# Structural changes in a primeval beech forest at the landscape scale

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**A B S T R A C T**

Quantitative estimates of change of primeval European beech (*Fagus sylvatica* L.) forests at the landscape scale over time are scarce due to both the few remnants of such forests and the absence of repeated sample plot inventories. This forest ecosystem is thought to be relatively stable over time, but it remains unclear what drivers contribute to this stability. Here, we studied temporal change in one of the largest primeval beech forests. Our analysis is based on two consecutive inventories on 238 permanent sample plots in the Uholka-Shyrokyi Luh forest in Transcarpathia, Ukraine, covering 102.8 km$^2$. The inventories were carried out in 2010 and 2019.

This data allowed us to derive quantitative estimates for the main structural characteristics tree density, basal area and volume on a landscape scale and to characterize the demographic processes that shape this forest ecosystem. The structural characteristics tree density (2010: 441 N ha$^1$, 2019: 458 N ha$^{-1}$), basal area (2010: 35.9 m$^2$ ha$^{-1}$, 2019: 35.4 m$^2$ ha$^{-1}$), and standing volume (2010: 578 m$^3$ ha$^{-1}$, 2019: 584 m$^3$ ha$^{-1}$) of the living trees remained stable between the two inventories. The species composition, characterized by a pronounced dominance of beech, remained virtually unchanged as well, with 97.9% of the stems being beech trees in the first and 97.1% in the second inventory. In contrast, we observed a relatively high dynamic when looking at the demographic processes more closely. About 11% of the trees found alive in 2010 died until 2019, resulting in an annual mortality rate of 1.3%. Ingrowing trees compensated for trees that died or decayed regarding tree density, but only to a small extent regarding volume. The volume lost was largely compensated by the growth (8.0 m$^3$ ha$^{-1}$ year$^{-1}$) of the surviving trees.

This work characterizes the change of forest attributes in a primeval beech forest at the landscape scale over a time of period of nine years and provides baseline indicators on the development and dynamics of primeval beech forests. It broadens our understanding about the contribution of the main demographic processes to the pronounced structural and compositional continuity of primeval beech forests.

## 1. Introduction

As a result of more than 5000 years of land use, forest clearing for the cultivation of crops, and the use of wood as fuel resource (Kaplan et al., 2009), only few remnants of primeval forests still exist in Europe. We define primeval forests as forests extending to the landscape scale with the highest level of naturalness (Buchwald, 2005). In Europe, remnants of such forests can be mainly found in the eastern and northern part of the continent (Sabatini et al., 2018). Easily accessible lowland and montane forests such as European beech (*Fagus sylvatica* L., henceforth beech) forests have been particularly altered by forest management and wood pasture. Sabatini et al. (2020) found less than 1% of all forests in the zone of lowland and montane beech forests in Europe to be primary (i.e. forests with a high level of naturalness, see Buchwald (2005)). Only 27 primary beech forests in Europe were found to cover more than 10 km$^2$ (1000 ha, Sabatini et al., 2018).

Beech forests would, without human intervention, cover a large proportion of Central and Western Europe as beech is the most successful tree species in its distribution range (Peters, 1992). This is based on the species' wide ecological niche in terms of soil nutrient and water availability (Leuschner et al., 2006). In addition, the disturbance regime dominating the temperate zones of Europe, characterized by low to intermediate severity (Fischer et al., 2013) favours the species (but see Frankovič et al., 2021)). This disturbance regime creates canopy gaps

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which are mostly smaller than 200 m$^2$ (Hobi et al., 2015). Small gaps favour beech over other species, as it is very shade tolerant and can survive suppression periods of more than 150 years (Trotsiuk et al., 2012; Petrovska et al., 2021). Moreover, only few herbivorous insects feed on beech (Brändle and Brandl, 2001), and large-scale insect calamities are not known to occur even after major disturbances in beech forests. All of the above-mentioned characteristics contribute to a forest structure which is vertically and horizontally complex (Hobi et al., 2015).

Primeval beech forests are dominated by a mosaic of patches in different successional stages (Korpel', 1995; Remmert, 1991), resulting in varying structural characteristics depending on the spatial scale. At small spatial scales, forest patches are thought to pass through different developmental stages from regeneration and early growth through maturity and aging to decay, followed by a new tree generation. At a larger spatial scale, primeval beech forests may be described as ecosystems in dynamic steady state. Bormann and Likens (1979) define steady-state ecosystems as driven not primarily by exogenous disturbances such as wind, fire or insects, but by endogenous disturbances, i.e. single-tree mortality. This disturbance pattern subsequently results in an ecosystem where variables like mean stem diameter at breast height (DBH), basal area, number of trees and biomass or volume remain relatively stable over time although they may vary considerably between patches.

Various studies have explored different aspects contributing to the steady-state nature of beech forests, such as stand structure (e.g., von Oheimb et al., 2005; Emborg et al., 2000), dead wood accumulation (e. g., Meyer and Schmidt, 2011; Christensen et al., 2005), development phases (e.g., Král et al., 2010; Zenner et al., 2020) and gap frequency (Drößler and Von Lüpke, 2005; Hobi et al., 2015). Besides the above-mentioned structural attributes the demographic processes mortality (e.g., Wunder et al., 2007; Hülsmann et al., 2016) and regeneration and their spatial distribution in dependence of canopy openings (e.g, Jaloviar et al., 2020; Stiers et al., 2019; Feldmann et al., 2020) may contribute to the steady-state nature of this ecosystem. Tree mortality is thought to be following a distinct U-shape, i.e. high mortality in both small and large trees and low mortality in medium sized trees (e.g., Holzwarth et al., 2013; Hülsmann et al., 2016).

Owing to the small size of the remaining primeval forests, most of the above-mentioned studies have used one or several usually small permanent plots with one or multiple measuring cycles. Even if several hectares large, such plots cannot cover a broad environmental gradient influencing the dynamics of forests at the landscape scale. Drawing conclusions on the development of an entire forest ecosystem from few plots might therefore be problematic (Peck et al., 2015).

Sample plot inventories allow to study structural dynamics on both large and small scales through randomized sampling of the population of interest (Mandallaz, 2008). However, only few studies analysing structural attributes of primeval beech forests on a larger scale have been carried out (but see Nagel et al., 2010; Hobi et al., 2015; Commarmot et al., 2013; Frankovič et al., 2021). These studies make use of a single inventory, thus they miss to address the temporal dynamics of structural attributes and demographic processes of primeval beech forests. In this study, we use a unique dataset gathered in the primeval beech forest of Uholka-Shyrokyi Luh, Ukraine during two sample plot inventories on 238 plots, allowing us to derive quantitative estimates on structural change in a primeval beech forest over nine years. We wanted to determine if the steady-state hypothesis holds true for this particular forest. Specifically, we were interested in the *i)* change in the general forest attributes tree density, basal area, volume of both living and dead trees, and *(ii)* the influence of the main demographic processes recruitment, growth and mortality on these attributes.

## 2. Material and Methods

### 2.1. Study location

Covering 102.8 km$^2$, the primeval beech forest of Uholka Shyrokyi Luh is situated in south-western Ukraine (Fig. 1 a.) within the Carpathian Biosphere Reserve (CBR). It is part of the UNESCO world heritage *"Ancient and primeval beech forests of the Carpathians and other regions of Europe"* and is the largest forest included in this network. It is unique due to the minimal anthropogenic impact in the past and the absence of historical evidence of timber harvesting (Brändli et al., 2008). The forest consists of two almost equally sized parts, the Uholka massif covering the southern and the Shyrokyi Luh massif the northern part (Fig. 1 b.). They are characterised by three main valleys running from north to south, lateral side valleys, and undulating and steep terrain. The two massifs range between 400 and 1350 m a.s.l. The Uholka massif mainly consists of flysch formations, limestone and calcareous conglomerates. In contrast, silt and sandstone dominate the Shyrokyi Luh massif (Brändli and Dowhanytsch, 2003; Commarmot et al., 2013). The mean annual temperature at the meteorological station in Mala Uholka (430 m a.s.l.) was 7.7°C (1990–2010), with a mean July temperature of 17.9°C and a mean January temperature of −2.7°C. The mean annual precipitation was 1134 mm (1980–2010, Commarmot et al., 2013).

