1}^N BA_j(N - 1)} \quad (2)$$

TSCM was determined for each plot using historical records, when possible, as well as expert knowledge of the researchers involved in the monitoring (cf. [Table 1](#)). The uncertainty of assigning a specific calendar year to the cessation of management increases with TSCM itself. This was the case particularly for Bödmerenwald, Swiss National Park, Derborence and Scatlè (cf. [Table 1](#)). In the case of Scatlè, where no management has been recorded since the 13th century, the pragmatic decision was made to use 1700 as the last year in which management took place. This was done due to the impossibility of assigning a specific date, and to take into account the fact that it shares old-growth status with Derborence.

2.2.4. Climate variables

We used spatially interpolated monthly meteorological data at 100 m spatial resolution that were developed by the Landscape Dynamics group (Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Switzerland). They are based on the data of the climate stations of MeteoSwiss for the period 1930–2021, employing the DAY-MET method to derive spatially explicit data ([Thornton et al., 1997](#)). On a few occasions, the centroid of the plots is closer than 100 m and therefore the climatic values are the same. This is the case for 27 plots out of 224 plots (12 % of the plots) in 12 reserves.

We used monthly mean, maximum and minimum temperatures and the precipitation sum to derive annual mean and growing season (April to September) temperature and precipitation values, as well as maxima and minima. We calculated potential evapotranspiration (PET) using the Hargreaves equation implemented in the R package “SPEI” ([Begueria and Vicente-Serrano, 2017](#)). The climatic water balance (WBal) was calculated as precipitation minus PET. Finally, the degree-day sum (DDS) was calculated according to [Bugmann \(1994\)](#) using the modified sine wave method ([Allen, 1976](#)) and a threshold temperature of 5.5 °C. An annual value and a value for the growing season (April to September) were calculated for the variables PET, WBal and DDS.

2.2.5. Topographic and soil variables

Elevation, slope, and aspect of each plot were obtained from the digital terrain model DHM25 ([Federal Office of Topography swisstopo](#),

1994) with a resolution of 25 m x 25 m. It is based on the Swiss national map 1:25,000 and represents the three-dimensional surface of the country in the absence of infrastructure or vegetation. The clockwise measured aspect in degrees was transformed to Beers's aspect (Beers et al., 1966) using the cosine function (Eq. 3). It transforms aspect along an axis running from north-east to south-west to reflect the combined influence of bright illumination and high afternoon temperatures that maximally affect south-west facing slopes in the Northern hemisphere. Beers's aspect takes values between zero (south-west facing slopes) and two (north-east facing slopes).

$$\text{Beers' aspect} = 1 + \cos(45 - \text{aspect}) \quad (3)$$

Although soil characteristics play an important role for the growth rates and the amount of biomass a site can sustain, they are difficult to assess due to scarce data. In the NFR network, over 20 % of the permanent plots fortunately have a soil profile. Soil profiles were analysed to a depth of 1 m or until the bedrock was reached. Mean soil pH and available water capacity (AWC) were determined for each profile. AWC was derived from soil depth, texture, bulk density, organic carbon content and rock content of each soil horizon according to Teepe et al. (2003). In permanent plots where no soil surveys were available, mean soil pH and AWC were calculated for the adjacent available soil profiles with comparable geology, climate, elevation, slope, aspect, vegetation type and mean height of the tallest 20 trees (as a proxy for site productivity and thus soil fertility). The mean value of the variables calculated for the neighbouring similar soil profiles was taken as an approximation of the value of the permanent observation plot without soil analysis.

2.3. Development of biomass

To answer research question i), we used the calculated amount of biomass in each plot for each inventory and plotted the trajectories of each plot by reserve to visually assess biomass development.

2.4. Statistical modelling

We developed two linear mixed effects models (LMMs) to answer research questions ii) and iii). We developed the first model (hereafter referred to as "biomass model") to study the relationship between biomass and TSCM while controlling for other confounding factors such as forest stocking (measured as SDI). We included an interaction with elevation to further test our expectation of finding lower aboveground

biomass at higher and cooler locations. We created a second model (hereafter referred to as "biomass change model") to analyse the effects of abiotic and biotic drivers on annual biomass change, including variables that characterise (1) forest structure, (2) climatic conditions and (3) site conditions (see Table 2). To prioritize maximum statistical power for the biomass model, we retained the single-time inventories in this analysis, instead of using identical datasets for both models.

