

Limited sink but large storage: Biomass dynamics in naturally developing beech (*Fagus sylvatica*) and oak (*Quercus robur*, *Quercus petraea*) forests of north-western Germany

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Abstract

1. Currently, the dynamics underlying the storage and acquisition of biomass, and thus carbon, in naturally developing forests are under debate. A better understanding of the biomass dynamics of forests is needed to clarify the role played by naturally developing forests in the mitigation of climate change.
2. Long-term monitoring data from unmanaged strict forest reserves (SFRs) in north-western Germany were used to analyse the biomass dynamics of pure beech, mixed beech and mixed oak forests. A complete balance of above-ground woody biomass (biomass) and growth, density-dependent and -independent mortality, as well as deadwood decay was derived. Density-independent mortality served as a proxy for disturbance severity.
3. After a time since abandonment (TSA) of 50 years, the average biomass ranged between 334 t/ha in mixed oak and 478 t/ha in pure beech stands. The net change in biomass was positive in all forest types. Density-independent mortality and decay rates were much lower than the growth rates. Pure beech forests reached higher levels of biomass, a higher net change in biomass, and more growth than either of the mixed forest types. Biomass increased linearly with TSA in pure beech stands but followed an asymptotic course in the mixed forests. In the latter, the net change in biomass and growth were consistent with a unimodal development pattern. The development of biomass could not be explained by the ageing of the tree communities.
4. *Synthesis.* We hypothesized that the observed biomass dynamics are a result of the interaction between resource supply within a limited growing space and the resource-use efficiency of the tree stand in conjunction with disturbances. The still-linear increase in the biomass of pure beech forests was assumed to reflect the high resource-use efficiency of beech, especially its use of light. The above-ground capacity of naturally developing broadleaved forests to store and acquire carbon is substantial. Accordingly, allowing broadleaved forests to develop naturally can contribute substantially to carbon storage and sequestration. However,

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our study also suggests that the above-ground carbon sink decreases after several decades.

KEYWORDS

carbon storage, climate change, disturbances, tree demography

1 | INTRODUCTION

While it is beyond a doubt that the conservation of forests harbouring high stocks of biomass is imperative for climate protection (IPCC, 2020; Watson et al., 2018), it is less clear how long old forests can serve as carbon sinks (Luyssaert et al., 2008; Nord-Larsen et al., 2019) and to what degree forests set aside from active management are able to store and acquire biomass and thus carbon (Griscom et al., 2017; Schulze et al., 2020).

According to the 'respiration hypothesis', as forests age, their net primary production gradually approximates zero because autotrophic respiration increases and eventually equals or even rules out gross primary production (Odum, 1969). However, the 'respiration hypothesis' could not be supported by measurements (Kutsch et al., 2009). Instead, alternative explanations for an age-related decline in forest growth have been discussed (Binkley et al., 2002; Ryan et al., 1997). While Pregitzer and Euskirchen (2004) reported decreasing net primary production of forests with increasing age globally, there is also accumulating evidence that old-growth forests continue to increase their biomass stock for a surprisingly long period of time (Carey et al., 2001; Curtis & Gough, 2018; Knohl et al., 2003; Luyssaert et al., 2008). Halpin and Lorimer (2016) have shown that, in the later stages of old growth, biomass may indeed decline. These results have led to diverging positions regarding the climate protection potential of naturally developing unmanaged forests (Griscom et al., 2017; Höltermann et al., 2020; Jandl et al., 2019; Krug, 2019; Kun et al., 2020; Schulze et al., 2020).

The maximum attainable biomass stock of an ecosystem will ultimately be limited by environmental constraints (Körner, 2017; Molina-Valero et al., 2021). The fundamental concept of growth towards an upper limit is mostly modelled using the logistic function originally applied by Verhulst (1838) to human population growth. After growth has reached an exponential phase and has passed the inflection point, it decreases asymptotically. This temporal course has been interpreted as reflecting the interaction between the intrinsic tendency of natural entities to grow exponentially and the restraints of a finite environment (Hutchinson, 1978). A corresponding paradigm of forest growth and yield science (Pretzsch, 2009) and of ecology (Pastor, 2008) is that, in a steady state, ecosystem biomass oscillates around a certain upper limit. In ecology, growth is mostly modelled as a function of time while in forest growth and yield science it is seen as a function of stand age.

Odum (1953) was the first to refer to the asymptote of the logistic growth curve as representative of the carrying capacity. Gupta and Rhao (1994) then introduced the concept of the carbon carrying

capacity, defined by Keith et al. (2009) as 'the mass of carbon able to be stored in a forest ecosystem under prevailing environmental conditions and natural disturbance regimes, but excluding anthropogenic disturbance'. Although carrying capacity is a widely used concept, its definition and conceptual basis are ambiguous (Chapman & Byron, 2018; Dhondt, 1988). In particular, it is unclear whether carrying capacity is static or variable and thus either empirically or theoretically questionable (Sayre, 2008). This problem is especially relevant in the light of the human-induced alterations in environmental conditions that are affecting forest growth (e.g. in central Europe; Pretzsch et al., 2021).

Given the difficulties in determining an upper limit of biomass storage in forests, studies of unmanaged stands are essential to gain further insights into biomass dynamics (Hoover et al., 2012). However, empirical long-term data in this field are still scarce (Keith et al., 2010). Natural biomass dynamics are expected to differ between forest types and regions. Regions with a long-lasting history of intensive land management, such as central Europe, often lack natural forests as study objects (Sabatini et al., 2018). To compensate for this deficiency, in many European countries, strict forest reserves (SFRs) have been set aside from active management and monitoring schemes have been implemented (Parviainen et al., 2000). In Germany, SFRs were first established in the 1960s and 1970s (Bücking, 2007). Consequently, a large body of SFR monitoring data has been obtained. To make better use of this resource, a conceptual model for monitoring tree communities in SFRs and for unbiased hypothesis building based on explorative data analysis was proposed (Meyer, 2020).

In the present study, long-term data on tree communities and deadwood in the SFR of Lower Saxony, Germany were used to examine the biomass dynamics of naturally developing forests in this region. Our study was restricted to beech (*Fagus sylvatica*) and oak (*Quercus petraea*, *Quercus robur*) forests, which are the most important natural forest types in central Europe (Suck et al., 2014). The hypotheses that emerged from this study followed the conceptual model for explorative research in SFRs (Meyer, 2020) as well as the classical theories of growth and yield science (Pretzsch, 2009):

Specifically, we hypothesized that with ongoing time since abandonment (TSA)

1. total above-ground woody biomass and stand density increase asymptotically; consequently,
2. the net rate of change in biomass will be positive but will also decrease.
3. The asymptotic course of biomass is a result of the decreasing growth rates that occur with the ageing of tree communities.

4. Biomass, the net change in biomass and the growth rate differ between forest types and site conditions.

Our aim was to derive a complete balance over time for biomass and the processes that determine biomass, that is, the rates of growth, density-dependent mortality (DDM), density-independent mortality (DIM) and deadwood decay.

As a matter of convenience, we use the term biomass for both living trees and deadwood, although, strictly speaking, deadwood is part of necromass (Allaby, 2010). Because the carbon content in dry woody biomass amounts to an invariant proportion of roughly 50%, the results of our study can readily be interpreted in terms of climate protection.