Besides the sample plots established in 2010, the research infrastructure in the Uholka massif contains a 10 ha permanent plot, established in 2000 and since remeasured every 5 years (Stillhard et al., 2019).

### 2.2. Data acquisition

Our analyses build on two sample plot inventories carried out in the primeval beech forest of Uholka-Shyrokyi Luh. In the first inventory, which took place in 2010 (Commarmot et al., 2013), 314 circular sample plots were assessed in the core, buffer and transition zones. In summer 2019 we revisited 238 plots lying in the core zone of the reserve where all management is prohibited. The measurement teams were able to retrieve the exact location of all plots but one and considered all plots to be accessible.

The sample plots are distributed as non-stratified, systematic clusters of two plots per cluster on a grid of 445 x 1235 m with the plots of one cluster being 100 m apart from each other (Fig. 1 b). If one of the sample plots of a cluster was not measured during the first inventory or lies in one of the zones that we omitted, it was not assessed. For the analysis the sample plots formed 132 clusters. The 238 sample plots assessed in both inventories lie on a mean elevation of 821 m a.s.l. (± 142 m, mean ± one standard error of the mean, range 534 to 1202 m a.s.l.).

Sample plots consisted of a circular sample plot of 500 m$^2$ in area (horizontal radius = 12.62 m, adjusted for inclination), three regeneration subplots of 5, 10 and 20 m$^2$ located 10 m to the west and three line transects used for line intersect sampling (LIS) of coarse woody debris (CWD) of 15 m horizontal length (Fig. 2). All dead and living trees standing on the sample plot with a diameter at breast height (DBH) ⩾6 cm (sample trees) were identified to species, their status (alive/ dead/ missing) and position (standing/lying) assessed and their DBH measured (Stillhard et al., 2019). All trees were stem mapped by measuring azimuth and distance from the plot centre. On a subsample of about 25% of all sample trees, the tariff trees, we measured height, crown length and stem diameter at 7 m height (D$_7$) to allow to derive stem volume functions.

CWD was included to the inventory if the mean diameter of two crosswise measurements was ⩾7 cm at the intersection with the line transects. For every piece we recorded the degree of decay in 5 classes (fresh, solid, rotten, mould and duff, Table S5).

Regeneration was surveyed in three regeneration classes, i.e. seedlings (10–39.9 cm height, 5 m$^2$ subplot), saplings (40–129.9 cm height, 10 m$^2$ subplot) and recruits (⩾130 cm height up to 5.9 cm DBH, 20 m$^2$
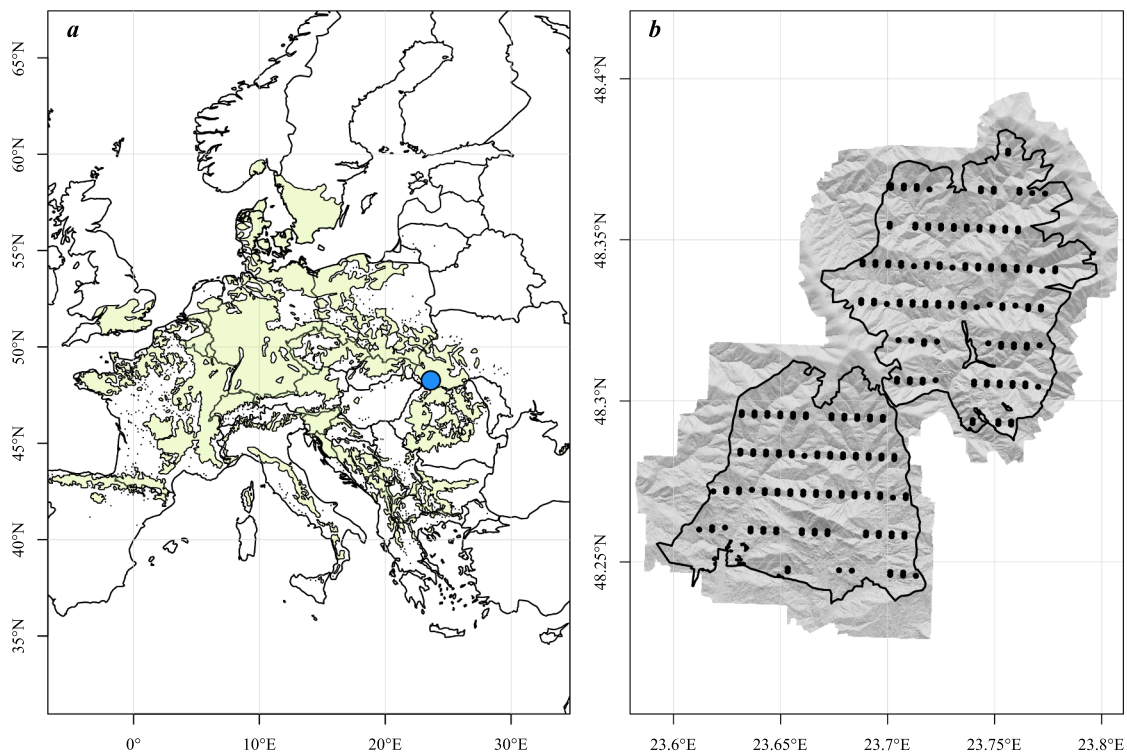
**Fig. 1.** a) Location of the Uholka-Shyrokyi Luh forest (blue dot) within Europe and the distribution of beech (green) according to EUFORGEN (2009) and b) distribution of the sample plot clusters (black dots) within the two parts of the forest, Uholka in the south and Shyrokyi Luh in the north with a shaded relief of a digital elevation model as background.
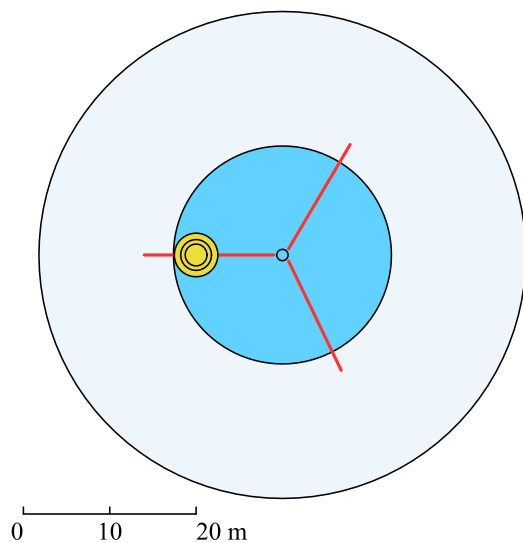


**Fig. 2.** Sample plot design. Light blue: interpretation area (2500 m$^2$), blue: sample plot (500 m$^2$), red: three CWD tranSections (15 m), yellow: three regeneration subplots (5, 10 and 20 m$^2$).

subplot). On recruits, we measured DBH, further dividing this class into 6 classes of 1 cm width. On all seedlings, we assessed browsing of the terminal shoot.

On a circular interpretation area of 2500 m$^2$ (horizontal radius = 28.2 m), topographic features, the occurrence of anthropogenic traces, and characteristics of the forest structure were visually assessed by the inventory teams. The information on forest structure includes the dominant height of the stand, the degree of cover, and the number of layers. In addition, the occurrence of gaps was visually assessed in 7 size classes (no gap, 20–50, 50–200, 201–500, 501–1000, 1001–5000 and >

5000 m$^2$). A gap was recorded if the plot center lay within a gap of the respective size.

In the 2010 inventory, all data was collected on paper forms and subsequently digitized. In 2019 we used OpenForis Collect (Open Foris Initiative of the FAO, 2019) to gather the data.

### 2.3. Data analysis

Data was analysed using R 4.0.4 (R Core Team, 2021) and the package 'forestinventory' 0.2.0 (Hill et al., 2017) according to a non-stratified, one-phase, one-stage cluster random sampling scheme (Mandallaz, 2008).