First, in the biomass model, we modelled biomass as a function of TSCM and elevation SDI and tree density. We checked the correlation between the explanatory variables using the R package "corrplot" (Wei and Simko, 2021) and verified that their correlation coefficients were <0.7 (Fig. A1). We included SDI at the first inventory as a proxy for the initial stocking state after the cessation of management. The hypothesized peak and decline pattern of biomass (Bormann and Likens, 1979) may be too subtle to be evident in field data with a decade-long remeasurement interval (Halpin and Lorimer, 2016). Therefore, to account for the expected equilibrium of the biomass curve, TSCM was modelled using the logarithm (Keeton et al., 2011). As the TSCM >200 years in Derborence and Scatlè is a minimum value, their true TSCM might be much longer. To test the effect of a potential longer TSCM in these reserves, we fitted an alternative model where we increased their TSCM by 2000 years to evaluate the influence of these extreme values. We furthermore created a model that excluded all plots with a TSCM >170 years, i.e. the reserves Derborence, Scatlè and Swiss National Park, to further test the effect of high values.

Second, in the biomass change model, we examined the response of the annual biomass change to abiotic and biotic drivers. We first assessed the multicollinearity of the explanatory variables using the R package "corrplot" (Wei and Simko, 2021) and selected those variables with a correlation coefficient <0.7 that we considered to have the highest environmental relevance (Figs. A3 and A4). The final predictor variables used in this LMM were (1) BA, tree density and the Gini coefficient of the stands in the previous inventory, to characterise forest structure; (2) annual degree-day sum and annual precipitation, both averaged over the inventory period, to represent climatic conditions; and (3) slope, aspect and soil AWC, to account for site conditions. We formulated the models based on our ecological hypotheses. To decide whether a variable needed to be transformed we plotted the response variable against each predictor variable. Variables were then transformed using log transformations and quadratic terms (see Table 2).

Both models were constructed using the basic LMM structure, including each plot nested within the corresponding reserve as grouping variables of random effects, to account for the hierarchical structure and

Table 2

Response and explanatory variables used in the (1) biomass and (2) biomass change models, and structure of their fixed effects. The number of observations used in each model is represented by n. The column SD shows the standard deviation of each variable, and the column 'Model' shows the structure and interactions between variables in their respective models.

	Response variable and number of observations	Explanatory variables	Unit	Acronym	Min	Median	Max	SD	Model
(1)	Biomass (Mg ha ⁻¹) n = 695	Time since cessation of management	years	TSCM	1.0	47.0	319.0	54.1	$\log(\text{TSCM}) + \text{ele} + \text{SDI} + \text{N} + \log(\text{TSCM}) \times \text{ele} + \log(\text{TSCM}) \times \text{SDI}$
		Elevation	m a.s.l.	ele	334.0	647.0	2227.0	492.0	
		Stand density index in first inventory	unitless	SDI	363.6	733.8	1385.9	185.7	
		Stand tree density	stems ha ⁻¹	N	163.9	726.2	2720.5	939.2	
		Annual degree day sum	°C days	DDS	556.6	1900.7	2495.8	497.2	
		Annual total precipitation	mm	prcp	802.2	1167.7	2447.3	304.9	
		Stand basal area in previous inventory	m ² ha ⁻¹	BA	15.8	38.1	84.6	10.5	
(2)	Annual change of biomass (Mg ha ⁻¹ year ⁻¹) n = 471	Stand tree density in previous inventory	stems ha ⁻¹	N	173.3	754.9	2720.5	397.9	$\text{Gini} + \text{slp} + \text{asp} + \text{AWC} + \text{DDS}^2 \times \text{prcp} + \text{BA}^2 \times \text{N}^2$
		Gini index in previous inventory	unitless	Gini	0.3	0.5	0.7	0.1	
		Slope	%	slp	1.0	39.0	122.0	25.0	
		Beers's aspect	unitless	asp	0	0.8	2	0.7	
		Available water capacity	mm m ⁻¹	AWC	23.0	108.9	254.0	43.5	

repeated measurements of the data (several plots within reserves were measured several times):

$$Y_{fii} = \beta_0 + \beta_m \times z_{fii}^m + b_f + b_{fi} + \varepsilon_{fii} \quad (4)$$

where Y represents the response variable of interest and z the explanatory variables (Table 2). The indices represent the reserve f , the plot t and the measurement at a point in time i , and the index m represents an explanatory variable. The fixed effects parameters associated with each variable z are represented by β , and b_f and b_{fi} represent the random effects associated with the reserve and the plot within the reserve ($b_f \sim N(0, \tau_1^2)$, $b_{fi} \sim N(0, \tau_2^2)$). Finally, ε_{fii} represents the error associated with each observation i of plot t within reserve f ($\varepsilon_{fii} \sim N(0, \sigma_2^2)$).