2 | MATERIALS AND METHODS

2.1 | Selection of strict forest reserves and research plots

The recording plots were so-called 'core areas', which have been monitored since the designation of the SFR in the 1970s. The square plots are mostly 1 ha in size and representative of the respective forest stands. All plots dominated by beech (*Fagus sylvatica*) or oak (*Quercus petraea*, *Quercus robur*) were selected, provided that they had been remeasured at least twice and that the censuses covered a period of >25 years. In three SFRs, two plots of the same forest type were available, one fenced and the other unfenced. Only the fenced plots were included in our study, to ensure that all SFRs within each forest type were of equal weight. Finally, 21 plots were selected (Table 1; Figure 1). The pure and mixed beech forest stands were mature, with ages close to the end of the regular rotation period (target diameter cutting starts at an age of ~100 years). While the pure beech stands represented typical single-cohort stands, in some mixed beech stands a second cohort had become established. The mixed oak stands varied considerably in age and most comprised two cohorts (regular rotation age of oak of 180–220 years). The dominant height of the stands ranged between 26 and 37 m (Table 1), indicating relatively fertile site conditions.

2.2 | Dataset and computational methods

Data processing and analysis as well as graphical representations were carried out using SAS 9.4 and R statistic software (R Core Team, 2019).

Deriving a full balance of biomass and the processes that determine biomass dynamics required the development of computational methods specific to the available dataset. An overview of the methods is provided below, with further details available in the Supporting Information.

2.3 | Dataset

The living tree community and the deadwood pool within the plots were divided into three compartments: (1) standing (standing trees and snags ≥ 7 cm DBH), (2) lying (lying deadwood pieces and living lying trees ≥ 7 cm either at the butt end or at the DBH respectively) and (3) regeneration (trees and shrubs with a DBH < 7 cm and older than 1 year). In the last (second) census, compartments (1) and (2) had been fully assessed (for details, see the Supporting Information). Regeneration was sampled in a 20×20 m grid on square plots of 50 m^2 for trees ≥ 1.5 m in height and 20 m^2 for trees < 1.5 m in height. Inventories of deadwood and regeneration were missing for all first censuses and for seven (deadwood) and eight (regeneration) plots at the second census. Data gaps for deadwood were filled by modelling (see Section 2.4.6). For tree regeneration, change rates were employed as the estimation method (see Section 2.4.6).

Information on the species-specific age for trees ≥ 7 cm DBH was obtained from forest management data. Nutrient and water supply were estimated on the basis of available site maps.

2.4 | Computational methods

2.4.1 | Biomass and growth

The biomass of living trees ≥ 7 cm DBH was calculated according to Riedel and Kändler (2017). Their methodology is the standard used to inventory German national forests (details in the Supporting Information). For trees and shrubs < 7 cm DBH, the biomass functions of Annighöfer et al. (2016) were employed. The biomass of deadwood ≥ 7 cm DBH was calculated on the basis of the computed volume, with the species-specific wood density and decay stage also taken into account and the results extrapolated to total deadwood (details in the Supporting Information). Finally, biomass was calculated as the sum of the biomass of living stands ≥ 7 cm DBH, regeneration < 7 cm DBH and total deadwood (details in the Supporting Information).

The growth rate was calculated as the sum of the growth of remaining and in-grown trees and half of the growth of those trees that died within the respective period. The annual net change in biomass was defined as the difference in biomass between two consecutive censuses divided by the period length. Further details on the calculations of the growth rate, deadwood decay and the net change in biomass are given in the Supporting Information.

2.4.2 | Time since abandonment

It was assumed that, on average, the last forest intervention took place in the middle of the 10-year taxation period preceding the designation of the SFR. Thus, the TSA of a census was defined as the

TABLE 1 Core areas selected for the data analysis and their main characteristics. Site conditions are encoded as ordinal variables as follows: nutrient supply 1 = low, 2 = medium and 3 = high; water excess and water shortage: 0 = largely absent, 1 = occurring and 2 = severe; f = fenced and u = unfenced

Stand type	Same SFR	Plot name	Plot size (ha)	Stand age (first census)	Years observed period	Number of cohorts	Dominant height	Nutrient supply	Water excess	Water shortage
Pure beech (n = 6)	Großer Freeden	GF1u	1.2	81	33	1	33.6	3	0	0
	Großer Staufenberg	GS2u	0.48	90	43	1	32.0	3	0	0
	Meinsberg	ME1f	1	91	45	1	36.6	3	0	0
	Limker Strang	LI2f	1.5	98	31	1	33.7	1	0	0
	Vogelherd	VO1f	1	109	38	1	31.1	1	0	0
	Franzhorn	FR1f	1	115	36	1	37.4	2	1	1
Mixed beech (n = 8)	Großer Freeden	GF2u	0.56	71	33	2	32.3	3	0	0
	Großer Staufenberg	GS1u	0.96	76	43	1	31.4	2	0	0
	Königsbuche	KO1f	1	78	32	1	36.4	2	0	0
	Oderhang	OD1u	1.01	96	34	1	34.7	3	0	0
	Rieseberg	RI1f	1	98	33	2	29.2	3	0	0
	Stöberhai	SH1f	1.8	100	30	1	33.5	1	0	0
	Haringer Berg	HA1f	1	111	38	2	26.6	3	0	2
	Hünstollen	HU3f	1	124	34	2	33.8	3	0	1
	Herrnholz	HE1f	1	78	31	2	25.9	3	2	0
	Nordahner Holz	NO2u	1	100	29	2	27.9	2	2	0
Mixed oak (n = 7)	Franzhorn	FR2u	1	101	36	1	31.2	2	2	0
	Friedeholz	FH1f	1	121	36	2	26.8	3	2	0
	Landwehr	LA1f	1.48	129	44	2	21.1	1	2	0
	Walbecker Warte	WA1f	1.2	178	41	3	29.2	2	2	0
	Göhlder Eichen	GO2f	1	212	44	2	26.0	1	0	1



FIGURE 1 Map showing the location of the studied strict forest reserves (SFR) in Lower Saxony, Germany

time since the year of designation plus 5 years, except for the SFR 'Limker Strang', where an intervention in the year of SFR designation had been documented. TSA values ranged from 31 to 50 years.

2.4.3 | Determination of stand density

The stand density (Zeide, 2005) was calculated using the stand density index (SDI; Reinecke, 1933) developed for mixed and uneven-aged stands by Shaw (2000) and Woodall et al. (2005). SDI was calculated per plot and census by first computing the species-specific values for 10-cm DBH classes, then correcting these values to account for different species-wise coefficients and for diameter classes (Pretzsch & Biber, 2005) and, finally, calculating the sum over species and diameter classes (Equation 1).

$$SDI = \sum_{i=1}^n \sum_{k=1}^m \left(N_{ik} \times \left(\frac{25}{d_i} \right)^{a_k} \right) \times KORR_{ik}, \quad (1)$$

where SDI represents the stand density index (number of trees at an average diameter of 25 cm), i represents the DBH classes 1 to n , k represents species 1 to m , $N_{ik} \text{ ha}^{-1}$ is the stem number of species k per hectare in diameter class i , d_i is the midpoint of diameter class i (cm), a_k is the species-specific coefficient (from Vospernik & Sterba, 2015 and Wördehoff, 2016); $KORR_{ik}$ is the species-specific correction factor per DBH class (Pretzsch & Biber, 2005).