Based on local densities ($Y$) of the target variable $X$ in each sample plot, standardized to one ha, depending on the size of the sample plot within the forest ($f$) (Eq. 1), we calculated the local density of each cluster $M(x)$, $M(x)$ being the arithmetic mean of the local densities of all plots within the cluster that are part of the area of interest $f$.

$$Y\left(x\right) = \sum_{i=1}^{N(x)} X_i f_i \tag{1}$$

We then calculated the estimate for the mean spatial density $\widehat{Y}_c$ of the target variable $X$ using Eq. 2 where $s_2$ is the sample of clusters that lie within $F$.

$$\widehat{Y}_c = \frac{\sum_{x \in s_2} M\left(x\right) Y_c\left(x\right)}{\sum_{x \in s_2} M\left(x\right)} \tag{2}$$

The variance of $\widehat{Y}_c$, $\widehat{Var}(\widehat{Y}_c)$, was calculated using Eq. 3, where $M_2$ is the average number of plots per cluster in $F$ and $n_2$ the total number of plots.

$$\widehat{Var}\left(\widehat{Y}_c\right) = \frac{1}{n_2(n_2-1)} \sum_{x \in s_2} \left(\frac{M(x)}{M_2}\right)^2 \left(Y_c\left(x\right) - \widehat{Y}_c\right)^2 \tag{3}$$

We calculated all ratios as the ratio of means as shown in Eq. 4 and the respective variance, shown in Eq. 5, following Mandallaz (2008).

$$\widehat{R}_{1,2} = \frac{\widehat{Y}_c^{(1)}}{\widehat{Y}_c^{(2)}} \tag{4}$$

$$\widehat{Var}\left(\widehat{R}_{1,2}\right) = \frac{1}{n_2} \frac{1}{\widehat{Y}_c^{(2)}} \frac{1}{n_2-1} \sum_{x \in s_2} \left(\frac{M(x)}{M_2}\right)^2 \left(Y_c^{(1)}\left(x\right) - \widehat{R}_{1,2} Y_c^{(2)}\left(x\right)\right)^2 \tag{5}$$

We performed two-sided t-tests, corrected for multiple testing, to determine if estimates differ significantly between the inventories, and report 95% confidence-intervals.

Volume was calculated using the function published in Commarmot et al. (2013). It includes the total volume of the stem down to 7 cm diameter and the branch volume of branches with a diameter ⩾7 cm. The function was derived using tree height, DBH and diameter at 7 m ($D_7$) and includes the variables DBH, elevation of the plot, crown length, and the binary variable bifurcation. For entire dead standing trees, the volume was assumed to be the same as for living trees whilst for broken trees, we assumed a linear decrease from the measured snag height to the measured DBH. This decrease rate was estimated using the $D_7$ measured on tariff trees.

### 2.4. Coarse woody debris

We calculated the volume of CWD based on LIS following the formula by Böhl and Brändli (2007) shown in Eq. 6, where $h$ is the number of transects per plot, and $L_k$ the horizontal length of the $k$-th transect, $N(k)$ the number of CWD pieces on the $k$-th transect, $D1$ and $D2$ are the crosswise-measured diameters $i$ and $\alpha$ is the measured angle. The estimates of the CWD amount as derived from the LIS includes not only dead lying stems but all deadwood with a crosswise mean diameter ⩾7 cm.

$$Y\left(x\right) = \frac{1}{h} \sum_{k=1}^{h} \frac{\pi^2}{8L_k} \sum_{i=1}^{N(k)} \left(\frac{D1_i + D2_i}{2}\right)^2 \frac{1}{cos(\alpha_i)} \tag{6}$$

### 2.5. Mortality probability

Mortality rates ($M_{rate}$) were calculated as the ratio of trees that have died or disappeared ($t_m$) since the first inventory to all trees present in the first inventory, including surviving trees ($t_s$, Eq. 7).

$$M_{rate} = \frac{\sum(t_m)}{\sum(t_m + t_s)} \tag{7}$$

$M_{rate}$ was then scaled to the yearly mortality rate following Monserud (1976) as shown in Eq. 8.

$$M_{prob} = 1 - (1 - M_{rate}))^{\frac{1}{9}} \tag{8}$$

The mortality probability ($M_{prob}$) was calculated as the ratio of means where we first calculated the overall estimate of $t_s$ and $t_m$ which was then scaled to yearly values. The variance of the respective estimates was calculated according to Eq. 5.

### 2.6. Change components

The state observed during the second inventory is a result of components of change that happened since the first inventory. Following Lanz et al. (2019), these can be split into: i) net change (i.e. increase or decrease of the respective variable), (ii) mortality, (iii) ingrowth, and (iv) survivor growth. We analysed the contribution of these components

to the overall change but omitted growth of trees that died between the inventories as the calculation of this component requires an interpolation of the growth to the unknown point in time at which a tree disappeared or died. This omission may result in a slight underestimation of the growth of those individual trees, leading to an underestimation of the total growth too (Lanz et al., 2019).

## 3. Results

### 3.1. Forest characteristics

The dominant stand height, estimated by the field teams on the interpretation area, changed from 35.1 m in 2010 to 36.8 m in 2019 (Table 1). Most of the stands at the location of the sample plots were considered to consist of three horizontal layers (67.2% in 2010 and 70.6% in 2019) and only few stands (< 7%) were single-layered. A layer was considered as present if it reached a degree of cover of 20%. The degree of cover slightly increased in the lower layer, but remained relatively constant in the middle and the top layer. Although during both inventories we observed sporadic disturbances and indicators for large disturbance events (up to several ha) in the past, such as stands with a relatively homogeneous diameter distribution and pit-mound micro-relief, only few plots were considered to be lying within recent gaps larger than 200 $m^2$ (2010: 13.0%, 2019: 18.9%).

### 3.2. Standing trees

#### 3.2.1. Living trees

On the 238 plots we assessed a total of 5624 trees in 2010 and 5960 trees in 2019. The tree with the maximum DBH was a Scotch elm (*Ulmus glabra*) and had a DBH of 150 cm in 2010 and 154 cm in 2019 whilst the maximum height, measured on a beech tree, was 53.3 m in 2010 and 55.1 m in 2019 (Fig. S2).

In both inventories, we found 9 tree species and 3 shrub species in living trees (Table S1). *Fagus sylvatica* was the dominant species with a share of the basal area of 97.87 (± 0.69)% in the first and 97.64 (± 0.66)% in the second inventory (Table 2 and Table S4). Other species with N ⩾10 appearances in both inventories were *Acer pseudoplatanus*, *Carpinus betulus* and *Abies alba*.

Changes in tree density, basal area and volume from 2010 to 2019 were small and not significant. In total, we found 441.4 (± 25.6) trees per ha in 2010 and 458.5 (± 27.5) trees per ha in 2019, with a basal area of 35.9 (± 1.7) m² ha⁻¹ in 2010 and 36.3 (± 1.6) m² ha⁻¹ in 2019. The volume slightly increased from 578.9 (± 29.7) to 584.5 (± 28.7) m³ ha⁻¹ in the same time (Table 2).

The DBH distribution was exponentially decreasing, with most of the living trees being smaller than 20 cm (Fig. 3). The number of very large trees (VLT, trees with a DBH ⩾80 cm) per ha was 7.8 (± 1.5) in 2010 and 8.6 (± 1.9) in 2019.

#### 3.2.2. Dead trees

As in the living trees, we did not observe significant changes in the density and the volume of dead standing trees (snags). The density was 30.2 (± 5.0) snags per ha in 2010 and 25.9 (± 4.3) snags per ha in 2019 (Table 2), whilst the volume slightly increased from 21.7 (± 5.1) m³ ha⁻¹ in 2010 to 26.3 (± 7.1) m³ ha⁻¹ in 2019. Similar to the living trees, the DBH distribution of snags is right-skewed with more than 50% (2010: 57.7%, 2019: 50.7%) of the snags having a DBH below 20 cm (Fig. S3). Dead VLTs were found relatively often, with 1.2 (± 0.6) ha⁻¹ in 2010 and 1.8 (± 0.7) ha⁻¹ in 2019.