We developed and applied the LMMs using the R package "lme4" (Bates et al., 2015). The residuals were assessed using the R package "DHARMA" (Hartig, 2022). We used R version 4.2.1 (R Core Team, 2022) for all statistical analyses as well as for data visualization.

3. Results

3.1. Development of biomass

After the cessation of management and in the absence of major natural disturbances, biomass increased gradually in most forest reserves (Fig. 2). Nevertheless, there were large differences in biomass development among reserves and among the plots within a reserve. In some cases, they were due to a large variation in elevation between reserves and plots, associated with differences in species composition and thus forest types. The variations among the plots within the same reserve may also be due to terrain heterogeneity (e.g., slope, soil depth, or rock outcrops) or management history. While in some reserves biomass has increased steadily since the first inventory (e.g.,

Langgraben, Strassberg), in others an initially strong increase was followed by small changes in subsequent inventories (e.g., Unterwilerberg, Tariche Haute Côte). In some cases, little change was observed over the entire monitoring period (e.g., Scatlè).

We found biomass values across all plots in all reserves ranging from 101 Mg ha⁻¹ to 851.2 Mg ha⁻¹, with a median of 362.1 Mg ha⁻¹ (SD = 122.5 Mg ha⁻¹). The belowground component (tree roots) represented on average 19 % of total biomass, ranging from 11.7 % to 27.2 % (SD = 2.6 %), depending on the species composition of the stand.

The differences in biomass storage among plots and reserves are also mirrored in the rate of change of biomass. The highest positive rate of 9.5 Mg ha⁻¹ year⁻¹ was observed in a permanent plot in the Strassberg reserve between 1987 and 2001. This plot was characterized by 542 Mg ha⁻¹ of biomass, 66.7 m² ha⁻¹ of stand BA and 1590 stems ha⁻¹ in 1987. In the next inventory in 2001, biomass increased to 675 Mg ha⁻¹ and tree density decreased to 1130 stems ha⁻¹. In general, we found low biomass change rates or even a loss of biomass (up to -7.7 Mg ha⁻¹ year⁻¹) in plots with high BA and low tree density, or when tree density was very high (>2500 stems ha⁻¹).

3.2. Biomass and TSCM

The biomass model showed that on average, more biomass was found with increasing TSCM (Fig. 3, Table A1). A rapid increase of biomass occurred during the first 100 years since the cessation of management, and this trend continued even with high TSCM albeit at a lower rate, as shown by the shape of the modelled saturation curve.

For the same TSCM, plots at higher elevation had lower biomass (Fig. 3; statistically significant with $p < 0.001$). The interaction term between elevation and TSCM was not significant ($\beta = 0.02$; $p = 0.285$), which indicates no difference in the slope of the curves between elevation zones. Most of the plots studied have low values of TSCM, and we