2.4.4 | Determination of tree age

Tree age has a large influence on biomass dynamics. In our study, tree age was determined using the age information available in the forest management data for those compartments where the respective plot was situated. Typically, stand and tree age are registered when a certain forest stand is being regenerated, with the

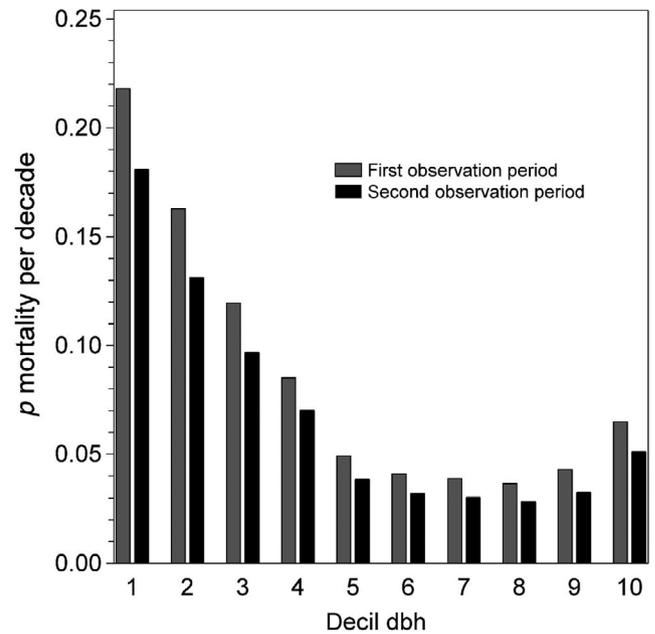


FIGURE 2 Logistic models of mortality per decade as a function of DBH deciles for the first and second observation period (p = probability)

information then being updated every 10 years over the course of management planning. In case that age information for a single species was missing, the age of the ecologically nearest species was used; for example, if information for birch was present, this age was applied to other pioneer species, such as *Salix caprea*. It was assumed that tree species with a similar successional trait, such as light-demanding pioneer species or shade-tolerant climax species, will also have a similar age structure, such that applying the known age of trees of the same group can be justified. Otherwise, the mean age was attributed to this species. In case of different age classes, the diameter distribution was assessed and the result used to set a diameter threshold separating the respective age classes.

Age determination for in-grown trees is highly error-prone, as the suppression by upper tree layers may have caused a significant slowdown in growth. Thus, it can be difficult to estimate how long in-grown trees would need to reach a DBH of 7 cm. To avoid this problem, for all trees, only the age at a DBH of 7 cm (age_{d7}) was considered. The age_{d7} for in-grown trees was calculated as half of the length of the observation period at which the trees were first registered. To calculate the age_{d7} of trees for which age information was already available, a reduction value was derived by first determining the site index of the tree species present and then interpolating the number of years until a DBH of 7 cm was reached based on growth and yield tables for light thinning from below (Schober, 1987).

2.4.5 | Estimating density-independent mortality

Density-dependent mortality was distinguished from DIM by analysing the change in mortality with changing competition pressure.

For this purpose, deciles of the DBH distribution were used as proxies for the social position of a group of trees. DDM was assumed to be the main process in lower deciles and was therefore expected to decrease with increasing decile. The opposite pattern was expected for DIM. If both DDM and DIM occur, the U-shaped curve typically observed in natural stands (Holzwarth et al., 2013; Hülsmann et al., 2016) will result and can be interpreted as comprising two separate curves.

The probability of mortality per decile and period was modelled using a GLMM (proc glimmix under SAS 9.4) for binary data, with a logit link and SFR as a random effect. The fixed effects were decile (categorical: 1-10), period (categorical: first, second) and the duration of the observation period (integer). Since tree species did not prove to be a significant predictor, it was subsequently ignored. In the final model, all fixed effects were highly significant. Mortality followed the expected U-shaped course (Figure 2). The minimum of the curve was interpreted as the intersection point between the separate DDM and DIM curves. Consequently, a numerical determination of the intersection point was conducted, and the proportions of DIM per decile and period were derived.

The intersection point between the DDM and DIM curves was determined according to Equations 2 and 3.

$$\text{DDM}(x|\alpha, \beta) = \alpha \times F_{\text{Gamma}}(X = x | k = \beta), \quad (2)$$

$$\text{DIM}(x|\alpha, \delta) = \alpha \times (1 - F_{\text{Gamma}}(X = x | k = \delta)) \quad (3)$$

where $F_{\text{Gamma}}(X = x | k)$ is the probability distribution function of a real-valued and strictly positive gamma-distribution random variable X , evaluated at $X = x$, depending on the shape parameter $k = \beta$ for DDM and $k = \delta$ for DIM. Parameter α , shared by the two models, served as a rescaling constant.

Based on the mortality data $\{0 < p_{\text{mort},i} < 1; i = 1, \dots, 10\}$, the most plausible point estimates $(\hat{\alpha}, \hat{\beta}, \hat{\delta})$ for the unknown parameters (α, β, δ) were obtained by numerically minimizing the squared loss, as shown in Equation 4.

$$(\hat{\alpha}, \hat{\beta}, \hat{\delta}) = \arg \min_{(\alpha, \beta, \delta)} \left(\sum_{i=1}^{10} (p_{\text{mort},i} - (\text{DDM}(i|\alpha, \beta) + \text{DIM}(i|\alpha, \delta)))^2 \right). \quad (4)$$

This was carried out using function `stats::optim()` of the R software (R Core Team, 2019). A numerical determination of the decile value \bar{x} , where DDM is equal to DIM, that is,

$$\bar{x} = \arg \min_x \left| \text{DDM}(x|\hat{\alpha}, \hat{\beta}) - \text{DIM}(x|\hat{\alpha}, \hat{\delta}) \right|$$

was carried out using R function `stats::uniroot()` (R Core Team, 2019). The numerical determination of the decile value x^* , at which the overall mortality reaches a minimum, that is,

$$\frac{d}{dx} (\text{DDM}(x = x^*|\hat{\alpha}, \hat{\beta}) + \text{DIM}(x = x^*|\hat{\alpha}, \hat{\delta})) = 0$$

TABLE 2 Proportions of density-independent mortality per decile for the first and second observation period

Decile	First period	Second period
1	0.00	0.00
2	0.00	0.00
3	0.00	0.00
4	0.00	0.00
5	0.03	0.03
6	0.17	0.17
7	0.49	0.52
8	0.79	0.83
9	0.93	0.95
10	0.98	0.98

was carried out using R function `stats::optimize()` (R Core Team, 2019).

Density-independent mortality proportions were defined as the ratio between the DIM and total mortality and calculated for each decile and for the first and second observation periods (Table 2).

As the trees in the observed stands were still relatively young compared to their expected life span (Piovesan et al., 2005; Trotsiuk et al., 2012), DIM was assumed to be mainly disturbance driven. Disturbance severity was then estimated by summing the biomass values of trees that died, weighted by the DIM proportion of the respective decile.