### 3.3. Regeneration

We observed a significant decrease in the density of seedlings but only small and insignificant changes for saplings and recruits. The

**Table 1**

Description of stand variables. Dominant height, degrees of cover and number of layers were visually assessed on the interpretation area of 2500 m², for the assessment of gap size the position of the sample plot center within a gap was relevant whilst the stand density index was calculated based on the trees measured on the plot.

| Variable | | 2010 | | | | 2019 | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Ŷ | $CI_{95}$ | Min | Max | Ŷ | $CI_{95}$ | Min | Max |
| Dominant height | | 35.1 | 0.7 | 0 | 50 | 36.8 | 0.6 | 20 | 50 |
| Degree of cover [%] | Upper layer | 59.9 | 2.1 | 0 | 90 | 55.6 | 2.7 | 5 | 90 |
| | Middle layer | 32.6 | 2.1 | 0 | 80 | 33.2 | 2.1 | 2 | 90 |
| | Lower layer | 38.2 | 3.6 | 0 | 95 | 45.7 | 3.2 | 0 | 100 |
| | All layers | 130.7 | 5.0 | 40 | 220 | 134.5 | 4.5 | 42 | 220 |
| Stand density index | | 641.7 | 27.0 | 160 | 1252 | 655.1 | 25.2 | 212 | 1383 |
| Proportion of number of layers [%] | One layer | 6.3 | 3.4 | | | 2.9 | 2.0 | | |
| | Two layers | 26.5 | 7.5 | | | 26.5 | 7.6 | | |
| | Three layers | 67.2 | 12.1 | | | 70.6 | 12.4 | | |
| Proportion of gap sizes [%] | Gap ⩽200 m² | 86.6 | 13.1 | | | 80.3 | 12.8 | | |
| | Gap 201–1000 m² | 10.1 | 3.9 | | | 14.3 | 5.3 | | |
| | Gap > 1000 m² | 2.9 | 2.0 | | | 4.6 | 2.6 | | |

**Table 2**

Estimates of forest population parameters. The estimates are based on 238 plots which were assessed in both inventories (2010 and 2019) and form 132 clusters. Column Ŷ contains the estimate for the respective parameter, column $CI_{95}$ the range of the 95% confidence interval. P-values of the t-test are indicated in column *p*.

| Population | Estimator | Species | 2010 | | 2019 | | p |
|---|---|---|---|---|---|---|---|
| | | | Ŷ | $CI_{95}$ | Ŷ | $CI_{95}$ | |
| **Living trees** | **Tree density [N ha⁻¹]** | *Fagus sylvatica* | 432.3 | 25.4 | 445.4 | 27.2 | > 0.05 |
| | | Other species | 9.1 | 4.3 | 13.1 | 7.3 | > 0.05 |
| | | Total | 441.4 | 25.6 | 458.5 | 27.5 | > 0.05 |
| | **Basal area [m² ha⁻¹]** | *Fagus sylvatica* | 35.2 | 1.6 | 35.4 | 1.6 | > 0.05 |
| | | Other species | 0.8 | 0.5 | 0.9 | 0.5 | > 0.05 |
| | | Total | 35.9 | 1.7 | 36.3 | 1.6 | > 0.05 |
| | **Volume [m³ ha⁻¹]** | *Fagus sylvatica* | 565.7 | 29.2 | 570.2 | 27.7 | > 0.05 |
| | | Other species | 13.2 | 8.4 | 14.3 | 8.3 | > 0.05 |
| | | Total | 578.9 | 29.7 | 584.5 | 28.7 | > 0.05 |
| **Dead trees** | **Tree density [N ha⁻¹]** | *Fagus sylvatica* | 23.4 | 4.2 | 22.7 | 3.6 | > 0.05 |
| | | Other species | 6.8 | 3.4 | 3.2 | 2.3 | > 0.05 |
| | | Total | 30.2 | 5.0 | 25.9 | 4.3 | > 0.05 |
| | **Volume [m³ ha⁻¹]** | *Fagus sylvatica* | 16.6 | 4.7 | 21.6 | 5.6 | > 0.05 |
| | | Other species | 5.1 | 2.5 | 4.6 | 4.0 | > 0.05 |
| | | Total | 21.7 | 5.1 | 26.3 | 7.1 | > 0.05 |

seedling density decreased from 18950 (± 6791) seedlings with a height of 10–39.9 cm per ha in 2010 to 6546 (± 1892) in 2019. In both inventories, beech was the most common species, accounting for 75.8 (± 14.7)% of the total number of seedlings in 2010 and 85.1 (± 10.2)% in 2019. *Acer sp.* accounted for 23.7 (± 14.6)% in 2010 and 13.6 (± 9.9)% in 2019.

In the sapling class (height 40–129.9 cm), the density did only slightly change with 6382 (± 2324) individuals per ha found in 2010 and 6210 (± 1651) in 2019. In this height class, beech accounted for more than 90% of the total (Table S3). As in the sapling class, we observed only slight changes in the recruits class (0.0–5.9 cm DBH). In 2010 we found 3699 (± 892) individuals per ha in 2010 and 3390 (± 671) in 2019 (Fig. 4).

### 3.4. Coarse woody debris

We found 146.2 (± 16.9) m³ ha⁻¹ of CWD in 2010 and 154.5 (± 21.1) m³ ha⁻¹ in 2019 (Table 3) and observed a significant decrease in duff deadwood but no significant changes for the other decay classes. However, there was an increase in fresh deadwood with a remarkable increase in the confidence interval (2010: 10.4 (± 4.5) m³ ha⁻¹, 2019:

15.1 (± 12.0) m³ ha⁻¹) whilst both the amount and the confidence interval remained relatively stable for the decay classes solid, rotten and mould.

### 3.5. Mortality probability

We observed the highest mortality rates for VLT's (trees with DBH ⩾80 cm) with an annual mortality probability of 3.11 (± 0.84)% and for small trees of DBH 6 cm to 9 cm with 1.58 (± 0.31)%. For the DBH-classes in-between, the annual mortality probability was around 1 % with a minimum value of 0.90 (± 0.41)% (Fig. 5, Table S2). We did not observe an increased yearly mortality probability for trees just above the callipering threshold of 6 cm (Fig. S5).