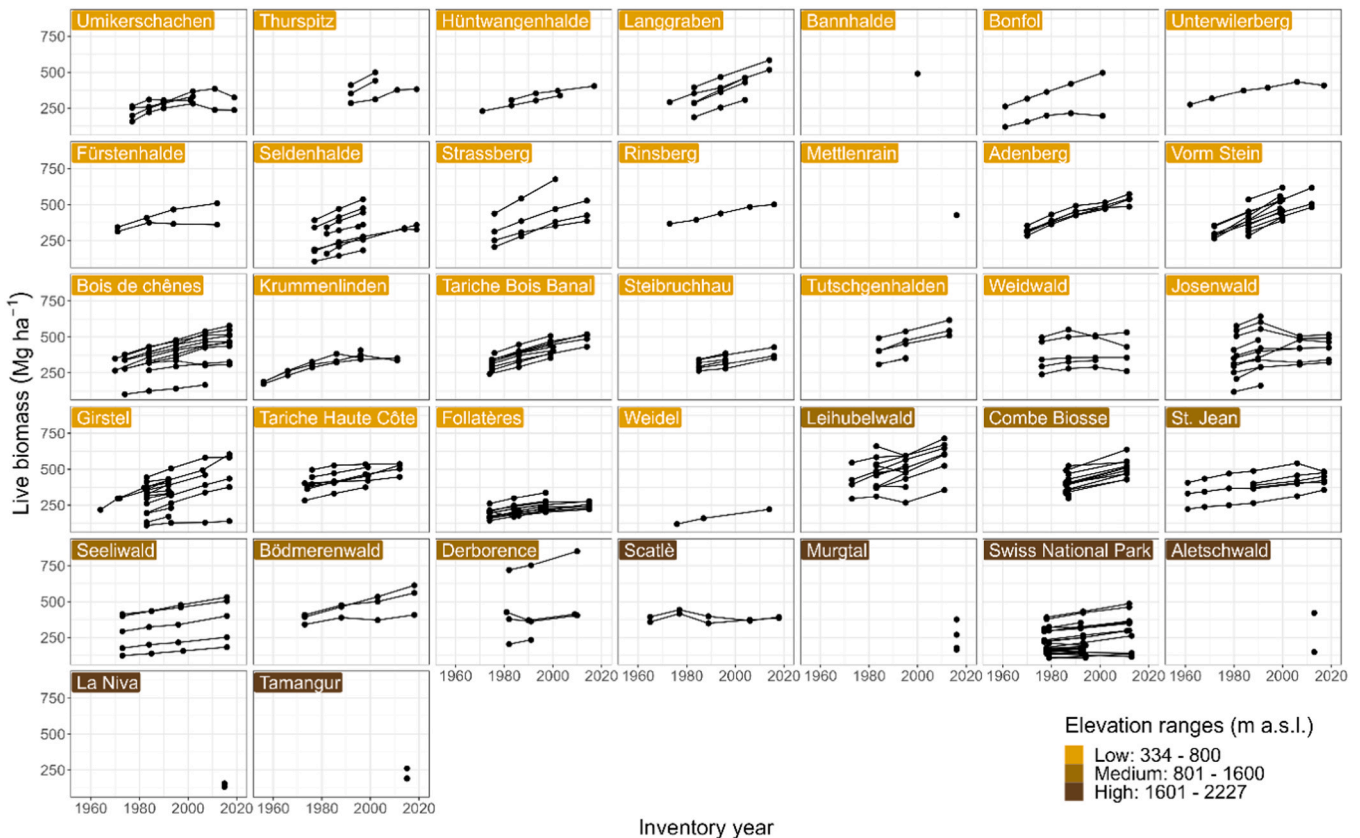


Fig. 2. Live biomass (Mg ha⁻¹) in the 37 Swiss forest reserves used in this study. Each panel represents a forest reserve, each line within a panel a permanent plot, and each dot a measurement (inventory year). The panels are ordered from low to high elevation.