2.4.6 | Estimating missing values

All attempts to model biomass regeneration as a function of forest type and/or the biomass of stands ≥ 7 cm DBH failed. Instead, the rates of relative annual change were derived for those plots in which data from two censuses were available. The rates were calculated as shown in Equations 5 and 6; also see Table 1.

$$B_{t1} = B_{t0} \times (1 + d_r)^t, \quad (5)$$

$$d_r = \sqrt[t]{\frac{B_{t1}}{B_{t0}}} - 1, \quad (6)$$

where d_r is the relative rate of change per year; t is the duration of the period of observation (years); and B_{t0}, B_{t1} = biomass at the start (t_0) and end of the observation period.

On the basis of these individual rates, values for regeneration biomass at the first census were estimated, starting with the measured value of the second census and considering the length of the observation period. For those plots without values for the second census, the same procedure was followed but using the average annual rate of change for the plots, using data from the third census.

In the case of deadwood (standing and lying) biomass ≥ 7 cm DBH, the absolute annual rate of change could be modelled

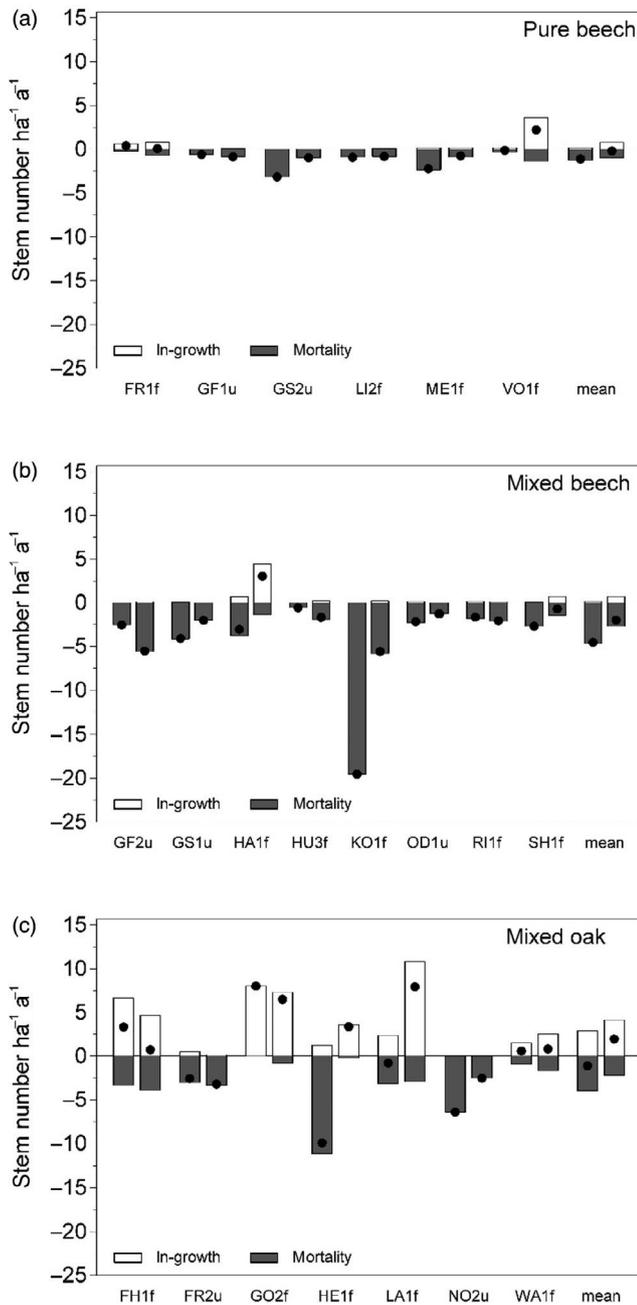


FIGURE 3 Rates of mortality and in-growth in the studied plots. The left column shows the rate during the first observation period and the right column that during the second observation period. The dots indicate net changes

as a function of the annual input of deadwood due to the mortality of trees from the corresponding living stand ≥ 7 cm DBH ($\Delta\text{deadwood ha}^{-1} \text{a}^{-1} = -0.541 + 0.889 \times \text{mortality ha}^{-1} \text{a}^{-1}$; r^2 : 0.8537, $p > F < 0.0001$). Missing values were estimated using the value of the available census of the respective plot, after which the mortality-related annual input into the deadwood pool was calculated by applying the derived model function. The resulting values were further corrected for species-specific and decay stage-specific dry matter density and extrapolated by multiplying by

1.37 to arrive at the full amount of deadwood (see the Supporting Information).

2.5 | Data analysis

Hypothesis testing was performed by applying the selection procedures of general linear modelling (proc glmselect under SAS 9.4). In the first step of the analysis, the effects of TSA and forest type on biomass, SDI, the net change in biomass, the growth rate and the temporal courses of these variables were estimated by testing whether a simple linear approach, a log approach (natural logarithm), a square transformation of the TSA or a combination of these formulations yielded the best model as indicated by Akaike's information criterion (AIC). Biomass was analysed using the TSA values of the census years. For rates and processes (net change in biomass, growth rate, DIM, decay), the TSA in the middle of the observation periods was applied.

In the second step, the additional effects of the age of the tree communities and of site factors on biomass, the net change in biomass and the growth rate were tested. Community age was quantified by calculating the arithmetic mean age_{d7} (for all trees with DBH ≥ 7 cm) and the basal-area-weighted arithmetic mean age_{d7}, in which it was assumed that trees of different size occupy different shares of the available resource space. The site factors considered were nutrient supply (1 = oligotrophic, 2 = mesotrophic and 3 = eutrophic), water excess (0 = largely absent, 1 = occurring and 2 = severe) and water shortage (0 = largely absent, 1 = occurring and 2 = severe). Model building was conducted in three steps. First, the variables were tested for multicollinearity (proc reg under SAS 9.4 outest=vif). Those showing either a variance inflation factor >10 and/or a tolerance <0.2 were removed from the analysis. Second, the remaining variables were used to select the best model as indicated by the AIC. Third, the predictive effect of the remaining variables was checked for nonlinearity by applying general additive modelling (proc gam under SAS 9.4). In case of a significant smoothing component, the course of the smoothing plot was inspected to identify the appropriate relationship (log, exponential and unimodal); model building was then repeated by introducing the respective variable in a nonlinear formulation.

3 | RESULTS

3.1 | Rates of in-growth and mortality

The annual rates of in-growth and mortality differed considerably between the three forest types (Figure 3). In pure beech forests, only a minor turnover of the tree population was observed, while in mixed oak forests mortality and in-growth rates were higher and more variable. In mixed beech forests, the mortality rates were, on average, relatively high and not compensated by in-growth. The

amount of biomass attributable to in-growth was much lower (mean: $0.06 \text{ t ha}^{-1} \text{ a}^{-1}$ in the first and $0.07 \text{ t ha}^{-1} \text{ a}^{-1}$ in the second period) than the mortality rate (mean: $1.3 \text{ t ha}^{-1} \text{ a}^{-1}$ in the first period and $2.0 \text{ t ha}^{-1} \text{ a}^{-1}$ in the second period).