### 3.6. Change components

Changes in the two main forest characteristics volume and number of trees are illustrated as changes in the relevant components, i.e. survivors (including growth of the surviving trees), losses and ingrowth for both living and dead trees (Fig. 6 and Fig. S1). While most of the sample trees survived, 9 % died between the two inventories. About the same number
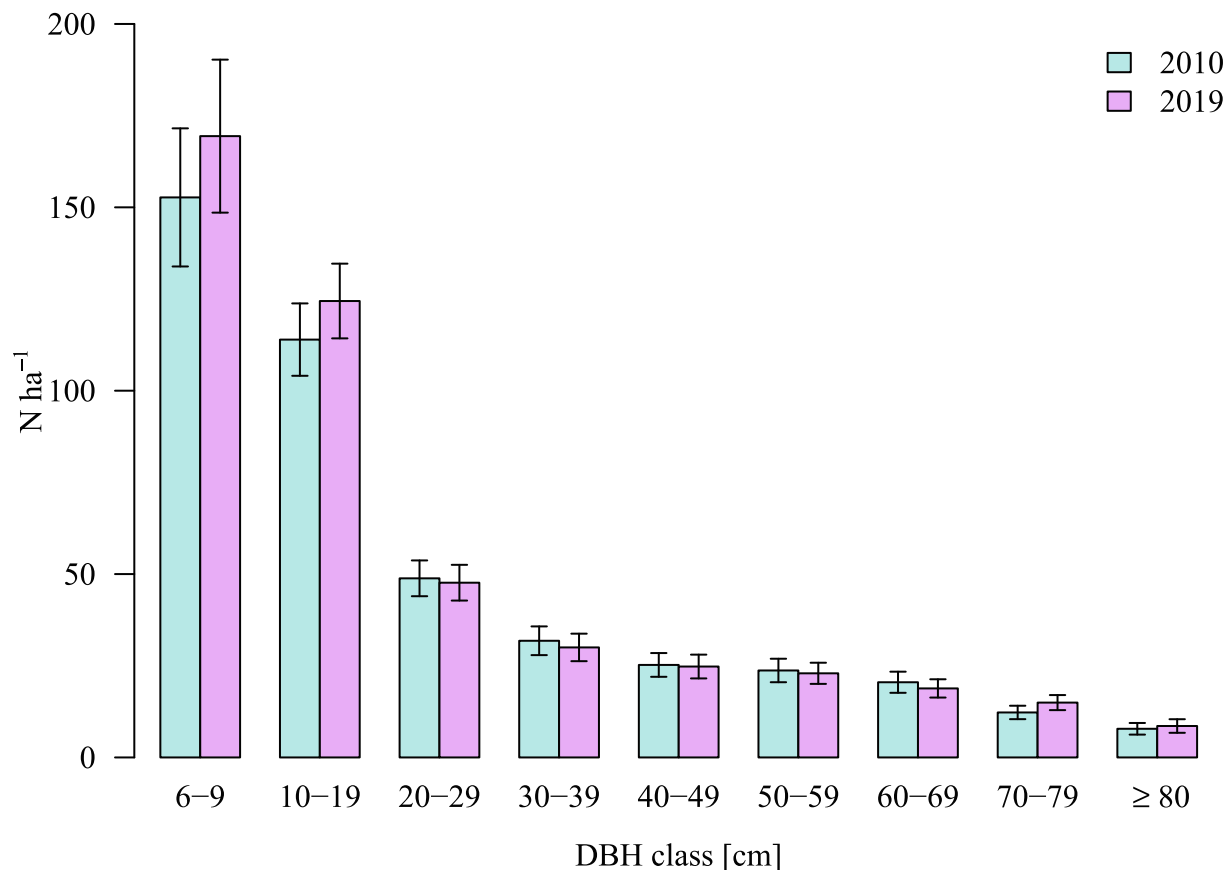
**Fig. 3.** DBH distribution of living trees, grouped in DBH classes. The first class contains all trees with a DBH ⩾6 cm to 9 cm, the classes up to a DBH of 79 cm are 10 cm wide and the class ⩾80 cm includes all trees with a DBH ⩾80 cm. Error bars represent 95% confidence intervals.

of trees that died since the first inventory were recorded as ingrowth in the second inventory, resulting in a stable number of living trees. The main driver of the increase of the dead trees in the second inventory were trees that died since the first inventory and not trees that grew over the callipering threshold and subsequently died between the inventories. Only 0.59 ($\pm$ 0.43) trees/ha with a volume of 0.7 ($\pm$ 0.7) m$^3$ ha$^{-1}$ surpassed the calliper threshold and were recorded as dead ingrowth in the second inventory. The volume of the trees that died or disappeared since the first inventory (72.6 m$^3$ ha$^{-1}$) was compensated for by growth of surviving trees (71.9 m$^3$ ha$^{-1}$), resulting in an annual growth of 8.0 m$^3$ ha$^{-1}$ for the surviving trees. Ingrowing trees contributed 10.2 m$^3$ ha$^{-1}$ to the volume of the second inventory, resulting in a total annual growth including ingrowth of 9.1 m$^3$ ha$^{-1}$. As we did not include the growth of trees that died between the inventories, this value might slightly underestimate total growth.

## 4. Discussion

In this study, we make use of a repeated sample plot inventory in one of the largest remnants of primeval beech forests. Besides that, to our knowledge, no repeated sample plot inventory covering several 1000 ha for primeval forests of this ecosystem exists. Another unique feature of our dataset is the high share of beech observed. This results in a very high number of observations for this species, whilst other species are not well represented. The dataset allows to quantitatively describe the development and change of this particular forest at a relatively large scale. However, extending the temporal extent of only 9 years might allow to gain important new insights not yet detectable in our data.

### 4.1. Forest characteristics

Most of the plots had a relatively high degree of cover, with a mean of 130.7% in 2010 and of 134.5% in 2019. This can be attributed to the high crown plasticity (Schröter et al., 2012) of beech which is able to fill gaps in the canopy very efficiently. The ability of beech to survive under closed canopies results in a vertically structured forest with less than 10% of the plots consisting of only one layer (2010: 6.3 ($\pm$ 3.4)%, 2019: 2.9 ($\pm$ 2.0)%). In both inventories, more than 80% of the plots were considered to lie under canopy or within a small gap up to a size of one tree crown (⩽200 m$^2$) and less than 5% of all plots to lie in gaps larger than 1000 m$^2$ (2010: 2.9 ($\pm$ 2.0)%, 2019: 4.6 ($\pm$ 2.6)%). This is in line with other studies who did not find large gaps in primeval beech forests (Meyer et al., 2003) with mean gap size ranging from 62 to 74 m$^2$ (Tabaku and Meyer, 1999) and earlier observational descriptions of primeval beech forests (Fröhlich, 1947; Fröhlich, 1954). The overall gap frequency is slightly higher than the one found by Feldmann et al. (2018) who report only 5 and 8% of the forested area in a primeval beech forest in the Slovakian Carpathians to consist of gaps in two consecutive transect surveys.

The studied forest is characterized by a small-scale disturbance regime leading to a multi-layered canopy structure (Hobi et al., 2015). A similar small to medium-scale disturbance regime with low to intermediate disturbances was found in primeval beech forests in the Slovakian Carpathians (Frankovič et al., 2021). Although larger (one to several ha) disturbances occurred in the study region in summer 2018, these events are, given the large forest area, relatively rare and have therefore only minor effects on a sample plot inventory deriving representative estimates for a large forest. Moreover, the time between the two inventories might have been too short to allow for the observation of such rare events.
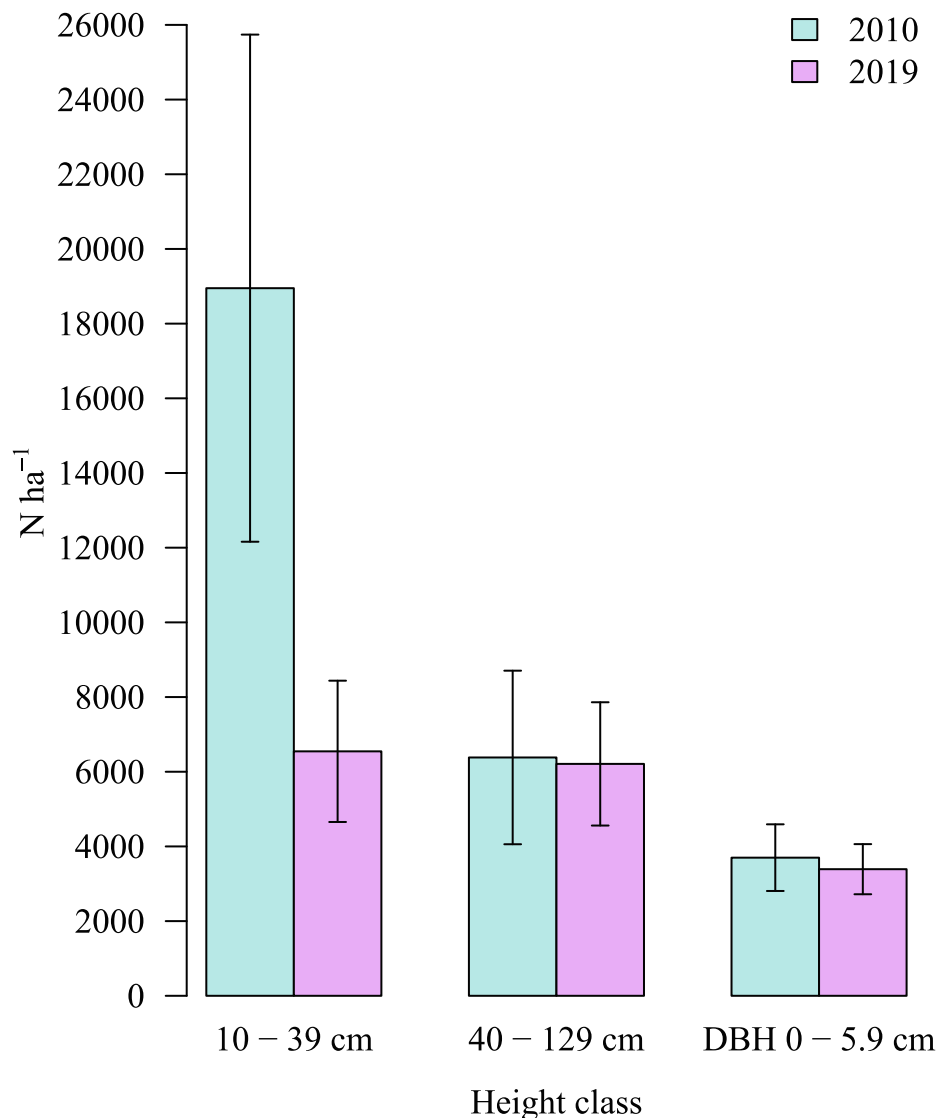
**Fig. 4.** Density of seedlings, saplings and recruits. Error bars represent a 95% confidence interval.