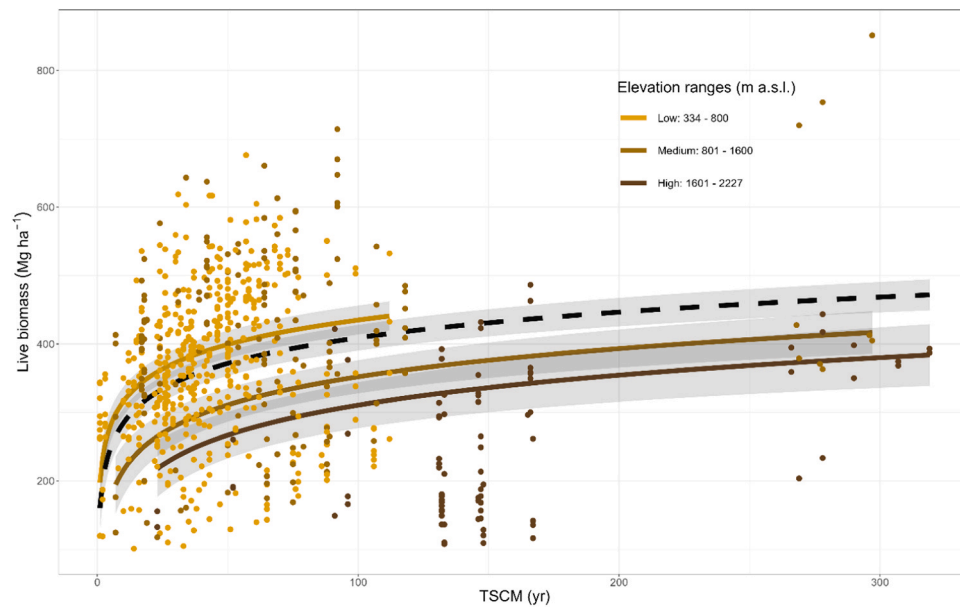


Fig. 3. Predicted live biomass as a function of the time since the cessation of management (TSCM) and elevation. Dots represent observed values of each plot, and the colour shows the corresponding elevation zone. The dashed line represents predictions for the mean elevation of all plots (850 m a.s.l.). These curves were predicted based on the mean value of all other variables in the model. The shaded area shows the 95 % confidence intervals. Predictions are restricted to the TSCM range covered by each elevation zone to avoid extrapolation. Model coefficients are shown in Table A1.

lack data on forest stands at low elevations that have been unmanaged for >120 years. Therefore, we do not extrapolate beyond this value.

The alternative model, in which TSCM of Derborence and Scatlè was increased to 2000 years to test its sensitivity to this uncertainty, did not feature noticeable differences. It had very similar coefficients, but lower statistical significance (Fig. A5, Table A2) compared to the original biomass model. The same pattern was found in the second alternative model, in which we excluded all plots with a TSCM > 170 years (Derborence, Scatlè and the Swiss National Park) (Fig. A6, Table A3).

3.3. Drivers of biomass change

Tree density and BA in the previous inventory, annual DDS and slope were the most important drivers of annual biomass change (Figs. 4 and

5; Table A4). Below, we present the results of the biomass change model according to variables representing (1) forest structure, (2) climatic conditions and (3) site conditions.

First, in terms of forest structure (Fig. 4), the highest change rates (>8 Mg ha⁻¹ year⁻¹) were found when BA in the previous inventory was high (>60 m² ha⁻¹) and tree density medium to high (1500 to 2000 stems ha⁻¹). At low BA and high tree density, we found a considerably lower biomass increase, and the same was found for low tree density and very high values of BA.

Second, we found the strongest positive rate of change of biomass of up to 6.7 Mg ha⁻¹ year⁻¹ in plots that experienced low precipitation (within the range covered by our data, cf. Table 1) and medium DDS (Fig. 5). We also found a high rate of change of biomass when precipitation was very high (>2000 mm annually), but overall the annual

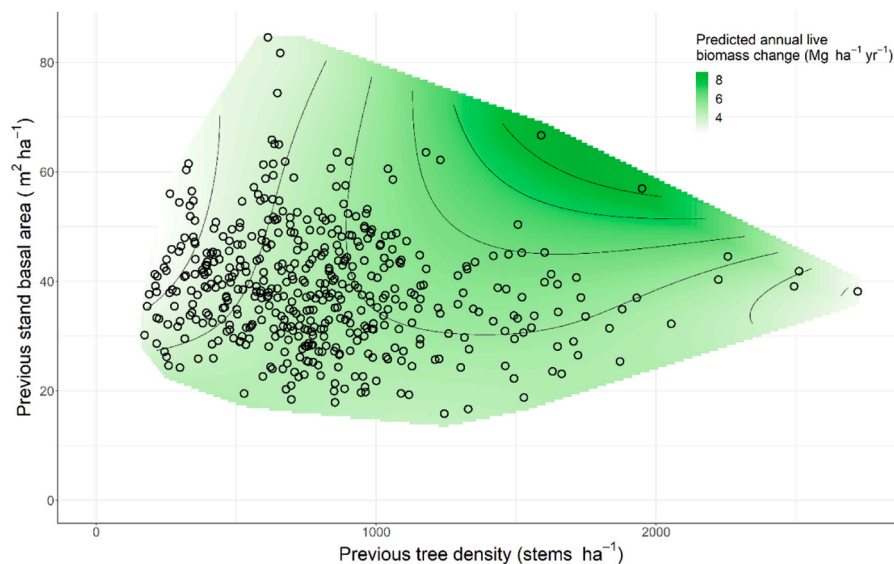


Fig. 4. Predicted annual live biomass change based on BA and tree density in the previous inventory. The circles represent the observed values of both explanatory variables in each plot. The heat map was predicted using the mean value of all other variables in the model. The coefficients of the model are shown in Table A4.