3.2 | Development of mean tree age

The unweighted (basal-area-weighted) mean age_{d7} at the cessation of active forest management was 93 (92) years in pure beech, 72 (79) years in mixed beech and 63 (102) years in mixed oak forests. Notably, the increase in the mean age began to decouple from the ongoing TSA, as shown in a calculation of the extra- and interpolated mean ages (proc expand under SAS 9.4, method = join) at the selected base years of TSA. Thus, while during the first 25 years after abandonment the mean age increased by 20 (23) years on average, during the next 25 years the increase was only 13 (20) years. The increasing lag between mean age and TSA was clearly due to in-growth and mortality within the tree communities. Because turnover was pronounced in the mixed oak forests, for a 50-year TSA (TSA₅₀) the increase in the mean age of this forest type was only 17 (28) years. The respective values were 35 (49) years for pure beech forests and 46 (51) years for mixed beech forests.

3.3 | Biomass pools at selected base years of TSA

At TSA₅₀, the biomass of pure beech forests was 478 t/ha, followed by mixed beech forests, with 434 t/ha, and mixed oak forests, with 334 t/ha (Table 3). In general, living stands contributed the most to biomass, whereas the regeneration mass was of minor importance. In the three forest types, deadwood reached proportions from 3% (pure beech) up to 9% (mixed oak). Distinct increases in the compartments living stand and deadwood were also determined (Table 3).

3.4 | Models of biomass and stand density as a function of TSA

In the models for biomass and SDI as a function of TSA and forest type, the latter was retained in the best model such that the model selection procedure was conducted for each forest type separately.

Biomass increased significantly with TSA but the respective models differed between pure beech forests, in which biomass increased linearly, and mixed beech and mixed oak forests, in which biomass followed an asymptotic course (Figure 4). The level of biomass reached at TSA₅₀ was highest in pure beech forests, followed by mixed beech and then mixed oak forests.

Stand density index increased with TSA in all forest types and the shape of the modelled increase mirrored that of biomass, except for pure beech stands (Figure 5). However, both the significance level and the adjusted R^2 values of the models were low, and for mixed oak forests there was no significant increase as a function of TSA.

3.5 | Rates of growth, disturbance and decay during certain base years of TSA

Values for the growth rate, the DIM and the decay of deadwood were interpolated for TSA of 15 and 30 years, which were the approximate midpoints of the first and second observation periods (Table 4). Although the decay rate was much lower than the growth rate in all forest types and during both base years, it increased markedly over time. Also, there was a clear increase in DIM with increasing TSA, apparently as a result of the increasing average biomass of dying trees (first period: 0.34 t; second period: 0.93 t), despite the decreasing probability of mortality (Figure 2). Consequently, increasing amounts of biomass were added to the deadwood pool over time.

Forest type	Compartment	Biomass (t/ha) per TSA (years)		
		5	25	50
Pure beech (n = 6)	Living ≥7 cm DBH	281.3	377.0	460.3
	Regeneration	0.4	0.7	1.2
	Deadwood	5.6	7.5	16.6
	Total	287.3	385.2	478.1
Mixed beech (n = 8)	Living ≥7 cm DBH	248.1	339.6	405.5
	Regeneration	0.6	0.9	2.7
	Deadwood	7.5	16.4	26.3
	Total	256.2	356.9	434.5
Mixed oak (n = 7)	Living ≥7 cm DBH	190.7	254.9	301.6
	Regeneration	1.7	1.1	1.2
	Deadwood	11.3	20.2	30.6
	Total	203.7	276.2	333.4

TABLE 3 Interpolated and extrapolated mean values of biomass for three base years (5, 25 and 50 years) after abandonment. Three compartments were distinguished: living trees with a DBH ≥7 cm, living trees <7 cm DBH (seedlings excluded) and standing and lying deadwood

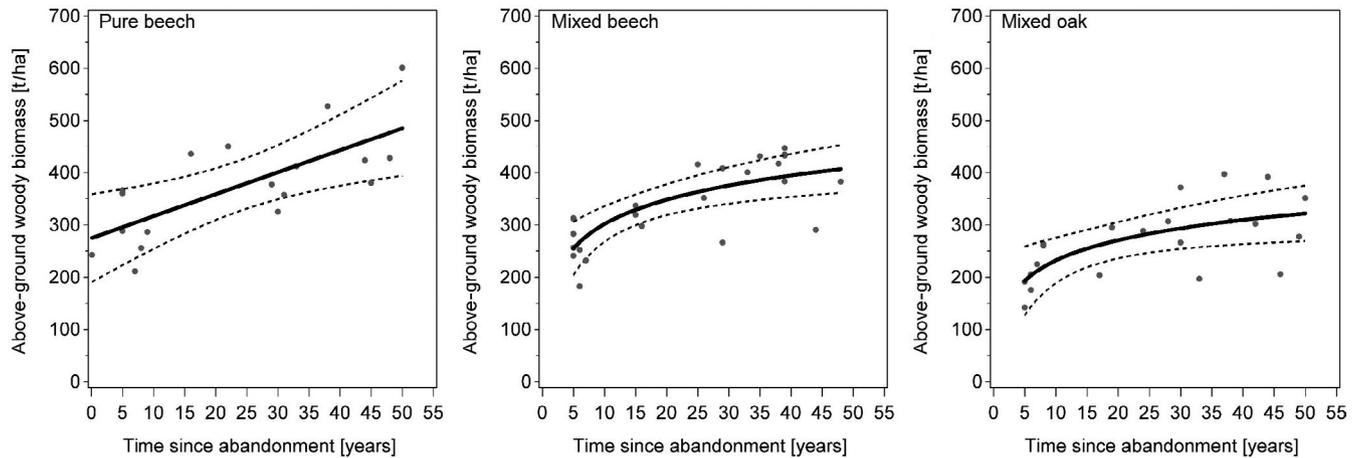


FIGURE 4 Models for biomass as a function of time since abandonment (TSA) for the three different forest types. The following models were derived for the three forest types: pure beech: biomass = $275 + 4.207 \text{ TSA}$ (adjusted R^2 : 0.4965, $p > F$: <0.0007); mixed beech: biomass = $146 + 67.380 \ln \text{ TSA}$ (adjusted R^2 : 0.5698, $p > F$: <0.0001); and mixed oak: biomass = $102 + 56.198 \ln \text{ TSA}$ (adjusted R^2 : 0.4097, $p > F$: 0.0010). The dashed lines show the 99% confidence intervals of the models and the grey dots indicate the data points