*4.2. Standing trees*

*4.2.1. Living trees*

With regards to the parameters basal area, volume and number of trees, the Uholka Shyrokyi Luh forest remained stable with only slight changes below a threshold of 5.0% between the two inventories. Given the relatively short inventory period of 9 years, this can be seen as a typical behaviour of beech forests.

Compared to other beech-dominated forest reserves in Europe (Vandekerkhove et al., 2018), the basal area of the Uholka-Shyroki Luh forest (2010: 35.9 ± 1.7, 2019: 36.3 ± 1.6 $m^2$ $ha^{-1}$) is at an average level. Whilst the highest value for basal area presented in that study is 45.2 $m^2$ $ha^{-1}$, most of the forests were found to have an average basal area between 30 and 40 $m^2$ $ha^{-1}$. Dividing the 10 ha plot in Uholka into 40 subplots of 0.25 ha each, Commarmot et al. (2005) found 23.0–51.8 $m^2$ $ha^{-1}$ with a mean of 38.5 $m^2$ $ha^{-1}$.

The total volume increment over the inventory period of 71.9 $m^3$ $ha^{-1}$, translating to an annual volume increment of 8.0 $m^3$ $ha^{-1}$, is within the range of managed mixed mountain spruce-fir-beech forests across Europe. For such forests, Hilmers et al. (2019) report an annual volume increment of 9.3 (± 3.3) $m^3$ $ha^{-1}$. This finding is in line with Glatthorn et al. (2017) who found that three primeval beech forests in Slovakia had a comparable growth to adjacent, managed forests dominated by beech.

The number of VLTs per ha (2010: 7.8 ± 0.8, 2019: 8.6 ± 0.94 N $ha^{-1}$) is in the lower range of the numbers for VLTs found by Vandekerkhove et al. (2018) for various beech-dominated forest reserves in Europe (13.9 ± 9.1 N $ha^{-1}$).

The species composition, characterised by a pronounced dominance of beech, did not change between the two inventories. In both inventories, the beech proportion in basal area was over 97 %. The absence of change in species composition over nine years is also an indicator for the disturbance regime which results in canopy gaps that are usually too small to allow for the ingrowth of other species. This is in line with the data presented in Vandekerkhove et al. (2018) for beech-dominated forests where silver fir (*Abies alba* Mill.) and Norway spruce (*Picea abies* (L.) H.Karst) are almost absent.

*4.2.2. Dead trees*

While the number of snags decreased by 14%, their volume increased by 17%. This might indicate that disturbances mainly affected larger trees or might be a legacy effect of disturbances that happened before the initial inventory and mainly affected smaller trees. We did not find a specific DBH class that made a particularly large contribution to the number of snags. The volume of dead standing trees (including bark and main branches), 21.7 (± 5.1) in 2010 and 26.3 (± 7.1) $m^3$ $ha^{-1}$ in 2019,
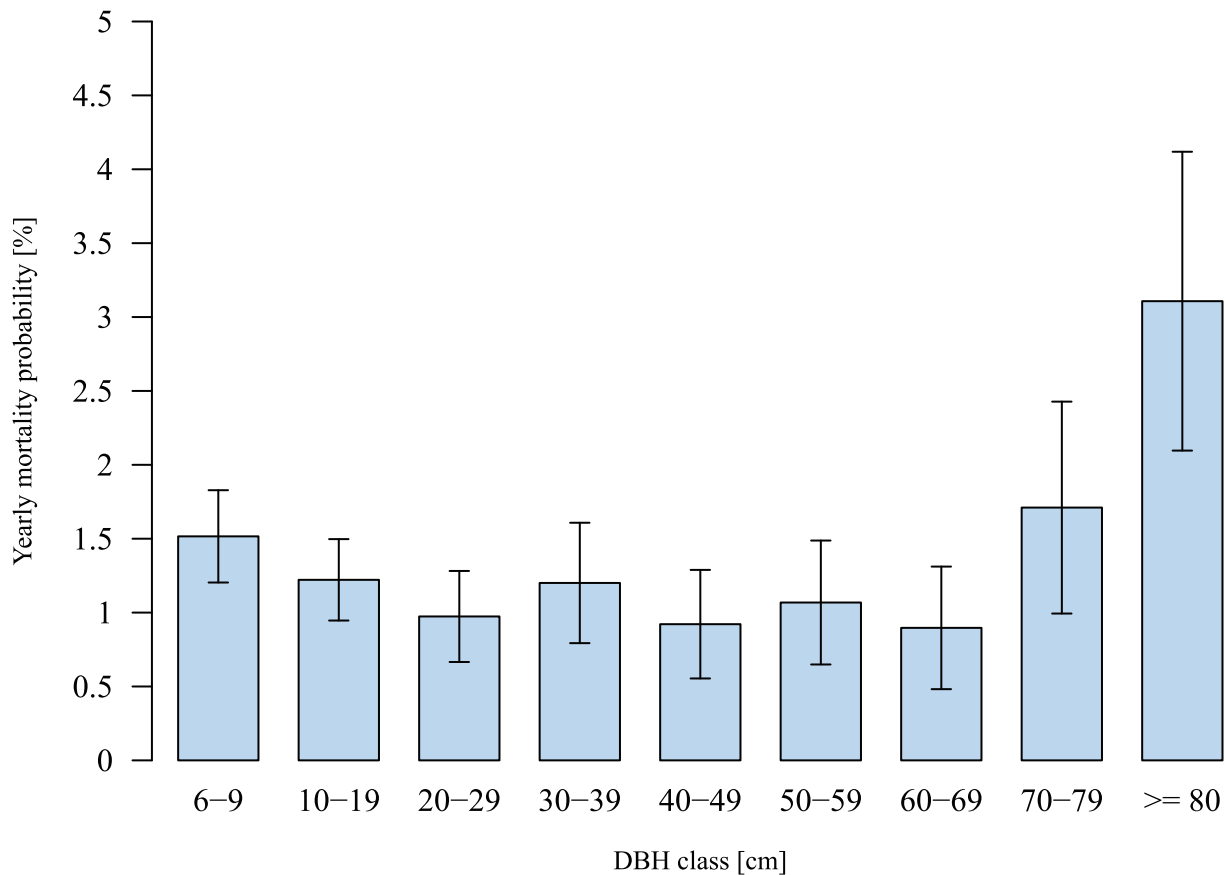
**Fig. 5.** Yearly mortality probability for trees alive in 2010 grouped in DBH classes. The first class contains all trees with a DBH ⩾6 cm to 9 cm, the classes up to a DBH of 79 cm are 10 cm wide and the class ⩾80 cm includes all trees with a DBH ⩾80 cm. Error bars represent a 95% confidence interval.

lay below the mean 39 m³ ha⁻¹ reported by Christensen et al. (2005) for 86 beech-dominated forest reserves throughout Europe with a range from 1 to 283 m³ ha⁻¹, but within the range provided by Vandekerkhove et al. (2009) who report a mean of 22 m³ ha⁻¹ and a range of 1 to 109 m³ ha⁻¹. The values provided by Christensen et al. (2005) are based on a wide range of beech forest types and sampling methods. With full cruises (mean: 48.9 m³ ha⁻¹) or on permanent plots (mean: 45.1 m³ ha⁻¹), higher snag volumes were found than with sample plot inventories in which snag volumes (mean: 31.9 m³ ha⁻¹) were similar as in our study. This might be attributed to a biased selection of stands surveyed in full cruises and permanent plots towards higher volumes (Holeksa et al., 2009; Peck et al., 2015).