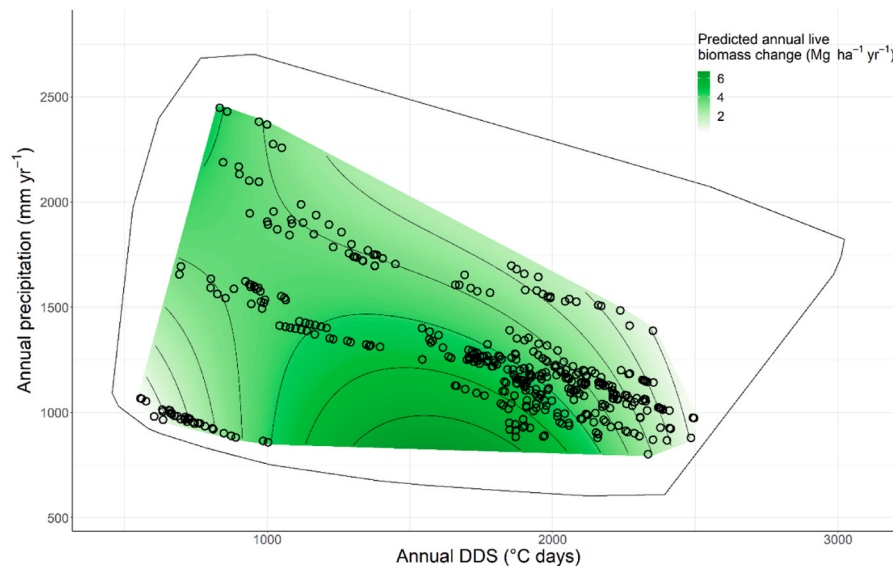


Fig. 5. Predicted annual live biomass change as a function of annual precipitation and annual degree-day sum averaged over the inventory period. The black polygon shows the climatic envelope covered by the Swiss National Forest Inventory plots. The circles represent the observed values of both explanatory variables in each plot. The heat map was predicted using the mean value of all other variables in the model. The coefficients of the model are shown in Table A4.

change in biomass was driven by DDS. Under both very low and very high annual DDS, biomass change was quite low ($0.2 \text{ Mg ha}^{-1} \text{ year}^{-1}$).

Third, the biomass change model (Table A4) suggests a minimal effect of site conditions. Slope angle had a negative effect ($p < 0.001$) on biomass change, and the effects of AWC and aspect were not significant, with their fixed effect estimates being zero or close to zero.

4. Discussion

4.1. Development of biomass

After the cessation of management and in the absence of high-severity natural disturbances, most forest reserves have gradually accumulated biomass. Similarly, unmanaged spruce-fir-beech forests in a strict reserve declared in 1957 in Serbia exhibited a comparable trend, in which BA increased from $42.4 \text{ m}^2 \text{ ha}^{-1}$ to $56.7 \text{ m}^2 \text{ ha}^{-1}$ between 1960 and 2010 (Keren et al., 2018). Some reserves in our study, particularly the old-growth forests Scatlè and Derborence, showed only slight changes of biomass over long time periods, possibly indicating that they are in the theoretical steady state, or are at least approaching it (Borrmann and Likens, 1979). A similar pattern was observed in 15 mixed mountain spruce-fir-beech old-growth forests in Slovenia, Croatia, Slovakia and Bosnia-Herzegovina, which showed rather constant BA over a long time (Diaci et al., 2011), as well as in the Uholka beech forest reserve in Ukraine over more than 100 km^2 during a 10-year inventory period (Stillhard et al., 2022). Furthermore, a semi-natural broadleaf forest in Denmark that was affected only slightly by human interventions over the last 200 years was found to be in steady state, as its net ecosystem production (NEP) approached zero (Nord-Larsen et al., 2019). Thus, while some Swiss reserves appear to be in a steady state already, most of them continue to accumulate biomass, with no clear sign of the biomass curve reaching an equilibrium.