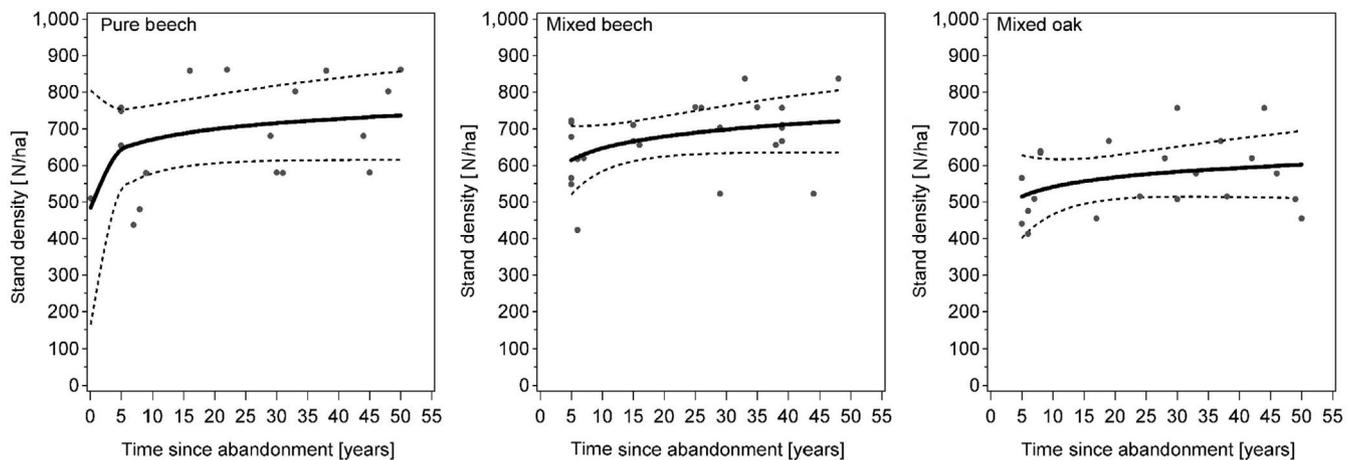


FIGURE 5 Models of SDI as a function of TSA for the three different forest types. The following models were derived for the three forest types: pure beech: SDI = $578 + 40.500 \ln \text{ TSA}$ (adjusted R^2 : 0.1333, $p > F$: 0.0754); mixed beech: SDI = $538 + 46.996 \ln \text{ TSA}$ (adjusted R^2 : 0.1303, $p > F$: <0.0466); and mixed oak: SDI = $453 + 38.181 \ln \text{ TSA}$ (adjusted R^2 : 0.0609, $p > F$: 0.1461). The dashed lines show the 99% confidence intervals of the models and the grey dots indicate data points

3.6 | Models of net change in biomass and the growth rate with increasing TSA

The net change in biomass changed significantly with increasing TSA (Figure 6). The linear decrease in pure beech forests contrasted with the unimodal course of mixed beech and mixed oak forests. The models for both mixed forest types indicated near zero or slightly negative values for the net change in biomass 40 years after abandonment.

Only in the case of pure beech forests did the selection procedure arrive at a solution for an intercept model of the growth rate as a function of TSA (Figure 7), whereas no such models could be derived for mixed beech and mixed oak forests. For the later, we derived no-intercept models instead. The respective models showed a steady decrease in the growth rate of pure beech stands and a pronounced unimodal course over the TSA for the mixed forest types. The empirically derived growth rates varied widely during the observation

period, ranging between 2.8 and 6.7 $\text{t ha}^{-1} \text{ a}^{-1}$ for pure beech, 2.2 and 6.7 $\text{t ha}^{-1} \text{ a}^{-1}$ for mixed beech and 1.7 and 4.6 $\text{t ha}^{-1} \text{ a}^{-1}$ for mixed oak.

3.7 | Additional effects of age and site factors on biomass, the net change in biomass and the growth rate

The inclusion of community age and site factors into the model-building process for biomass resulted in a complex model that explained >70% of the total variation (Table 5). Age and TSA had separate, positive effects on biomass. Water shortage had a negative effect, while biomass increased with an increasing nutrient supply. Additionally, forest type had a separate effect on biomass that closely corresponded to the differentiation described above (Figure 4; linear increase in pure beech forests and an exponential increase in mixed forests).

TABLE 4 Interpolated and extrapolated mean values of the growth rate, density-independent mortality and the decay of deadwood for 2 base years (15 and 30 years) after abandonment

Forest type	Process	Time since abandonment (years)	
		15	30
Pure beech (<i>n</i> = 6)	Growth	5.1	3.9
	Density-independent mortality	0.3	0.9
	Decay	0.5	0.9
Mixed beech (<i>n</i> = 8)	Growth	4.7	4.7
	Density-independent mortality	0.5	0.8
	Decay	0.8	1.3
Mixed oak (<i>n</i> = 7)	Growth	3.2	3.5
	Density-independent mortality	0.7	1.3
	Decay	0.9	1.3

4 | DISCUSSION

4.1 | Plausibility of the biomass estimates

Given the need to estimate the missing data for deadwood and regeneration, our results must be interpreted with caution. However, the average values of deadwood biomass (18–37 t/ha) estimated at TSA_{50} were plausible and within the 10–68 t/ha (Mund, 2004, converted from t C by multiplying by 2) and 86 t/ha (Glatthorn et al., 2017) reported for primeval broadleaved forests. This was also the case for the average biomass of tree regeneration, as our values of 1.1–2.6 t/ha at TSA_{50} were comparable to those reported by Glatthorn et al. (2017) in their study of primeval (2.9 t/ha) and managed (0.5 t/ha) beech forests of eastern Slovakia. Our estimates for the biomass in living trees ≥ 7 cm DBH of 405 t/ha (mixed beech) and 460 t/ha (pure beech) at TSA_{50} corresponded to the upper limit of the values derived by Mund (2004) for beech forests subjected to different management regimes (shelterwood system: 390–394 t/ha; average selection system: 292 t/ha; average unmanaged beech forests: 410 t/ha), but they exceeded the average living biomass of primeval beech forests in Slovakia (379 t/ha, Glatthorn et al., 2017).

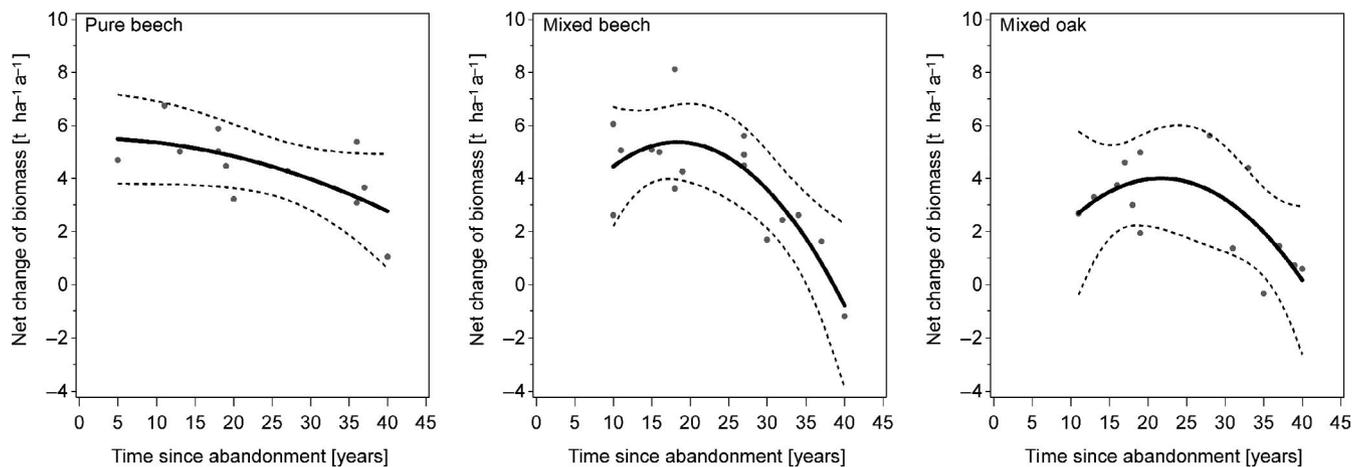


FIGURE 6 Models of the net change in biomass (NCB) as a function of TSA. The following models were derived for the three forest types: pure beech: $NCB = 5.528 - 0.0017 TSA^2$ (adjusted R^2 : 0.3717, $p > F$: 0.0208); mixed beech: $NCB = 0.946 + 0.482 TSA - 0.0131 TSA^2$ (adjusted R^2 : 0.6059, $p > F$: 0.0009); and mixed oak: $NCB = -1.394 + 0.498 TSA - 0.0155 TSA^2$ (adjusted R^2 : 0.3834, $p > F$: 0.0279). The dashed lines show the 99% confidence intervals of the models and the grey dots indicate the data points