*4.3. Regeneration*

Similar as for living trees above the callipering threshold of 6 cm, the density of saplings and recruits was strongly right skewed in the first inventory but not the second inventory. We attribute the observed decrease (2010: 18950 ± 6791, 2019: 6546 ± 1892 N ha⁻¹) in the height class 10–39.9 cm to masting events that occurred in the years before the initial inventory. Beech is known to show strong masting (Pidek et al., 2010) producing up to 7 million seeds per ha (Övergaard et al., 2007). Although there is no masting data for the Ukrainian Carpathians available, Ascoli et al. (2017) report a good to full mast year for Romanian plots in 2008, and given the dependence of masting on regional climate, it can be assumed that this event was also important in our study area. The height classes 40–129 cm (2010: 6382 ± 2324, 2019: 6210 ± 1651 N ha⁻¹) and DBH ⩾0 cm - DBH < 6 cm (2010: 3699 ± 892, 2019: 3390 ± 671 N ha⁻¹), containing trees already established, are not influenced by masting events. The density of saplings and recruits in

these classes remained stable through time. Whilst beech accounted for 75.8 (± 14.7) % in 2010 and 85.1 (± 10.2) % in 2019 in the height class 10–39 cm, the pronounced dominance of beech can be observed already in the height class 40–129 cm, where beech accounts for a share of more than 90% in both inventories. This suggests that beech becomes increasingly competitive already in early life stages. This increased competitiveness of beech over other species can be attributed to the high shade tolerance of beech resulting in a competitive advantage over other species such as *Acer spp.* (Petrovska et al., 2021).

*4.4. Coarse woody debris*

In contrast to the snag volumes, the volume of CWD remained stable throughout both inventories. CWD values in the Uholka-Shyrokyi Luh forest (2010: 146.2 ± 8.6 m³ ha⁻¹, 2019: 154.5 ± 10.7 m³ ha⁻¹) are markedly higher than in six Swiss beech-dominated forest reserves (20.1–100.5 m³ ha⁻¹, mean 43.6 ± 12.3 m³ ha⁻¹ Hermann et al. (2012)), in Italian beech-dominated forest reserves (22.6–76.5 m³ ha⁻¹, Castagneri et al., 2010), in forest reserves in NW-Germany (18 m³ ha⁻¹, Meyer and Schmidt, 2011) in which management ceased about 10 years before the first inventory, in 74 beech dominated, previously managed forests in North-Western and Central Europe (55.7 m³ ha⁻¹ Vandeker-khove et al. (2009)) and the value of 104 m³ ha⁻¹ reported by Burras-cano et al. (2013) for beech-dominated old-growth forests in Europe. These differences can be attributed to legacy effects of former management resulting in lower CWD values in formerly managed forests through lower mortality rates for large trees and smaller dimensions of these, even in forest reserves where management was abandoned decades ago (Hülsmann et al., 2016), resulting in a lower supply of CWD through mortality of large trees.

The relative stability of both the total amount of CWD and the

**Table 3**
CWD [$m^3$ $ha^{-1}$] of broadleaved and coniferous trees according to decay status. The estimates are based on 238 plots which were assessed in both, the 2010 and 2019 inventory and form 132 clusters. Column $\hat{Y}$ contains the estimate for the respective parameter, column $CI_{95}$ the range of the 95% confidence interval. P-values of the t-test are indicated in column $p$.

| Decay class | Group | 2010 | | 2019 | | p |
|---|---|---|---|---|---|---|
| | | $\hat{Y}$ | $CI_{95}$ | $\hat{Y}$ | $CI_{95}$ | |
| **fresh** | Broadleaved | 10.4 | 4.5 | 15.1 | 12.0 | > 0.05 |
| | Coniferous | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Undefinable | 0.0 | 0.0 | 0.0 | 0.0 | |
| | Total | 10.4 | 4.5 | 15.1 | 12.0 | > 0.05 |
| **solid** | Broadleaved | 33.9 | 8.4 | 35.2 | 8.5 | > 0.05 |
| | Coniferous | 0.0 | 0.0 | 0.0 | 0.0 | > 0.05 |
| | Undefinable | 0.0 | 0.0 | 0.0 | 0.0 | > 0.05 |
| | Total | 34.0 | 8.4 | 35.2 | 8.5 | > 0.05 |
| **rotten** | Broadleaved | 25.4 | 6.6 | 33.2 | 8.9 | > 0.05 |
| | Coniferous | 0.0 | 0.0 | 0.3 | 0.5 | > 0.05 |
| | Undefinable | 0.0 | 0.0 | 0.2 | 0.3 | > 0.05 |
| | Total | 25.4 | 6.6 | 33.8 | 8.9 | > 0.05 |
| **mould** | Broadleaved | 43.0 | 8.5 | 46.9 | 9.6 | > 0.05 |
| | Coniferous | 0.4 | 0.6 | 1.1 | 1.8 | > 0.05 |
| | Undefinable | 0.0 | 0.0 | 0.4 | 0.6 | > 0.05 |
| | Total | 43.3 | 8.5 | 48.4 | 9.7 | > 0.05 |
| **duff** | Broadleaved | 29.2 | 6.3 | 17.7 | 4.7 | **0.005** |
| | Coniferous | 0.0 | 0.0 | 0.0 | 0.0 | > 0.05 |
| | Undefinable | 0.8 | 1.3 | 1.8 | 2.9 | > 0.05 |
| | Total | 30.1 | 6.6 | 19.5 | 6.0 | **0.023** |
| **Total** | Broadleaved | 141.9 | 16.6 | 148.2 | 20.4 | > 0.05 |
| | Coniferous | 0.4 | 0.6 | 1.4 | 1.9 | > 0.05 |
| | Undefinable | 0.8 | 1.3 | 2.3 | 3.4 | > 0.05 |
| | Total | 146.2 | 16.9 | 154.5 | 21.1 | > 0.05 |

respective small confidence intervals suggests that severe, large-scale disturbance did not occur recently in the study area. Such disturbances would result in a statistically significant higher amount of CWD in the classes fresh or solid deadwood and a higher variability between plots as long as only parts of the forest were affected. The increase of the amount of fresh deadwood between the inventories and the increase of the respective confidence interval (2010: 10.4 ($\pm$ 4.5) $m^3$ $ha^{-1}$, 2019: 15.1 ($\pm$ 12.0) $m^3$ $ha^{-1}$) might be a result of small- to medium-scale disturbances that occurred between the two inventories. The observed significant decrease in the amount of deadwood in the decay class duff might as well indicate a disturbance that happened some time before the first inventory. Although there is some variability in the amount of particular decay classes, the total amount remained stable and can be understood as an indicator for an almost steady-state ecosystem, with losses (through decay) and supply (through mortality) being similar.

### 4.5. Mortality rates

We observed an annual mortality rate for all trees of 1.30 ($\pm$ 0.22)%. This value is considerably higher than the rates found by Portier et al. (2021) for beech dominated latent reserves in the Swiss NFI, i.e. sample plots in the Swiss NFI that have not been managed for more than 70 years, with a mean annual mortality of 0.29 (confidence interval: 0.17–0.49)%, but is in line with the value reported by Runkle (1985) of about 1%. The general pattern of increased mortality rates for VLTs is consistent with another study based on data from the 10 ha plot in Uholka (Hülsmann et al., 2016) as are the mortality rates. However, we only observed a slightly higher mortality rate for small trees compared to trees of medium DBH, which together with higher mortality of larger trees usually lead to a distinct U-shaped mortality-DBH relationship

(Holzwarth et al., 2013).

We attribute this surprising finding to particular physiological properties of beech, its disturbance regime, and our sampling approach. Among the physiological properties of beech, the high shade tolerance resulting in the ability to survive long suppression periods of up to 177 years (Trotsiuk et al., 2012) reduces the mortality due to suppression and competition. The high shade tolerance and therefore low sensitivity to competition for light corresponds to the findings of Rohner et al. (2012) who found beech mortality rates to be unaffected by basal area in Swiss forest reserves.