The highest biomass value in our dataset (851.2 Mg ha^{-1}) occurred in the Derborence forest reserve, one of the few old-growth forests found in the Alps, which is dominated by silver fir and Norway spruce. This exceptionally high value was recorded in a small plot of 0.3 ha and may be a sign of the “majestic forest” bias (Phillips et al., 2004). Nevertheless, it is comparable to the value of 850 Mg ha^{-1} reported for old-growth silver fir forests in Spain (Molina-Valero et al., 2021), underlining the high biomass storage capacity of unmanaged forests.

4.2. Biomass and TSCM

The amount of biomass a forest stand can sustain depends strongly on abiotic and biotic conditions. Higher temperature and precipitation tend to have a positive effect (Zhu et al., 2018), and thus with decreasing elevation (i.e., increasing temperature), biomass is expected to increase (Hiller and McMichael, 1975). This was generally confirmed by the patterns observed in our data, albeit with exceptions such as Derborence (cf. above). We found a reduction by 148 Mg ha^{-1} of biomass per 1000 m of elevation gain, which is broadly consistent with the results of Whittaker (1966), who found a reduction by 230 Mg ha^{-1} of above-ground biomass per 1000 m of elevation gain in the Great Smoky Mountains in the US. This pattern is further influenced by other factors. Soil quality (i.e., nutrient availability) tends to increase with decreasing elevation unless water is becoming a limiting resource, thus boosting biomass at low elevations. High-elevation forests in our dataset, such as the plots in the Swiss National Park that lie above 1900 m a.s.l. , feature Swiss stone pine (*Pinus cembra* L.) and mountain pine (*Pinus mugo* Turra), which grow more slowly and do not reach biomass values as high as other forest types (Boden et al., 2010). Thus, not only site conditions have a strong influence on the amount of biomass a forest can sustain, but also the tree species mixture is important.

The elevational and thus climatic effect we found suggests that in a warmer climate – and provided that the other drivers do not change – unmanaged forests will have an even larger role as carbon sinks, since the biomass they can support would increase. However, the expected increase in the frequency and severity of natural disturbances, as well as reduced precipitation leading to more drought, may result in biomass losses (Albrich et al., 2022). For example, forests in central Europe experienced a historic drought linked to the 2018 heatwave (Hoy et al., 2020). Together with the weakening effect of previous years that were drier than usual (i.e., 2015 and 2017), this drought event had a strong effect on the vitality of many trees (Rohner et al., 2021), and it even led to widespread mortality (Schuldt et al., 2020). Additionally, even in the absence of changes in the annual precipitation sum, shifts in seasonal rainfall patterns may occur. This can result in more intense rainfall events, causing increased water runoff and subsequently reduced water availability for trees and other forest plants (Rummukainen, 2012; Lindner et al., 2014). Therefore, although there may be an increasing potential of carbon storage in set-aside forests under climate change, disturbances need to be taken into account, which may turn these

systems into net sources. Nevertheless, the disturbance-driven losses of live biomass increases the necromass and deadwood compartments, which can provide a buffer until potentially fast-growing new cohorts take over.

We expected the biomass curve to reach an equilibrium at high TSCM, from which one could derive how long formerly managed forests need to reach the upper limit of biomass storage. Meyer et al. (2021) found that mixed beech-oak forest reserves approached the upper limit of biomass storage 50 years after the cessation of management. However, they found a linear increase in biomass during the first 50 years without management in pure beech forest reserves (Meyer et al., 2021). This was further analysed by Nagel et al. (2023), who showed increasing biomass for approximately 50 years for forest reserves at different stand ages and including stands with TSCM >100 years. The Kersselaerspleyn beech forest in Belgium was even found to approximate a dynamic equilibrium merely ca. 20 years after the last management intervention (Vandekerckhove et al., 2005). Although we found a clear pattern towards this upper limit, biomass did not reach the expected equilibrium at the TSCM covered by our study. The majority of the NFRs in our study do not exceed 100 years of TSCM, which is still short relative to the length of a tree generation (Oliver and Larson, 1996).