A simple model was obtained for the net change in biomass, with TSA and forest type alone explaining nearly 55% of the variation (Table 6).

Model building for the growth rate resulted in a low coefficient of determination and a model that contained only the age_{d7} parameters (Table 7). Neither TSA nor forest type nor site factors proved to be significant predictors of growth. The effect of age_{d7} was very weak because the coefficients of both mean ages had different signs, thus cancelling each other out to a substantial degree. The negative sign of the basal-area-weighted age_{d7} suggested a slightly negative effect of the age of the dominant tree layer on growth.

4.2 | Consistency of the models

While the models for the net change in biomass and growth showed a decreasing (pure beech) or unimodal trend (mixed beech and oak), the derivation of biomass resulted in a constant (pure beech) or decreasing (mixed beech and oak) slope. This difference can be explained by the low number of observations and the different methods of TSA determination. In the biomass models, three censuses were at our disposal, whereas the net change in biomass and the growth rate were based only on the midpoints of two observation periods. Nonetheless, it can be assumed that a direct derivation of rates will yield more accurate results than obtained with indirect derivations from biomass curves.

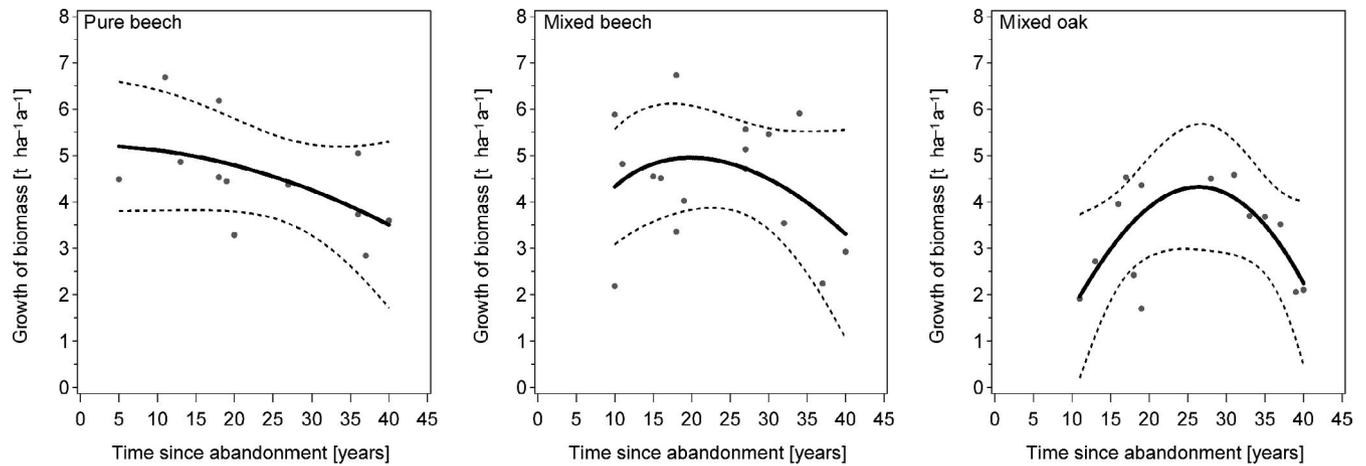


FIGURE 7 Models of growth (GRO) as a function of TSA. The following models were derived for the three forest types: pure beech: $GRO = 5.197 - 0.0010 \text{ TSA}^2$ (adjusted R^2 : 0.2417, $p > F$: 0.0404); mixed beech: $GRO = 2.077 \ln \text{ TSA} - 0.0026 \text{ TSA}^2$ (adjusted R^2 : 0.9439, $p > F$: <0.0001); and mixed oak: $GRO = 0.714 \times \text{TSA} - 1.837 \ln \text{ TSA} - 0.0122 \text{ TSA}^2$ (adjusted R^2 : 0.9337, $p > F$: <0.0001). The dashed lines show the 99% confidence intervals of the models and the grey dots indicate the data points

TABLE 5 Final complex model of biomass ($p > F < 0.0001$)

Variable	Cumulative adj. R^2	Parameter estimate	$p > t $
Intercept		138.249	0.0010
Mean age _{d7}	0.4598	1.124	0.0007
TSA	0.6086	2.935	<0.0001
Nutrient supply	0.6554	21.902	0.0075
Pure beech	0.6821	0	0
Mixed beech	0.6821	-15.947	0.3291
Mixed oak	0.6821	-64.523	0.0023
Water shortage	0.7190	-35.713	0.0051

TABLE 6 Final complex model of the net change in biomass ($p > F < 0.0001$)

Parameter	Cumulative adj. R^2	Parameter estimate	$p > t $
Intercept		3.264	0.0238
TSA^2	0.3991	-0.008	0.0054
Pure beech	0.4896	0	0
Mixed beech	0.4896	-0.767	0.1658
Mixed oak	0.4896	-1.627	0.0060
TSA	0.5426	0.265	0.0453

4.3 | Interpretation of biomass storage and dynamics over time

While the pure beech forests in our study were characterized by an even-aged structure, in most of the mixed beech and oak stands a second or even third tree cohort was present. In-growth was prominent only in the mixed oak forests. Nevertheless, also in those forests, the tree populations aged throughout the study period. We

based our hypotheses on the classical insights provided by growth and yield science, that as trees age, their growth declines (Binkley et al., 2002). This should be reflected in the asymptotic course of biomass per unit of ground area over time. Differences in population structure (see Figure S1 in the Supporting Information for DBH distributions) were addressed indirectly in our model calculations, via forest type and age parameters.

Biomass in the pure beech forests deviated from the asymptotic course postulated in hypothesis (1), in contrast to the biomass of more complex, structured mixed beech and oak forests, which followed this pattern. The net change in biomass largely remained positive throughout the observation period (hypothesis 2). Pure beech forests also differed from mixed forests in their steady decreases in both the net change in biomass and the growth rate, with unimodal curves obtained for mixed forests over time. Thus, concerning hypothesis 2, only partial evidence was found. An additional characteristic of the pure beech forests was that their biomass levels, SDI, net change in biomass and growth were higher than in other forest types.