Disturbances in beech forests are generally of low to intermediate severity (Frankovič et al., 2021). Hobi et al. (2015) found that about 60% of all gaps detected using spectral image analysis in the Uholka-Shyrokyi Luh forest were between 20 and 50 $m^2$ in size. Although some larger disturbances occurred in the study area between the two inventories, the absence of higher mortality rates in small trees might as well be an effect of an observation period with relatively few disturbances resulting in low values for both, the overall mortality and the mortality of small trees induced by crushing by falling of larger trees (Holzwarth et al., 2013).

There are indicators for historical disturbances of large extent and high severity such as patches covering several thousand square meters with a relatively uniform DBH distribution, pronounced pit-mound micro-relief or high proportion of stems of more light demanding species such as *Acer sp.* Given the small spatial extent and the rarity of disturbances, these might not be detected using sample plot inventories as locally increased mortality rates are averaged out when analysing such data (Fisher et al., 2008). Conversely, making use of data gathered on large permanent plots data without replication as done by Hülsmann et al. (2016) might result in an overestimation of mortality rates. This is in particular true for the 10 ha plot in Uholka, which is not representative for the entire forest (Peck et al., 2015), having a lower number of stems per ha (293 vs. 414 N $ha^{-1}$, cf. Peck et al. (2015)) and a higher number of VLTs per ha (23 vs. 9 N $ha^{-1}$, cf. Peck et al. (2015)).

Given the factors mentioned above and that we observed only very few trees that grew over the calliper threshold and died between the two inventories (Fig. S1), we conclude that increased mortality in small trees most probably occurs before they reach the calliper threshold of 6 cm. Finally, the short time between the two sampling inventories, with by chance few disturbances, may have contributed to the low mortality rates observed.

### 4.6. Change components

The analysed change components support the steady-state hypothesis for this ecosystem. Looking at the volume of living trees, growth has compensated for the volume lost due to tree mortality between the initial and the second inventory. The few trees that disappeared in between are not important here. In comparison, ingrowth contributed only little to volume increment. Ingrowing trees, however, contribute to the stability of the ecosystem regarding the number of trees, since they replace about the number of trees having left the living component since the first inventory. These results explain why the system remained stable regarding the structural attributes tree density and volume, although there is considerable demographic change (about 6.5% of all trees and about 12% of the living volume have been replaced in 9 years). A quantitative characterization of the different components of change has, to our knowledge, not yet been published for a primary forest in general and for a primeval beech forest in particular.

### 5. Conclusions

Two consecutive sampling inventories of a large primeval beech forest of more than 100 $km^2$ enabled us to capture the changes of its characteristics over a period of nine years, giving important insight into the dynamics and demographic processes of this ecosystem. We found
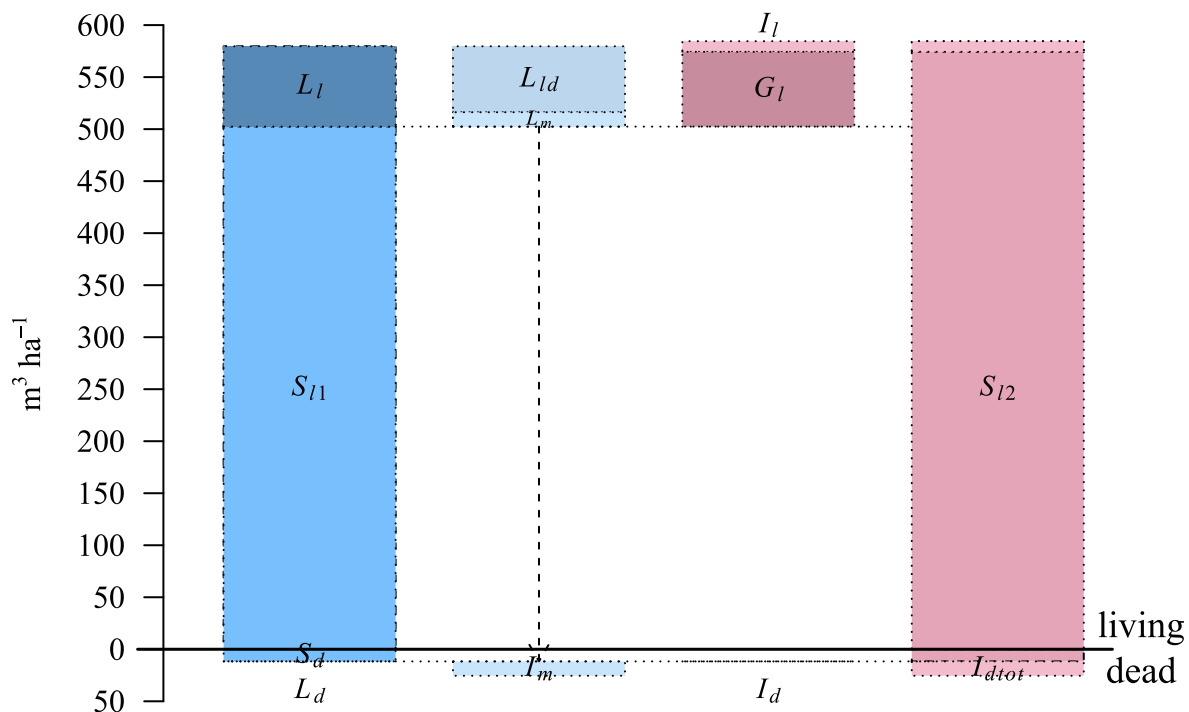
**Fig. 6.** Changes in volume in different components. $S_{l1}$ and $S_{l2}$ denote the volume of trees living in both inventories (502.4 ($\pm$ 27.7) m$^3$ ha$^{-1}$ and 574.31 ($\pm$ 29.3) m$^3$ ha$^{-1}$), $S_d$ the volume of the dead trees first measured during the first inventory and remeasured in the second inventory (11.7 ($\pm$ 4.2) m$^3$ ha$^{-1}$), $L_l$ total losses from living trees (71.9 m$^3$ ha$^{-1}$). These split into living trees that decayed and have therefore not been remeasured ($L_{ld}$, (58.1 ($\pm$ 24.7) m$^3$ ha$^{-1}$)) and trees that died but have been remeasured ($L_m$) and form the component $I_m$, ingrowth from mortality (13.8 ($\pm$ 5.1) m$^3$ ha$^{-1}$). $I_l$ denotes the living ingrowth (10.2 ($\pm$ 7.8) m$^3$ ha$^{-1}$) and $I_d$ the dead ingrowth (0.7 ($\pm$ 0.7) m$^3$ ha$^{-1}$). $I_m$ and $I_d$ together form the total dead ingrowth ($I_{dtot}$). $L_d$ denotes the trees that were found dead during the first inventory and decayed (7.8 ($\pm$ 4.0) m$^3$ ha$^{-1}$). $G_l$ denotes the growth of the living trees (71.9 ($\pm$ 5.1) m$^3$ ha$^{-1}$).

less than 5% of the sample plots to lie within a canopy gap larger than 1000 m$^2$. The few sporadic disturbances that affected patches of one to a few hectares during the inventory period did not affect the species composition and the structural attributes such as basal area or number of trees of the primary forest leaving it largely unchanged at the landscape scale.

We were able to elucidate some of the factors that contribute to this pronounced continuity and support the steady state hypothesis. Ingrowth did replace dead trees, compensating for the stem number lost, and the increment of the surviving (and to a small extent the ingrowing) trees compensated for the volume lost. Moreover, there is little and only observational evidence for larger disturbances before the first inventory.

However, it is not fully clear if the last decades in general and the inventory period we chose in particular, are representative for disturbances in this region. Additionally, it is uncertain whether the observed steady-state of this forest under current climate will be maintained under a changing climate. Future extreme drought events could cause widespread and/or severe disturbance, altering the current small-scale disturbance regime.

**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.

**Appendix A. Supplementary material**

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2021.119836.

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