These literature findings are partly contrasting our results, particularly for the reserves at low elevations that continued to accumulate biomass well beyond the reported TSCM. This discrepancy could be due to the difference in biomass stocks between the reserves of each study just after the cessation of management. Nevertheless, our results are consistent with findings showing the above-mentioned asymptotic curve of biomass accumulation with longer TSCM (Halpin and Lorimer, 2016; Meyer et al., 2021; Nagel et al., 2023). Overall, our results suggest that most of the reserves have not yet reached a biomass equilibrium and are still acting as carbon sinks in tree biomass. This highlights the potential of forest reserves to accumulate biomass over long periods of time, which is consistent with the findings of Glatthorn et al. (2018) and Luyssaert et al. (2008).

4.3. Drivers of biomass change

Contrary to our expectations, we found high positive rates of biomass change when BA was high and tree density was medium. This may be because most of the reserves were already well stocked with a high density of canopy trees at the beginning of the monitoring. These mature, large trees grew – and therefore produced biomass – at high rates. Similar results were found in old-growth beech forests in Slovakia, where the heterogeneous canopy structure was the primary driving force (Glatthorn et al., 2018). However, the positive effect of BA became smaller at very high values, possibly indicating that the carrying capacity of the site was reached.

We expected to find the largest positive changes of biomass under warm and wet conditions (Hilmers et al., 2019). However, we observed the highest positive rates of change at medium annual DDS values. We found no effect of annual precipitation, indicating that water availability is overall not a limiting factor in the forest reserves studied here, since annual precipitation was always above 900 mm. This suggests that even though biomass acquisition benefits from a longer growing season, there is a limit to this positive effect, likely dictated by site-specific conditions such as site fertility (Holeksa et al., 2009). Thus, our results cannot be extrapolated to warmer and drier sites which can be found in some areas of Central Europe, where a decrease of biomass storage would be expected (Zhu et al., 2018).

The effects of forest structure, climate, and site conditions on biomass change were potentially confounded by the successional phase of the forest plots (Oliver and Larson, 1996). For example, sites with similar BA and tree density may follow different biomass trajectories depending on their respective successional phase (i.e., biomass may increase in the mature phase whereas it may decrease if the stand is already in the decay phase; cf. Brang et al., 2011). Thus, the mixed

effects models developed here may not be generally valid, but they represent the effects of forest structure in the various successional phases represented in our dataset under current climatic conditions.

5. Conclusion

It is crucial to better understand biomass dynamics in unmanaged forests due to their role in climate change mitigation. Our study puts into perspective the usefulness and importance of long-term permanent plots covering a wide environmental gradient for studying these dynamics. We showed that biomass storage has increased in the majority of the studied forest reserves since monitoring began. Biomass development followed an asymptotic saturation curve with longer TSCM, and although our dataset covered a wide range of TSCM, the biomass trajectory did not reach the expected equilibrium. This indicates that these forest stands have not yet reached their biomass carrying capacity. Elevation had a negative effect on the total biomass sustained by the sites, which indicates a positive effect of temperature under conditions where water is not a primary limiting factor. We furthermore showed that forests with a structural optimum of high basal area and medium levels of tree density have the highest rate of biomass increase.

In future analyses on biomass dynamics, it would be especially important to include further carbon pools, such as standing and lying deadwood as well as soil carbon. Ultimately, establishing forest reserves appears as a fast and relatively simple means for enhancing biological carbon storage. However, there is a limit to their storage capacity, and the demand for timber requires keeping a large share of managed forests in the landscape. Lastly, it will be essential to find a good balance between carbon storage through the promotion of wood products on the one hand, and the promotion of the transition of forests to mature stages on the other hand.

CRedit authorship contribution statement

Idoate-Lacasia Jokin: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Stillhard Jonas:** Data curation, Formal analysis, Methodology, Writing – review & editing. **Bigler Christof:** Formal analysis, Supervision, Writing – review & editing. **Bugmann Harald:** Conceptualization, Supervision, Writing – review & editing. **Hobi Martina Lena:** Conceptualization, Supervision, Writing – review & editing. **Zimmermann Stephan:** Resources, Writing – review & editing. **Portier Jeanne:** Formal analysis, Methodology, Writing – review & editing. **Brang Peter:** Conceptualization, 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.

Data Availability

Data and script to reproduce the analysis are available at the Environmental Data Portal EnviDat (<https://www.envidat.ch/dataset/biomass-dynamics-temperate-forests-in-europe>).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.121697.

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