In summary, we were able to demonstrate that the studied pure beech forests differed from the mixed oak forests with respect to biomass storage and acquisition (hypothesis 4). Mixed beech forests occupied an intermediate position between these two forest types. Both nutrient supply and water shortage showed the expected effects on biomass, whereas these site variables had no effect on either the net change in biomass or the growth rate (hypothesis 4).

In contrast to our initial hypothesis (3), we found no clear relationship between either the net change in biomass or the growth rate and the ageing of the tree community. Mean stand age gradually decoupled from time, as a result of the turnover within the tree communities. A process of self-renewal set in, that was much more pronounced in mixed oak than in mixed and pure beech forests. However, in-growth does not fully compensate for the loss of dying canopy trees. At least, a slightly negative effect of the age of the

Parameter	Intercept model		
	Cumulative adj. R^2	Parameter estimate	$p > t $
Intercept		5.179	<0.0001
Basal area weighted mean age	0.1270	-0.027	0.0043
Mean age	0.2756	0.021	0.0014

TABLE 7 Final complex model of the growth rate ($p > F = 0.0007$)

dominant tree layer on growth was indicated. Although the decrease in growth with increasing age is paradigmatic for even-aged stands (Binkley et al., 2002), whether this relationship also holds true for more complex (uneven-aged, mixed, naturally developing) forests is thus far unclear (Carey et al., 2001). Results from plant physiology cast doubt on a simple negative effect of age on growth, as clear evidence for genetically programmed senescence in plant tissues has yet to be presented (Munné-Bosch, 2008; Piovesan & Biondi, 2021). In fact, shade-tolerant tree species in old-growth forests typically survive several suppression phases (Canham, 1989; Nagel et al., 2007) and after their release they continue to grow without an obvious negative age trend (Hobi et al., 2015). Moreover, in complex forest ecosystems, age is difficult to operationalize because it varies between tree individuals and thus can be transferred only to the stand scale, by employing mean values or parameters of variability.

Rather than ageing, we hypothesize that the observed development of biomass, the net change in biomass and the growth rate resulted from increasing exploration of the environmental and species-specific growing space over time. Growing space can be taken as a proxy for above- and below-ground resource supply in terms of light, water and nutrients. In forest stands, which constitute communities of sessile organisms, the above- and below-ground growing spaces are gradually accessed by trees increasing their size. A limit is given above-ground by constraints in height growth (Kutsch et al., 2009) and below-ground by the rootable soil volume. Within this growing space, trees compete for vitally important resources.

The studied stands showed a saturating stand density and the canopy trees were quite mature. The linear increase of biomass in the pure beech forests suggested that these stands are not yet approaching a limit to area-based growth. However, declining net change in biomass and growth rate might already indicate the proximity to a potential maximum. Consequently, the course of biomass would be expected to become asymptotic in the near future. In terms of demography, the population structure of the pure beech forests is not balanced, but subject to further ageing. According to model calculations, the structural conversion towards a balanced demographic structure (steady state) involves fluctuation in biomass levelling out at a lower level than that reached by the initial cohort (Halpin & Lorimer, 2016). This assumption is supported by the fact that the level of biomass reached so far is well above that, documented for primeval beech forests in Slovakia (Glatthorn et al., 2017).

The saturating biomass and the unimodal course of net change in biomass and growth rate in both mixed forest types indicate

that these have come close to a limitation in the acquisition of biomass, or sequestered carbon respectively. However, in these forests, the mortality rate in canopy trees of oak and other, more light-demanding tree species, was disproportionately high while the opposite was observed for beech. Probably, on the long run, beech might out-compete this species and the resulting turnover in species composition might lead to an upward shift of the potential biomass storage.

The higher values of biomass, as well as of net change and growth, of pure beech forests compared to mixed forest types also showed that the generally assumed positive relationship between tree species richness and productivity (Forrester & Bauhus, 2016; Liang et al. 2016; Pretzsch & Schütze, 2016) does not necessarily apply to mature and naturally developing forests. Beech forests are highly efficient in their light use (Leuschner, 1998; Leuschner & Meier, 2018) and in their ability to acquire below-ground resources (Hertel, 1999), both of which explain their large capacity to store and acquire biomass (Glatthorn et al., 2017). Our results are consistent with these findings while also showing that admixing less productive tree species can have a negative effect on overall productivity (Pretzsch et al., 2017). In accordance, the limitation of biomass acquisition of the mixed forests might be only temporary, as the proportion of beech continuously increases.

The interpolated average rates of growth and DIM showed that the biomass dynamics of the studied stands were mainly driven by internal processes, not external disturbance agents. There was no indication of an increase in the relative importance of disturbances that eased the intrinsic control of biomass dynamics. However, as wood decay, even for beech, requires rather long periods of time (Přivětivý et al., 2016), the dead wood pool can buffer a biomass reduction in the living stand substantially for several decades. The onset of turnover within the tree communities suggests that, even if disturbances became more important, regeneration could compensate for increased DIM.

5 | CONCLUSIONS

In response to the call for long-term ecological studies (Franklin, 1989), the availability of long-term data has increased considerably. Our study demonstrates the potential value of such datasets. However, due care must be taken in hypothesis building (Meyer, 2020) and in developing solutions for data analysis within the limitations of the specific dataset.

Our study showed the difficulties in explaining and determining the biomass acquisition limit of naturally developing forests based on age. Instead, the degree of resource exploration within a limited growing space in conjunction with disturbances offers a straightforward explanation. The finding that tree age paralleled the degree of space exploration in even-aged stands may have led to a misinterpretation of age as independent explanatory factor.

The validity of our results is restricted to the medium-term development of mature beech and oak forests that have been set aside within the past few decades. Nonetheless, our findings contribute to a better understanding of the consequences of nature protection strategies aimed at increasing the area of naturally developing forests, as is the case for the German Biodiversity Strategy (Engel et al., 2016).

Although biomass, and thus carbon, acquisition per hectare seems to be limited in naturally developing broadleaved forests, the storage capacity of these forests was shown to be substantial. Accordingly, forests that are allowed to develop naturally are likely to play important roles in carbon storage and sequestration (Keith et al., 2010). Apart from their above-ground carbon storage, SFRs and other naturally developing forests have the potential to store additional carbon in the soil (James & Harrison, 2016; Mayer et al., 2020; Zhou et al., 2006).

Whether an upper limit, such as that of the carbon carrying capacity, can be considered as constant or variable is open to debate, as is, in the latter case, whether a fluctuation that evens out at a lower level of biomass at the old-growth stage is probable (Halpin & Lorimer, 2016). Against this backdrop, both continued monitoring and research in naturally developing forests and the combination of empirical data with statistical modelling are crucial to further improve our as yet limited understanding of long-term natural biomass dynamics.

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CONFLICT OF INTEREST

The authors confirm that they do not have any conflict of interests to declare.

AUTHORS' CONTRIBUTIONS

P.M. conceived the idea of this study, designed the methodology, carried out the data analysis and led the writing of the manuscript; R.N. and E.F. revised the manuscript, improved the data analysis and contributed to references. All authors contributed critically to the drafts of the manuscript and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/1365-2745.13740>.

DATA AVAILABILITY STATEMENT

The dataset our analysis is based on is archived in the Dryad Digital Repository <https://doi.org/10.5061/dryad.b2rnbzsfv> (Meyer et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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